CHAPTER 11

Rhizosphere

Ann C. Kennedy

> *To own a bit of ground, to scratch with a hoe, to plant seed, and watch the renewal of life—this is the most commonest delight. . .*
>
> —Charles Dudley Warner

To a soil microorganism, the rhizosphere is like a lush oasis in the desert. In comparison to the near-starvation conditions of the bulk soil, the rhizosphere is a place where nutrients are plentiful, life is good, and microorganisms flourish. The rhizosphere is the zone of altered microbial diversity, increased activity and number of organisms, and complex interactions of microorganisms and the root. The significance of the rhizosphere arises from the release of organic material from the root and the subsequent effect of increased microbial activity on nutrient cycling and plant growth. The microbial community in the rhizosphere can influence plant growth in beneficial, neutral, variable, or harmful ways (Fig. 11–1).

The term **rhizosphere** was first used by Hiltner in 1904 to describe the zone of soil under the influence of roots (Hiltner, 1904; Box 11–1). The rhizosphere can extend more than 5 mm from the root and, more importantly, is the area of increased microbial activity (Fig. 11–2). The area of increased microbial activity around the seed is called the **spermosphere** (Slykhuis, 1947). This term arose because the seed was commonly referred to as the sperm; hence the word "spermosphere" paralleled the areas of influence of the root, or rhizosphere. The spermosphere can extend 1 to 10 mm from the seed, but distances up to 20 mm have been reported. Seed colonization is the first step toward root colonization in the soil. Microorganisms established on the germinating seed can multiply and colonize the length of the root as it emerges and grows through the soil. Thus, colonization of the imbibing seed may predispose future colonization of the root.

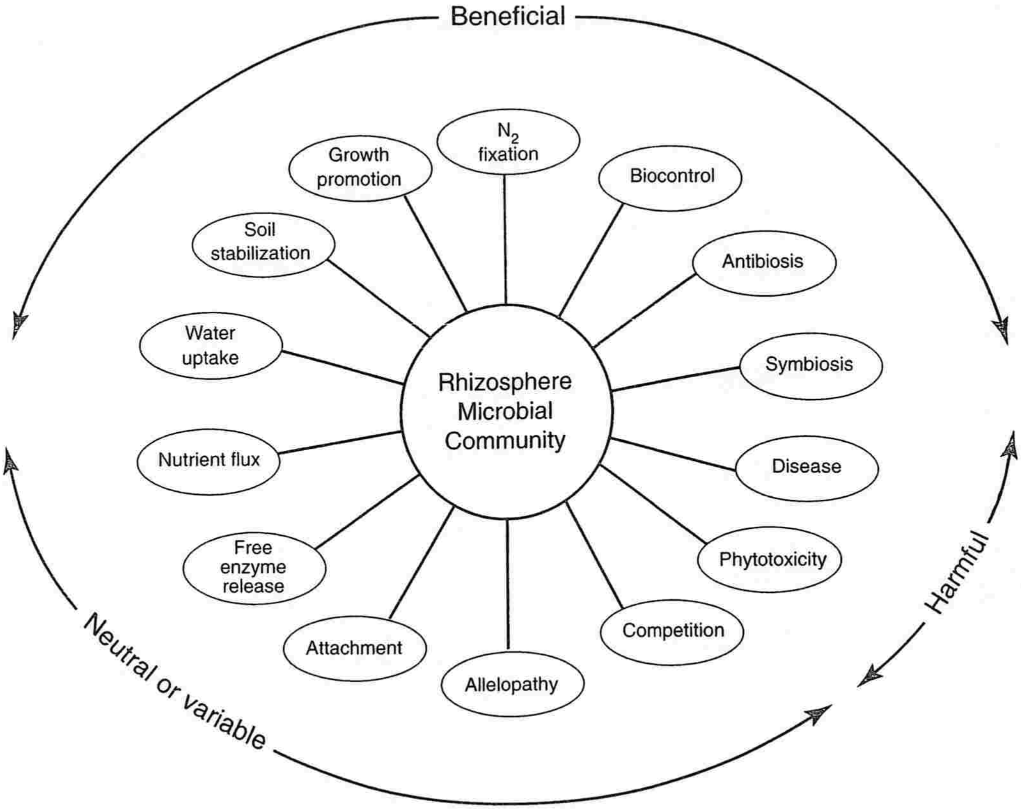

FIGURE 11–1
Beneficial, harmful, and neutral or variable effects of the rhizosphere microbial community on plant growth.
Adapted from Lynch, 1990. Used with permission.

BOX 11–1

Terminology

Hiltner coined the term "rhizosphere" based on observations of symbiotic dinitrogen-fixing bacteria on the legume root. The term has now been expanded to represent, in a more general way, the volume of soil surrounding and under the influence of the roots of all plants. It is important to recognize that definitions may change as our understanding changes.

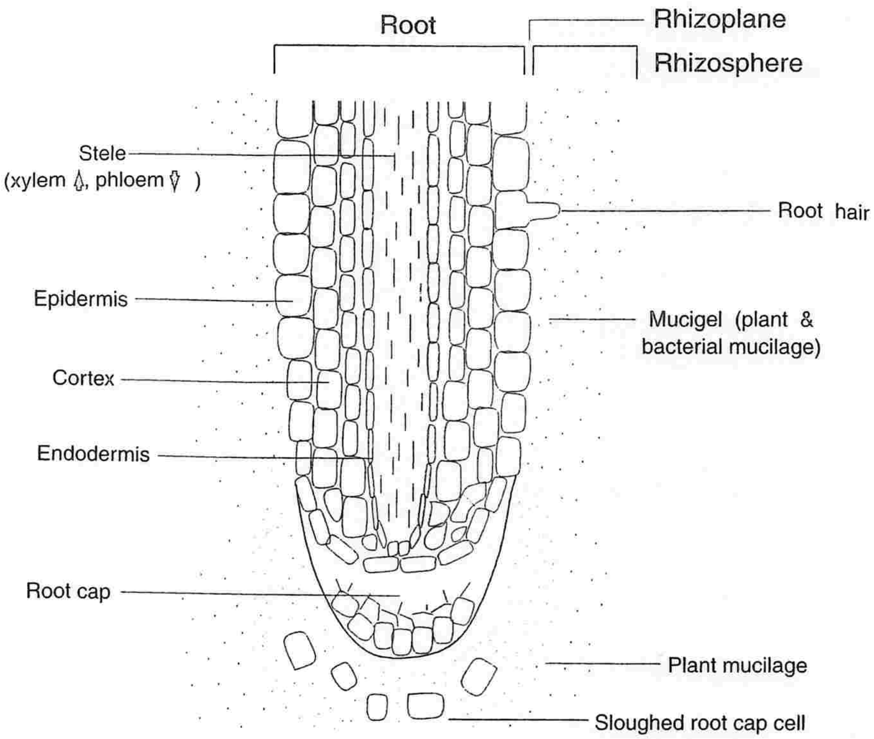

FIGURE 11–2
A root and corresponding rhizosphere and rhizoplane.

