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Rhizosphere ecology

The study of interactions among the biotic and abiotic components within the narrow region of soil surrounding plant roots. The rhizosphere (the soil region subject to the influence of plant roots and characterized by a zone of increased microbiological activity) extends from the root surface to less than 5 mm (0.2 in.) from the root. The close proximity of plant roots to the soil provides abundant simple sugars and amino acids that sustain large populations of microorganisms. The diffusion of gases through roots creates habitats rich in oxygen, which further supports zones of high microbial activity within the soil matrix. The interactions of plants, soil, and microorganisms within the rhizosphere heavily influence the biogeochemical cycling of carbon, nitrogen, and phosphorus through ecosystems. *See* BIOGEOCHEMISTRY; CARBON-NITROGEN-OXYGEN CYCLES; MICROBIAL ECOLOGY; RHIZOSPHERE; ROOT (BOTANY); SOIL CHEMISTRY; SOIL ECOLOGY; SOIL MICROBIOLOGY.

Components of the rhizosphere. The rhizosphere has a number of components, which contribute to the various features and interactions found in rhizosphere ecology.

Plants. Plant roots and rhizomes (belowground stems) are the defining features of the rhizosphere. The depth of root penetration in the soil determines the vertical boundaries of the rhizosphere. In forested ecosystems, the rhizosphere typically extends 1–3 m (3.3–10 ft) below the soil surface. In sharp contrast, the rhizosphere under turf grasses, such as those found on golf courses and lawns, reaches only a few centimeters in depth. Plant roots provide habitat for microorganisms, nematodes, and protozoa, as well as their nutritional and physiological needs.

Root exudation of sugars and amino acids fuels the metabolic demands of heterotrophic microorganisms. Up to 40% of the net amount of photosynthates is exuded from roots through secretions of polysaccharides or sloughing of plant cells from roots. Additionally, the exudation of organic acids and enzymes from roots aids in nutrient acquisition. Organic acids released into the rhizosphere can solubilize calcium, iron, and aluminum phosphates for biological uptake. Similarly, the secretion of extracellular enzymes frees phosphorus bound in organic form. Plant roots also provide a pathway for gas exchange that maintains high levels of oxygen in the rhizosphere. The rhizosphere creates important microsites of aerobic habitat for microorganisms in ecosystems that are characterized by waterlogged and anoxic (oxygen-deficient) soils. *See* OXYGEN; PHOSPHORUS; PLANT.

Soil. The soil matrix is an important abiotic reservoir for elements and molecules that sustain metabolic reactions and nutrient transformations. Soil is composed of sand, silt, and clay particles in differing proportions that influence soil texture. Soils that have a high proportion of sand particles relative to clay and silt hold less water but have improved water drainage and gas diffusion. Soils with high clay content are less permeable to water and can restrict root growth. Soil texture also influences the pore size within the soil matrix, which can limit the motility and distribution of microorganisms, nematodes, and protozoa through both the rhizosphere and bulk soils. *See* SOIL.

Microorganisms (fungi, bacteria, and archaea). Fungi are eukaryotic microorganisms that inhabit the rhizosphere in diverse forms. Arbuscular mycorrhizal fungi (AMFs) and ectomycorrhizal fungi (EcMs) are both symbiotic fungi that form mutualistic relationships with plants. AMFs enter plant roots and extend their hyphae into the cell membranes. Highly branched structures termed arbuscules or balloon-like vesicles are formed within the roots and aid in nutrient exchange. In contrast, EcMs form a thick sheath around roots, with a network of hyphae (termed the Hartig net) penetrating between epidermal and cortical cells. Whereas AMFs are ubiquitous across most plant families, the EcMs are associated primarily with trees and shrubs. Other nonsymbiotic fungi that inhabit the rhizosphere can serve a commensalist or antagonistic relationship. Saprotrophic fungi found in the rhizosphere can compete with mycorrhizal fungi for access to plant carbon, without providing direct benefits to the plant. Saprotrophs play a critical role in the decomposition of cellulose and lignin into reduced forms, providing other microorganisms and plants with the necessary substrates to carry out metabolic functions. Antagonistic fungi show pathogenic traits that inhibit root growth and seed germination; sometimes, they kill the adult plant. Fungal pathogens play an important role in maintenance of plant populations by influencing plant competition and reproductive fitness. *See* CARBON; ECTOMYCORRHIZAL SYMBIOSIS; FUNGAL ECOLOGY; FUNGI; MYCORRHIZAE.