THE SEED AND ROOT ENVIRONMENT

The volume of soil influenced by root and seed is neither uniform nor well understood. The rhizosphere and spermosphere consist of several different gradients that change as the distance from the root or seed increases. The heterogeneity of this zone and the many different processes occurring within it make it difficult to measure and study. The rhizosphere and spermosphere are dynamic, and both can change quickly in space and time sufficiently enough to alter rhizosphere characteristics. These changes can influence the associations between the plant and the microbial community.

Spermosphere

Microorganisms established on the germinating seed can multiply and colonize the length of the root as it emerges and grows through the soil. Although the spermosphere is not as well studied as the rhizosphere, the potential for change is immense. For example, colonization of the spermosphere may predispose future colonization of the root, change plant establishment, and affect physiological maturity. Many of these effects are seen at harvest. The spermosphere and rhizosphere effect begins with the release of compounds from the seed. Once the seed coat is damaged or broken and moisture is present, the seed imbibes water and, in so doing, releases nutrients for nearby microorganisms. The greatest amount of exudate originates from the embryo end of the seed; therefore, the corresponding initial microbial colonization is greater at this end than elsewhere.

Root Growth Through Soil

The elongating tip of a root is sterile, and as the root grows into the soil, contact is made with colonies of microorganisms distributed throughout the soil (Box 11.2). Roots normally grow into air-filled pores larger than 10 μm in diameter. Properties of the soil affect root diameter, root hairs, and the branching pattern of lateral roots. The distribution of roots is influenced by species and cultivar, soil texture, physical and chemical properties, and temporal changes. Root growth rates often are more influenced by soil type and physical conditions than by plant varietal effects.

Root Hairs

Root hairs are extensions of the epidermal cells of the plant root. The functions of root hairs are still debated among researchers, but root hairs are important in ion uptake from soil, especially with immobile ions like $H_2PO_4^-$ and Zn^{2+}. More root hairs are found in coarsely aggregated soils (aggregate size of 3 to 5 mm) than in finely aggregated soils (less than 1 mm). Root hairs may penetrate adjacent soil aggregates and take up nutrients within them.

Root Cap

The primary function of the root cap is to protect the meristem as the root moves through the soil. The cap produces **mucilage** and may release substances that enhance plant cell growth. This nutrient-rich area provides a lush region for microbial growth. Root cap cells may elongate and persist in the soil surrounding the root for many centimeters behind the root tip. The mucilaginous sheath (sometimes called mucigel layer) functions as a nutrient absorptive area and protects the root tip from chemicals in the soil that could injure the root. This covering reduces desiccation and abrasion damage to the root tip or apical region of the root.

Rhizosphere Boundaries

The boundaries of the various sections of the rhizosphere and spermosphere are difficult to demarcate. A simple solution is to divide this area into the rhizosphere, rhizoplane, and root. As previously defined, the rhizosphere is the zone of

BOX 11–2

Overview of Scale

Roots are much larger than bacteria and fungi. For example, a soil bacterium may be 0.5 µm wide and 5 µm long; a fungal hypha may be up to 20 µm wide and more than 1,000 µm long. It is difficult to estimate the length of individual fungal hyphae in soil because most sampling techniques break these filamentous structures. In contrast, plant roots are about 1,000 µm wide and extend 1,000,000 µm down the soil profile. An average root hair is 10 µm wide and 500 µm long. Compared to an average soil bacterium and fungus, root hairs and roots may be approximately 1 to 1,000 times wider and 1 to 100,000 times longer.

BOX 11–3

Practical Rhizosphere Analysis

How does one determine which organisms inhabit the various areas of the rhizosphere when these regions are indistinct? Rhizosphere analyses are often limited by the procedures to identify the microorganisms of these zones. Rhizosphere microorganisms are considered to be those microorganisms removed when the roots and adhering soil are shaken gently in water. Rhizoplane microorganisms are considered to be those left when the washed roots are transferred to fresh diluent and shaken vigorously. Finally, endophytes are those microorganisms that are recovered after the root is surface-sterilized and macerated.

soil influenced by roots and their exudation of substances that affect microbial activity. The **rhizoplane** is the surface of a plant root and any strongly adhering soil particles. The area within the root has been defined in many ways, but it is best considered as the root itself rather than a portion of the rhizosphere. The microbial populations that colonize the interior of the root and form intimate associations with the root are considered **endophytes**.

The rhizosphere, rhizoplane, and root are easier to conceptualize than to study (Box 11–3). For example, if the rhizosphere can extend from 1 to 4 mm or more from the root surface and the rhizoplane with adhering soil can be up to 2 mm in width, then the rhizoplane and the rhizosphere are difficult to differentiate. Furthermore, inhabitants in the rhizosphere may be difficult to distinguish from those of the rhizoplane because of mucilages secreted by the root. The soil–root interface is the area of greatest number and variety of plant–microbial associations.

THE RHIZOSPHERE ENVIRONMENT

The physical and chemical properties of soil were discussed in Chapter 2. This chapter focuses on how changes in some of these soil properties in the vicinity of a plant root affect microbial activity. The nutritional aspect of the rhizosphere will be covered in the next section.

Rhizosphere moisture will affect microbial colonization directly or indirectly as it affects plant growth. Cells at the surface of the root may experience severe changes in water potential (Fig. 11–3). On the one hand, soils above or near field capacity (approximately −0.03 MPa or a less negative potential) have little change in soil water potential even though plant transpiration can move a large amount of the soil water. On the other hand, in soils of −0.2 MPa or a more negative potential, the soil water potential near the root can stress microbial cells in the rhizosphere. At low soil water potential, motility and diffusion of nutrients can be reduced, dramatically influencing microbial growth. This does not mean that high soil water potentials are necessarily beneficial, because a large percentage of pore space is water-filled and oxygen may be limiting.

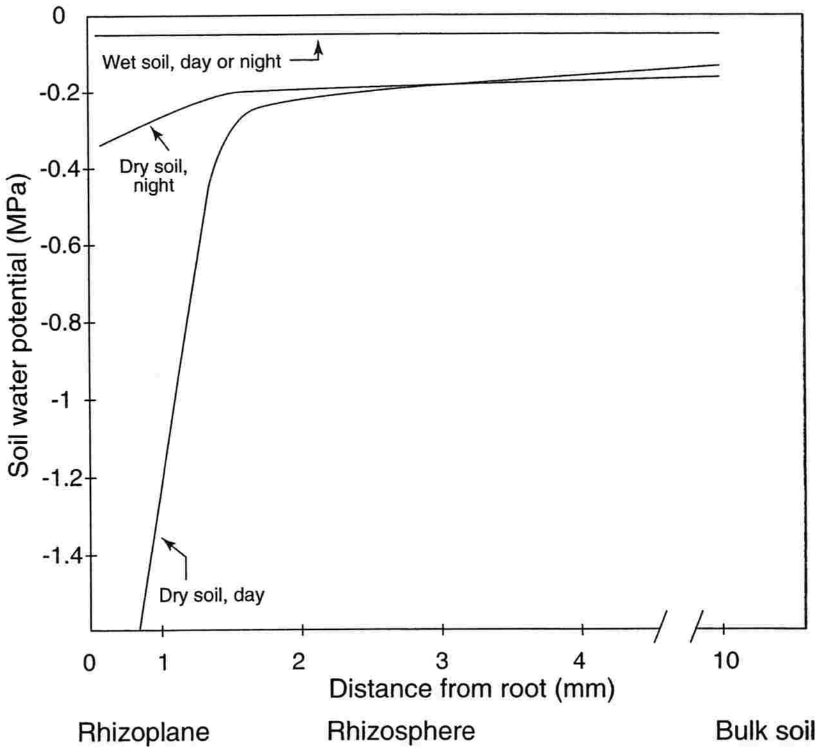

FIGURE 11–3
Effect of distance from root surface (rhizoplane) on soil water potential for day versus night, and wet versus dry soil conditions. *From Papendick and Campbell (1975). Used with permission.*

Soil texture can affect transport and root colonization by microorganisms. In general, bacteria move greater distances down the root in coarse-textured soils like sands than in fine-textured soils like clays. Similarly, soil texture may influence the rhizosphere effect to the greatest extent in sandy soils and least in heavy clay soils.

Temperature can play a role in colonization rates of the rhizoplane. Often microorganisms colonize best at temperatures below their optimum growth temperature. This difference may be because lower temperature reduces competition from the indigenous microflora or decreases the rate of root growth, thus allowing greater root colonization.

Soil pH can alter the survival and competitive abilities of microorganisms. Root-induced production of H^+, HCO_3^-, or organic compounds and their subsequent release into the rhizosphere affects ion uptake and thus pH (Box 11–4), which, in turn, alters the environment of the rhizosphere. Rhizosphere pH may fluctuate as much as one pH unit higher or lower than the bulk soil. The magnitude and direction of this pH change depends mainly on nitrogen nutrition; however, symbiotic relationships and microbial activity can also influence pH.

The plant community greatly influences the rhizosphere microbial community by the exudates it releases from the root and the composition of its plant residues. Plant species and even cultivars of the same species release different amounts and types of carbon to the rhizosphere. Even cultivars differing in disease susceptibility differ in their populations of rhizosphere bacteria; typically, susceptible lines support higher numbers of bacteria than nonsusceptible lines. Genetically modified plants often have distinct exudate patterns and residue composition compared to the wild type plant. Although these differences may result in changes in the microbial community, they may not be any greater than those seen among various cultivars.

Residue quality and management will influence the composition of the microbial community. Decaying residue and root systems serve as a source of nutrients for the surrounding microorganisms, and the quality of these crop residues may vary with species and cultivar. Similarly, crop species and varieties differ in their decomposition rate, and in the microbial populations they support. Crop rotation may allow for greater carbon inputs and diversity of plant material added to soils. Crop rotation enhances beneficial microbes, increases microbial diversity, interrupts the cycle of pathogens, and reduces weed

BOX 11–4

Effect of Nitrogen Source on Rhizosphere pH

The source of nitrogen influences ion uptake by the root and thus affects rhizosphere pH. When nitrate (NO_3^-) is supplied to the plant, the rhizosphere pH increases because more HCO_3^- is released than H^+. When ammonium (NH_4^+) is supplied, the reverse is true. Ammonium-based fertilizers such as urea, anhydrous ammonia, and aqua ammonia can reduce rhizosphere pH. In acid soils, rhizosphere acidification may reduce bacterial numbers.

and insect populations. Studies have long shown the positive effects of crop rotation on crop growth, attributing this effect to changes in microbial community composition.

As more and more genetically modified microorganisms are introduced into agricultural systems, their impact on native soil populations and plant productivity is being questioned. Differences are evident with the introduction of some of these organisms, but how these differences affect the soil microbial community, plant productivity, soil quality, and organic matter accumulation on a long-term basis is unclear. They may be case specific. The possibility exists that DNA from engineered strains of bacteria could be transferred to indigenous bacterial populations. Under laboratory conditions, gene transfer occurs in the rhizosphere and spermosphere of barley seedlings via transformation and transconjugation (Chapter 4). This genetic exchange may not be readily occurring in the soil or rhizosphere of field-grown plants. Studies of genetically modified bacteria under controlled conditions show that they are more susceptible to high temperature and low moisture stress in soil than the wild type. More studies on how genetically modified organisms affect the soil environment and indigenous microbial community are needed before these modified organisms can be soil-applied to enhance N_2^- fixation, promote plant growth, and assist in bioremediation and soil conservation.