Bacteria are the most abundant microorganisms in the rhizosphere, occupying one gram of soil with up to half a billion individual cells. Bacterial diversity in the rhizosphere is also high, with at least 2000–5000 bacterial species inhabiting a single gram. Bacteria perform a wide range of functions in the rhizosphere, including mediation of biogeochemical cycles, acquisition of nutrients, protection of the host plant from antagonistic microbial attacks, maintenance of plant populations, and production of secondary metabolites. Chemical transformations of molecules to bioavailable forms, such as conversion of organic nitrogen to ammonium and ammonium to nitrate, are carried out by saprotrophic and ammonia-oxidizing bacteria, respectively. Nitrogen-fixing bacteria are able to fix atmospheric N_2 into ammonia, which can be taken up directly by plants and microorganisms. Nitrogen fixers are found as symbiotic inhabitants on plant roots and as free-living bacteria within the rhizosphere. Rhizospheric bacteria also help maintain plant populations by serving as antagonistic or growth-promoting organisms. The antagonistic bacteria keep plant populations in check by suppressing plant growth, seedling elongation, and seed germination. Plant growth-promoting bacteria are common in the rhizosphere, providing plants with metabolites, nutrients, and antibiotics that protect the plant from pathogenic attack or enhance plant growth. *See* BACTERIA; NITROGEN; NITROGEN FIXATION; PLANT MINERAL NUTRITION.

Archaea are single-celled organisms that resemble bacteria in form and function, but they exist as a distinctly different domain of life from bacteria. Archaea were once thought to exist only in extreme environments of heat or salinity; however, since the late twentieth century, they are known to be ubiquitous in many environments. Within the rhizosphere, methane-producing archaea (methanogens) are involved with the production of the highly potent greenhouse gas methane. Methanogens are prevalent in rice paddies, wetlands, lake and ocean sediments, and other anoxic and flooded sediments. Archaea also play an important role in the nitrogen cycle as nitrogen fixers, denitrifiers, and ammonia oxidizers. Until the early twenty-first century, the ammonia-oxidizing capabilities of organisms such as *Nitrosomonas* were considered unique to bacteria. The extent of the role of archaea in the rhizosphere continues to be unknown, as new organisms and their functions are continually being discovered. *See* ARCHAEA; METHANE.

Nematodes and protozoa. Nematodes are small roundworms that were once considered detrimental to plant health, as almost half of all known nematode species are considered parasitic (approximately 16,000). Pest nematodes, including *Meloidogyne* (root-knot nematode), infect plant roots with disease. Predatory nematodes, on the other hand, can promote plant growth and suppress disease. Many species of predatory nematodes are now sold commercially to control prey populations that are antagonistic to plant health. In the rhizosphere, hundreds to over a thousand nematodes are found in a single gram of soil. They feed on bacteria, fungi, protozoa, algae, other nematodes, and organic matter. The wide-ranging feeding habits of nematodes aid in nutrient cycling, thereby benefiting plants through nutrient assimilation and mineralization. *See* NEMATA (NEMATODA).

Protozoa are single-celled eukaryotes that are prevalent in the rhizosphere, reaching populations of several thousands of protozoa per gram of rhizosphere soil. Protozoa are sometimes detrimental to plants, causing illness. More often, protozoa provide beneficial services, such as grazing on bacteria, which releases nitrogen and other nutrients into the rhizosphere. Protozoa also utilize organic compounds and feed on other protozoa. The grazing abilities of protozoa in the rhizosphere aid in suppression of plant disease through ingestion of plant pathogens. *See* PLANT PATHOLOGY; PROTOZOA.

Applications in rhizosphere ecology. Examination of the rhizosphere has led to advances in agriculture, environmental remediation, water filtration, medical discoveries, industrial applications, and many other fields. Both small- and large-scale agricultural practices require a good understanding of rhizospheric processes that aid in plant growth and disease suppression. Studying the complex interactions among the plant, soil, and microbial components of the rhizosphere is integral for sustaining healthy and high-yielding production systems. Various symbiotic microorganisms, including nitrogen-fixing rhizobia and AMFs, help improve soil fertility and plant growth. Additionally, plant pathologists study the rhizosphere to understand how microorganisms either promote or suppress plant diseases.

Beyond the many agricultural improvements that were developed from a detailed understanding of rhizosphere ecology, much advancement has occurred in other fields. Environmental remediation of pollutants from water and soil is heavily dependent on the biological and chemical breakdown of toxins. The rhizosphere is a rich source of microorganisms that can metabolize toxic substances into inert or safer compounds. Removal of particulates and pollutants through biological-based water filtration projects simulate rhizospheric processes, such as sedimentation, chemical transformations, and biological uptake. Many of the world's most notable medical discoveries were also isolated from rhizosphere microorganisms. Numerous antibiotics used in medicine are derived from the soil, and various plant root extracts have played important roles in aiding human health. In addition, enzymes and compounds produced in the rhizosphere by both plants and microorganisms provide useful applications in industry. For example, several pesticides and herbicides were originally isolated from rhizosphere inhabitants. *See* BIODEGRADATION.

The rhizosphere was once considered a "black box" of unknown processes and components, but it has become a more thoroughly studied system. Rhizosphere ecology continues to rise in importance with advances in genomics, mass spectrometry, and microscopy. The discovery of new microorganisms, chemical compounds, and genetic pathways continues to help elucidate the complex interactions of the abiotic and biotic components of the rhizosphere.

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