PLANT-DERIVED COMPOUNDS

Plant roots excrete various organic substances into the rhizosphere, and these substances provide a rich source of nutrients for the microbial community. Because most soils are low in readily available carbon for microbial growth, carbon-containing substances leaked by seeds and roots are of major importance to microbial growth. This importance is not too surprising because a typical microbial cell is approximately 50% carbon. Too often, the term *exudate* is used to define all compounds that come from the root. However, the organic fractions from the root are of various forms and composition and are better defined as exudates, secretions, mucilages, mucigel, and lysates (Table 11–1).

Exudate Composition

Exudate composition varies with the soil environment and the growth stage of the seed and root. It is difficult to determine which compounds are true exudates and which compounds are released from lysed root cells. Compounds in exudates include sugars, amino acids, vitamins, tannins, alkaloids, phosphatides, and unidentified substances (growth factors, fluorescent substances, nematode cyst or egg-hatching factors, and fungal growth stimulants and inhibitors).

Sugars provide readily available sources of carbon for microbial growth. Amino acids, whose percentages vary with plant species, are a readily available source of nitrogen for microbial growth. These compounds are the most-studied

TABLE 11–1 Carbon Compounds Originating from Plant Roots

Exudates	Compounds slowing oozing directly from epidermal cell walls into the soil or oozing indirectly into the intercellular spaces of the plant root and then into the soil. The release of these low-molecular-weight compounds is not the result of metabolic processes.
Secretions	Compounds released that are the result of metabolic processes. These compounds are both low- and high-molecular weight.
Lysates	Compounds released when epidermal cells autolyse.
Mucilages	Compounds (a) secreted by the Golgi apparatus in the root cap, (b) secreted by epidermal cells that still have only primary walls, (c) released from hydrolysed polysaccharides of primary cell wall (between epidermal cells and sloughed root cap cells), and (d) released from bacterial degradation of multilamellate primary cell walls of dead epidermal cells. These gelationous products, together with natural mucilages, bacterial cells and their metabolic products, colloidal minerals, and organic matter, form the mucigel, the gelatinous material on the surface of roots grown in soil. The mucigel maintains contact between the root and the soil as the root shrinks during daytime water stress, permitting continuous uptake of nutrients and water.

From Rovira et al. (1979). Used with permission.

root exudates and are thought to be associated with susceptibility or resistance of plants to root-infecting fungi. Organic acids can chelate metals, affecting pH and the absorption and translocation of nutrient elements. The range in quantity and variety of vitamins in exudates can account to some extent for differences in bacterial populations. Although most research has focused on water-soluble and nonvolatile exudates, water-insoluble and volatile exudates may affect the growth of soil microorganisms. Little is known about these latter exudates, although soluble and insoluble compounds are thought to be present in equivalent proportions in the exudate.

Exudation Rate

The actual rate of exudation from roots is difficult to calculate. Various gradients of release probably exist, with the greatest amount of exudate arising from those cells involved in cell elongation and lateral root formation. The concentration of carbon in the rhizosphere declines exponentially as the distance from the root increases. Increased exudation can result from extremes in temperature, water stress, phosphorus deficiency, increased light intensity, and increased populations of microorganisms. Exudation rate is also influenced by herbicides, pathogens, foliar treatments, symbiotic associations, and root and seed injury (Box 11–5). Decreased exudation can result from nitrogen deficiency, decreased light intensity, and decreased microbial populations.

Plant exudates are the substrates for microbial growth. As microbial activity increases, the growth of the root and plant is affected. Greater populations of microorganisms in the rhizosphere competing for nutrients may create a nutrient deficiency for the plant. In contrast, microorganisms may make nutrients from

BOX 11–5

Effect of Seed Scarification

Over a 24-h period, unblemished, moistened soybean seeds with intact seed coats exude an estimated 5.3 mg glucose equivalents (C) h^{-1} per seed. If the seeds are scarified (which breaks or injures the seed coat), then the seeds exude up to 217 mg C h^{-1} per seed! Thus, damaging the seed coat can vastly change the exudation pattern and the microbial community around that seed.

insoluble sources, such as phosphates and trace metals, available to plants. In addition, symbiotic associations of roots with rhizobia (Chapter 16) or mycorrhizal fungi (Chapter 12) increase root exudates. Mycorrhizal roots have enhanced nutrient-absorbing capacity, which subsequently increases plant growth. Plant pathogenic microorganisms (both foliage-infecting and root-infecting) can alter both the quality and amount of exudate and result in greater populations of microorganisms in the rhizosphere (Chapter 22).

Mucilage and Mucigel

The mucilage exuded by roots forms a sheath of slime on the external surface of the root. The principal site of mucilage release is the root tip or apical zone of a root, particularly the meristematic zone immediately behind the root cap. By definition, mucigel contains plant mucilages and plant products as well as bacterial cells and their products. The mucigel creates an intimate contact between roots or root hairs and soil particles. Contained in this sheath are organic materials excreted from living root cells or released from cortical cells, or senescent root hairs sloughed off from the root. This mucigel is more likely found on the root and root hairs than at the root tip.

ORGANISMS INHABITING THE RHIZOSPHERE

A vast number of species of microorganisms are present in the rhizosphere, and their numbers generally decrease as the distance from the root increases (Fig. 11–4). To measure the effect of the rhizosphere on a particular population, the number of microorganisms in the rhizosphere (R) and the number of microorganisms in the bulk soil (S, soil not influenced by the root) are compared. This R/S ratio provides an estimate of how strongly the rhizosphere affects a particular organism (Table 11–2). This relationship can also differ with plant species (Table 11–3). The R/S ratio is especially helpful in determining the **rhizosphere competence,** the ability of an organism to colonize the rhizosphere, of various organism-plant combinations. A microorganism with good rhizosphere competence is a good candidate for use as a microbial inoculant.

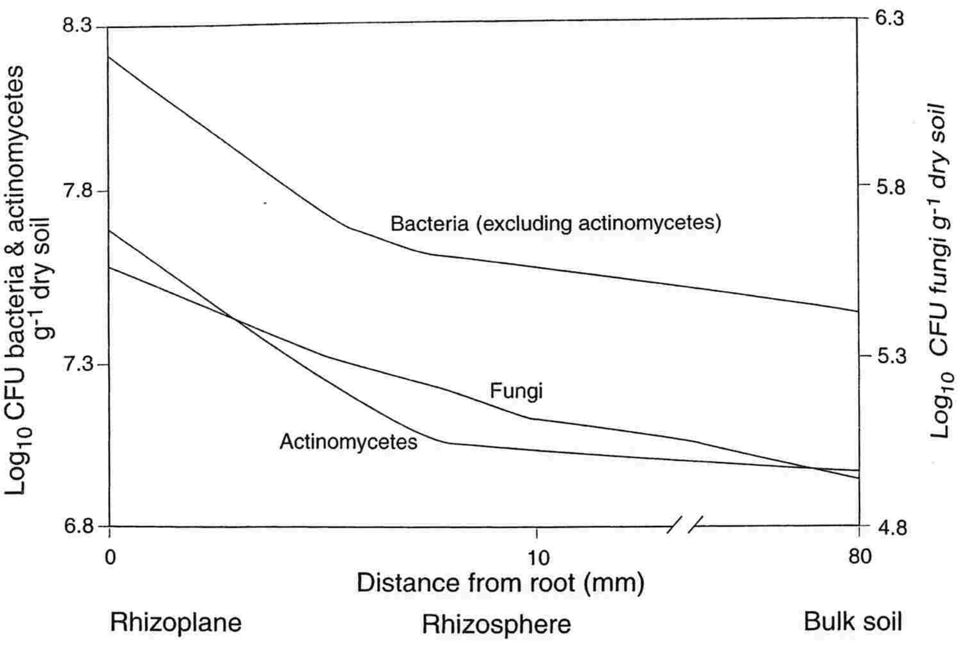

FIGURE 11–4
Distribution of naturally occurring actinomycetes, fungi, and bacteria on the rhizoplane and in the rhizosphere of spring wheat and bulk soil (CFU = colony forming units). *Modified from Papavizas and Davey (1961). Used with permission.*

TABLE 11–2 Colony-forming Units (CFU) of Microorganisms in the Rhizosphere (R) of Wheat (*Triticum aestivum L.*) and Nonrhizosphere Soil (S) and Their Resultant R/S Ratios

Microorganisms	Rhizosphere	Nonrhizosphere	R/S Ratio
	CFU g^{-1} Soil		
Bacteria	1.2×10^9	5.0×10^7	24.0
Fungi	1.2×10^6	1.0×10^5	12.0
Protozoa	2.4×10^3	1.0×10^3	2.4
Ammonifiers	5.0×10^8	4.0×10^6	125.0
Denitrifiers	1.3×10^8	1.0×10^5	1260.0

From Rouatt et al. (1960). Used with permission.

Bacteria

Bacteria, including actinomycetes, are the most numerous inhabitants of the rhizosphere—typically numbering 10^6 to 10^9 organisms g^{-1} of rhizosphere soil—although they account for only a small portion of the total biomass because of their small size. Many bacteria have a large R/S ratio, indicating marked stimulation in the rhizosphere. In general, nonsporulating rods are abundant in the rhizosphere.

TABLE 11–3 Colony-forming Units (CFU) of Bacteria in the Rhizoplane and Rhizosphere of Different Crop Plants and in Nonrhizosphere Soil

Plant	Rhizoplane	Rhizosphere	Nonrhizosphere	R/S Ratio
	CFU x 10^8 g^{-1} of Root or Soil Dry Wt.			
Red clover (*Trifolium pratense* L.)	38.4	32.6	1.3	25.1
Oats (*Avena sativa* L.)	35.9	10.9	1.8	6.1
Wheat (*Triticum aestivum* L.)	41.2	7.1	1.2	5.9
Flax (*Linum usitatissum* L.)	24.5	10.2	1.8	5.7
Barley (*Hordeum vulgare L.*)	32.2	5.0	1.4	3.6
Maize (*Zea mays* L.)	45.0	6.1	1.8	3.4

Adapted from Rouatt and Katznelson (1961). Used with permission.

Pseudomonads and other Gram-negative bacteria are especially competitive in the rhizosphere and occupy a large portion of the total bacterial population on the root. Actinomycetes account for approximately 10% to 30% of the total microflora in the rhizosphere, depending on the season or when the nutrients are added. Actinomycetes have smaller R/S ratios than other bacteria. Bacteria in the rhizosphere tend to be organisms exhibiting more of the "r" type strategists with rapid turnover rates, than "k" type strategists with slow turnover rates (Chapter 10). These factors further lead to the difficulty in following populations in the rhizosphere.

Fungi

Although plate counts of rhizosphere fungi generally are less than bacteria and actinomycetes, these counts are based on spores and mycelial propagules and may be misrepresentative. Direct microscopy shows considerable fungal growth along root surfaces; there may be as much as 12–14 mm of hyphae mm^{-2} of root surface. Population numbers may best be reported as ranges, most frequently 10% to 20% of the total microflora or 10^5 to 10^6 g^{-1} rhizosphere soil. The R/S ratios (ranging from 10 to 20) can be substantial. The rhizosphere and spermosphere favor initial colonization by zygomycetes and hyphomycetes because these fungi grow on simple sugars (Chapter 6). Several rhizosphere-inhabiting fungi are pathogenic, whereas others form symbiotic (mycorrhizal) associations with roots. Mycorrhizal fungi may be a major component of the microbial biomass in the rhizosphere. Because many of these fungi do not grow on artificial media in the laboratory, they are often overlooked.

FAUNAL POPULATIONS

As with the microfloral populations, micro-, meso-, macrofauna are affected by the rhizosphere. Protozoa (i.e., amoebae, flagellates, and ciliates), nematodes, mites (Acarina), and springtails (Collembola) exhibit the greatest rhizosphere effect (Chapter 8). Unsurprisingly, these organisms are not distributed throughout the soil uniformly, but are found where food is most plentiful. In the case of protozoa, they can feed selectively, and therefore, they can influence the composition of the bacterial population in the rhizosphere.

Root exudates influence abundance and behavior of nematodes directly or indirectly in a variety of crops, and the populations are much greater in the rhizosphere than in root-free soils. Root exudates can induce cyst- or egg-hatching of nematodes. Some plants stimulate hatching; others do not. Nematode larvae are usually found in the highest concentration at the region of greatest cell elongation behind the root tip. This enhanced population is not only a response to an increased food supply, but also in response to substances released that attract nematodes. Conversely, nematodes may also be repelled by some plant exudates.

Because many microarthropods are **mycophagous** (fungal-eating), they are more abundant near root surfaces. Mites and springtails predominate in the rhizosphere and feed on woody tissue, leaf tissue, fungi, bacteria, or algae. They follow plant roots to the available food supply. Like protozoa, mites and springtails can feed selectively on certain plants and bacteria. The high populations of bacteria and fungi in the rhizosphere encourage the buildup of many of these faunal species that graze on microorganisms. The faunal component is often overlooked in rhizosphere studies and yet it is a dynamic, integral factor in rhizosphere functioning.

MOVEMENT OF MICROFLORA IN THE RHIZOSPHERE

Dispersal

Microorganisms can move through the soil along the root and colonize the rhizosphere to its fullest extent. Microorganisms are thought to move along the root by three different mechanisms:

- motility of the organism (active transport),
- water movement on the surface of the root (passive transport), and
- movement of microorganisms on the root apex as the root cells elongate (passive transport).

Although bacteria inoculated on the seed will colonize roots within 3 cm of the seed in the absence of percolating water, their further dispersal along the roots is increased by water movement through the soil.

Root Colonization

A number of biotic and abiotic factors affect root colonization by soil microorganisms. These include, but are not limited by, the microorganisms themselves,

TABLE 11–4 Factors or Characteristics Influencing Rhizosphere Colonization

- Microorganisms
  - Nutritional versatility
  - Early growth rate
  - Cellulase production
  - Antibiotic tolerance or production
  - Siderophore production
  - Unique physiological attributes
  - Tolerance to fungicides or other chemicals
- Plants
  - Species
  - Age
  - Altered genetics
  - Foliar treatments
  - Abundance of unoccupied binding sites or niches
- Soil
  - Type
  - Texture
  - Moisture
  - Atmosphere
  - Temperature
  - Fertility
  - Applied pesticides

the plant, and the environment (Table 11–4). Although most scientists report colonization on a per root or root dry mass basis, electron micrographs show that microorganisms occupy only 7% to 15% of the root surface. For example, rhizoplane bacteria are typically scattered across the root in small colonies associated with only a small portion of the root surface (Fig. 11–5). Nor are these colonies uniformly scattered along the root, but are usually associated with holes, tears, crevices, and junctions of epidermal cells. The greatest colonization (approx. 10^7 CFU cm^{-2}) is found on older root surfaces, with the least ($< 10^3$ CFU cm^{-2}) at the root tip. Bacteria may attach to the surface of the root cell wall; fungal hyphae attach to the surface and also penetrate the wall. Recognition signals may play an important role in root colonization. For example, bacteria that agglutinate root exudates can better follow the downward growth of the root in the soil and colonize the rhizosphere than those with no agglutination activity. An introduced organism may colonize the entire rhizosphere after seeds are treated with that organism. In such a case, transport (active or passive) is not a problem. There are, however, many cases where neither bacteria nor fungi applied as an inoculant to the seed are transported along the root surface. Thus, transport of microorganisms in the rhizosphere can be highly variable and depends on the microorganism, the plant, and the environment.

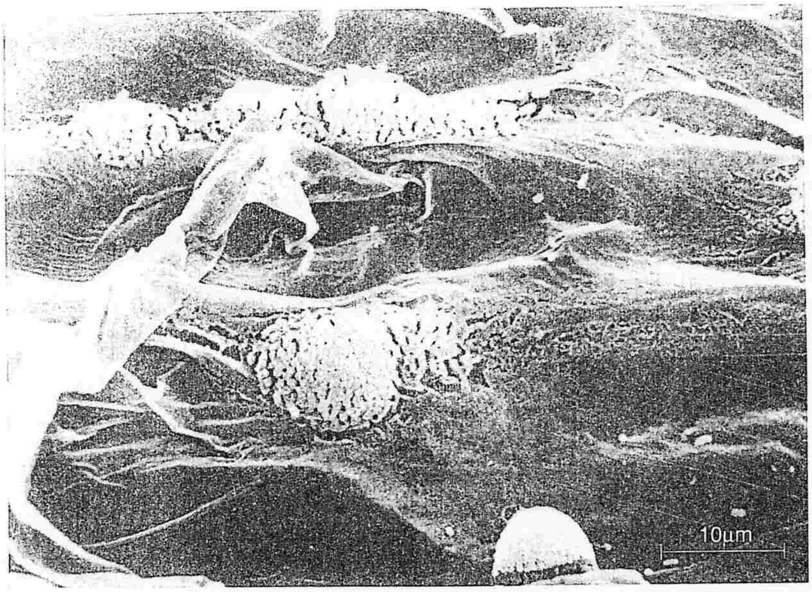

FIGURE 11–5
Colonization of the rhizoplane by bacteria. Note the clumping of colonies at intersection of cells. *Photo courtesy of Begonia et al. (1990). Used with permission.*

MICROBE–PLANT INTERACTIONS IN THE RHIZOSPHERE

The growth of a root through the soil increases the population of many microorganisms. Of interest and possible use are the microbial interactions that benefit plant growth (Table 11–5). The most intensely studied of these interactions are N_2-fixation, mycorrhizal associations, plant growth promotion, decomposition, and nutrient cycling.

Dinitrogen-fixing associations can add otherwise unavailable nitrogen to the plant (Chapter 16). Symbiotic rhizobia and related bacteria form nodules on the roots of plants, take dinitrogen from the air, and transform it to plant-available nitrogen. The plant provides nutrients and a competition-free home for the bacteria.

Mycorrhizal fungi form symbiotic associations with plant roots (chapter 12). They are involved in the nutrient cycling process, especially in stressed environments (e.g., phosphorus- and water-deficient soils). Mycorrhizal associations enhance nutrient solubilization and nutrient uptake in the rhizosphere and expand the volume of soil the root can explore. Benefits include increased rate of nutrient absorption, selective ion uptake, and protection from environmental extremes. This relationship may also impart some protection to plant roots from pathogens. Mycorrhizal associations are enhanced by crop rotation and management practices favoring minimum disturbance.

Plant growth-promoting rhizobacteria (PGPR) are specific strains of bacteria in the rhizosphere that enhance seed germination and plant growth (Chapter 22).

TABLE 11–5 Summary of Beneficial Activities of Microorganisms in the Rhizosphere

- Decompose plant residues and organic materials
  - Synthesize humus
  - Mineralize organic nitrogen, sulfur, and phosphorus
- Increase plant nutrient availability of phosphorus, manganese, iron, zinc, and copper
  - Increase root area (symbiotic mycorrhizae)
  - Produce siderophores
  - Cause oxidation–reduction reactions
  - Solubilize phosphorus
- Fix biological dinitrogen (symbiotic and asymbiotic bacteria)
- Promote plant growth
  - Produce plant growth hormone
  - Protect against root pathogens
  - Enhance nutrient use efficiency
- Promote biological control
- Increase biodegradation of synthetic pesticides or contaminants
- Enhance plant drought tolerance
- Improve soil aggregation

Many different mechanisms are responsible for plant growth promotion. PGPR have been used in biocontrol to protect against plant pathogens, biofertilization to fix atmospheric dinitrogen asymbiotically, and phytostimulation, which directly improves plant growth through the production of hormones. PGPR have the potential to reduce application of inorganic fertilizers and pesticides, and thus reduce pollution. For example, *Azotobacter* and *Azospirillum*, as well as other bacterial species (e.g., *Bacillus*) produce plant growth–stimulating hormones such as gibberellic and indoleacetic acid. Plant growth promotion may also be an indirect consequence of reducing pathogen colonization of the seed and root. For example, some microbes produce the iron-chelating compounds called **siderophores**. These compounds can make iron more available to a PGPR and less available to a plant pathogen. Because of the role iron plays in cellular metabolism (e.g., as a co-factor in some enzymes), this siderophore production may affect microbial growth.

PGPR may be *exophytic* or *endophytic*. The microbial populations that colonize the interior of the root and form intimate associations with the root are considered **endophytes**. Endophytic bacteria may increase plant growth, confer disease resistance, and aid the plant in withstanding stresses such as drought. Populations of endophytic bacteria can be introduced and manipulated in agricultural systems through the use of plant tissue culture, crop rotations, tillage systems, chemical inputs that encourage bacterial growth, and through cultivar selection, seed treatments, and genetic modification. A key to the success of endophytes may be the ability of the isolate to compete with other bacteria on the external or internal portions of plant roots. Bacteria are thought to increase mycorrhizal symbiotic efficiency. Inoculation with a helper bacterium (e.g., *Pseudomonas fluorescens*) may aid mycorrhizal colonization of tree seedlings, increase plant growth, and lower inoculum dose of mycorrhizae.

Introduction of a PGPR may change the overall composition of the microbial community, especially in the presence of plants. In one case where a PGPR was introduced in soil, populations of some bacteria were more affected than other bacteria (actinomycetes) and fungi. Total bacterial populations were generally reduced in the presence of the PGPR, especially in treatments without plants.

Associative N_2-fixing bacteria (Chapter 15) colonizing nonlegumes can be classified into three groups: (1) rhizosphere organisms, such as *Azotobacter paspali*; (2) facultative endophytes that colonize the rhizosphere or root interior of forage grasses and cereals, such as *Azospirillum* spp.; and (3) obligate endophytes that occur within plant tissues, such as *Acetobater diazotrophicus*, *Azoarcus* spp., *Herbaspirllum* spp., and *Burkholderia* sp. In low nitrogen soils, such as agricultural systems in the tropics, these organisms may contribute substantial amounts of nitrogen.

Plant growth-inhibiting microorganisms (Chapter 22) may colonize the rhizosphere and affect plant development in several ways. The traditional plant pathogen attacks plant tissue (Figs. 11–6 and 11–7) and causes disease symptoms. Other plant pathogens may parasitize root cells without causing distinct disease symptoms. Organisms may not parasitize the plant, but colonize the rhizosphere or rhizoplane and produce compounds that may harm root development and inhibit plant growth. Their detrimental effects on plant growth are due mainly to the production of metabolites that disturb plant physiological processes and include phytotoxins, plant growth regulators, volatile substances, and antibiotics. Host-specific organisms have been isolated that show potential as biocontrol agents for weed suppression (Fig. 11–8).

Microorganisms play a large part in the decomposition and subsequent mineralization of organic matter in the soil. Their activity yields various compounds, including nitrates, phosphates, sulfates, carbon dioxide, and water. These processes, as measured by microbial respiration, may be four times greater

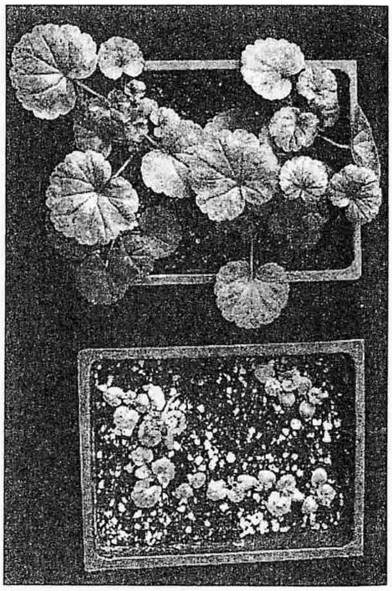

FIGURE 11–6
Biological control of the fungal pathogen *Pythium* with a PGPR on geranium (*Pelargonium graveolens*). Representative results are shown. All treatments received *Pythium* inoculum mixed into the planting medium. At planting time, the treatment on the top received seed inoculation with PGPR strains; the treatment on the bottom was unamended. *Courtesy of M. S. Reddy and J. W. Kloepper, Auburn University. Used with permission.*

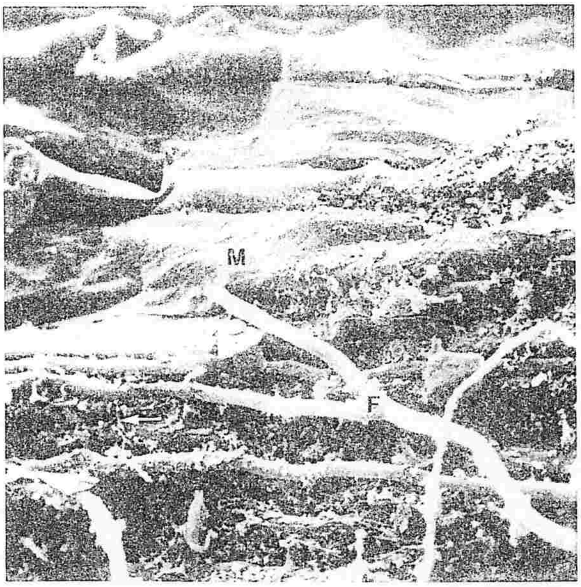

FIGURE 11–7
Edge of a *Gaeumannomyces* lesion in wheat. Entry of *Gaeumannomyces* hyphae induces the release of nutrients from the root cells, and large populations of bacteria build up in the mucigel (M) on the epidermal cells. Initially these bacteria are covered by the mucigel, but later this mucigel is removed by microbial lysis. Mucigel lysis results from the combined action of the fungal hyphae (F), bacteria, and actinomycetes (arrow) (× 4,000). *From Foster et al. (1983). Used with permission.*

FIGURE 11–8
Inoculation of downy brome (*Bromus tectorum*) with deleterious *Pseudomonas fluorescens* rhizobacteria. Downy brome is a weed in wheat fields. Representative results are shown. The noninoculated control plant is on the left and the inoculated plant is on the right.

in the rhizosphere than in the nonrhizosphere soil, though it is difficult to separate root and microbial respiration.

The principal interface for many plant–microbe interactions is the rhizosphere. The dynamics of these interactions will determine the health of the plant. Microorganisms inhabiting the rhizosphere, such as pathogens or microorganisms that produce phytotoxins, may be detrimental to plant health. The challenge is to enhance beneficial relationships and minimize harmful interactions.

INOCULANTS

Recognizing the impact that microorganisms have on plant growth has led to the development of inoculants for enhancing plant growth (Box 11–6). The introduction of a microorganism with the seed and the subsequent exposure of the microorganism to exuding nutrients will enhance microbial growth and establishment of the organism on the seed. Exposing specific microorganisms to a root increases the probability that they will flourish. Dinitrogen-fixing bacteria, PGPR, mycorrhizal fungi, and biological control agents all have potential as inoculants (Table 11–6). Inoculation will only be successful, however, if the microorganisms flourish when they are introduced into the soil or on the seed.

MODELING RHIZOSPHERE FUNCTION

Modeling the processes within the rhizosphere and spermosphere allows us to more fully understand the biology of these regions. In order to form a *conceptual model* of the rhizosphere, the separate components within the system must be

TABLE 11–6 Examples of Microorganisms That Have Shown Potential as Inocula for Soil or Rhizosphere

Microorganism	Effect
Agrobacterium tumefaciens	Controls crown gall in grapes (avirulent strains control crown gall in other plants species)
Alcaligenes spp.	Reduces *Fusarium* wilt in carnations
Bacillus subtilis	Increases germination and growth of cabbage
Azospirillum brasilense	Enhances uptake of NO_3^-, K^+, and $H_2PO_4^-$ Improves growth and dry mass of corn and sorghum
Pseudomonas fluorescens	Increases growth of seeds and cuttings of carnation, sunflower, *Vinca*, and zinnia Reduces damping-off of cotton seedlings Increases yields of potato and sugar beet Increases yield of radish Changes serogroup distribution of bradyrhizobia on soybeans Suppresses "take-all" disease of wheat Reduces stand, growth, and seed production of downy brome
Pseudomonas putida	Increases yield of sugar beet
Pseudomonas spp.	Reduces *Fusarium* wilt in flax, cucumber, and radish
Pseudomonas syringae pv. *tabaci*	Enhances growth, nodulation, and N_2-fixation of alfalfa
Trichoderma harzianum	Increases rate of seed germination and seed emergence Promotes earlier flowering and increased number of flowers Increases growth, height, and dry mass Promotes faster rooting of cuttings

BOX 11-6

Inoculation

Farmers have known for centuries about the benefits of adding a small amount of soil from a legume field to the seed or soil of another leguminous crop. *Rhizobium* inoculants have been successfully used from more than one hundred years and inoculation technology for PGPR is increasing. However, for inoculation to be successful, the organism must be consistently delivered, and it must be sufficiently competitive to survive and persist in the soil, rhizosphere, and rhizoplane. Care must also be taken to avoid laboratory acculturation, where repeated laboratory culturing reduces the survivability of a microorganism, much in the same way a pampered house pet would not have what it takes to survive in the wilds of Africa. Inoculant carriers such as peat, alginate, clay, plant bioproducts, or synthetic polymers can increase the likelihood of successful establishment. Co-inoculation or mixtures of organisms may have a synergistic effect by providing protection, increasing nutrients, or stimulating microbial growth.

brought together to form a network representing the interactions that occur. A *mathematical model* can then be developed to quantify the various interactions represented by the conceptual model. Although these models are often simplistic—perhaps a cylindrical porous membrane to represent the root, root segments, and various types of roots—the models do serve to indicate the outcome of events within the more complex rhizosphere or spermosphere regions. Any mathematical model is based on fundamental assumptions, and the validity of those assumptions in individual situations will determine the overall accuracy of the modeling results. Inoculants, plant infection and disease, and symbiotic colonization also lend themselves well to mathematical modeling. Modeling may assist investigations on the overlapping boundaries of the various regions of the rhizosphere, which may lead to further understanding in delineating these controversial, complex regions. Studies of rhizosphere and spermosphere ecology can use these models as a tool for testing subsequent hypotheses about the zone of soil around the root and seed.

SUMMARY

The rhizosphere is the volume of soil influenced by the root, and the spermosphere is the volume of soil influenced by the seed. In these areas, organic materials are released from the root or seed that alter microbial diversity and increase numbers of organisms, microbial activity, and interactions among microorganisms, the seed or root, and the soil. The microbial community in the rhizosphere can influence plant growth in beneficial, neutral, or detrimental ways, ultimately influencing the health, vigor, and productivity of the plant.

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STUDY QUESTIONS

1. Why is the rhizosphere a zone of increased microbial activity?
2. Why is the spermosphere an important area of study?
3. What role do exudates play in the rhizosphere?
4. Distinguish among rhizosphere, rhizoplane, and root.
5. How does microbial activity compare among the rhizosphere, rhizoplane, and soil?
6. By what mechanisms can bacterial populations be beneficial, detrimental, or neutral to plant growth?
7. What factors affect root colonization?