

# The Rhizosphere: Relation

Speaking before an audience of the Deutsche Landwirtschafts-Gesellschaft in 1904, Lorenz Hiltner (8), soil bacteriologist and professor of agronomy at the Technical College of Munich, stated: "If plants have the tendency to attract useful bacteria by their root excretions, it would not be surprising if they would also attract uninvited guests which, like the useful organisms, adapt to specific root excretions." Hiltner attributed *Bodennudigkeit* ("tiredness of soil") to the activities of harmful organisms in the "rhizosphere" of unthrifty plants and suggested that healthy plants formed a protective bacteriorrhiza, providing a measure of biological control.

The rhizosphere is that narrow zone of soil subject to the influence of living roots, as manifested by the leakage or exudation of substances that promote or inhibit microbial activity. The companion term "rhizoplane" refers to the actual root surface, which provides a highly favorable nutrient base for many species of bacteria and fungi. The two zones together are sometimes referred to as the soil-root interface. Other terms have been used to describe the active zone around seeds (spermatosphere), the peanut fruit (geocarposphere), and the base of plant stems at the soil line (laimosphere).

The years following Hiltner are marked with great advances in rhizosphere research as new techniques have been developed for the quantitative and qualitative assessment of microbial populations in soil, collection and analysis of root exudates, and study of microbial interactions at the root surface. Advanced light microscopy and the application of transmission and scanning electron microscopy have provided a better understanding of the spatial distribution of microorganisms on roots (14).

Rhizosphere investigations can be

divided into three distinct but interrelated phases to determine: 1) effects of roots on soil microorganisms, 2) effects of rhizosphere microorganisms on plant growth, and 3) rhizosphere influence on soilborne plant pathogens and disease. The first two phases provided a broad base of fundamental information on which the third phase developed. The classical investigations of R. L. Starkey of the New Jersey Agricultural Experiment Station between 1929 and 1940 demonstrated many of the principal effects of developing plant roots on soil microorganisms. Clarification of the nature and role of root exudates in contributing to the rhizosphere effect is based substantially on the work of A. D. Rovira and G. D. Bowen in Australia and V. Vancura of the Czechoslovak Academy of Sciences; many others also have contributed significantly. The research and philosophy of S. D. Garrett in England stimulated interest and activity

in the ecology of soilborne plant pathogens, and subsequently the significance of the rhizosphere came into focus as a featured topic in several international symposia.

## Components of the Rhizosphere

Crop plants in the field are under the influence of two very different environments (Fig. 1), the complex soil matrix in direct contact with root systems and the external environment that affects photosynthesis, transpiration, and other vital physiological processes. The roots and aerial parts of plants are interdependent, and environmental effects on one system are reflected in responses of the other. Pathogen growth and reproduction may be affected directly by root exudates of either host (suscept) plants or nonhost (nonsuscept) plants, or the pathogen may be affected by the microflora and small animals that proliferate in the presence of roots and exudates. Thus, the rhizosphere-rhizoplane zone (Fig. 2) is an environment created by the interactions between chemical substances released into the soil by living roots and microorganisms that either utilize these substances as nutrient sources or are inhibited by them. Sloughed root caps and epidermal cells also add to the total energy base for microbial activity. These interactions can be further altered by the nature of the physical soil environment at the root surface.

**Root exudates.** In recent years, the refinement of analytical techniques has permitted the elucidation of root exudate composition. A variety of sugars and amino acids commonly found in the exudate of plants have been studied extensively in relation to pathogen behavior. Other substances include organic acids, nucleotides, flavanones, glycosides, enzymes, vitamins, auxins, saponins, and a number of unidentified substances that attract nematodes, stimulate egg-hatch and fungal spore germination, or inhibit fungal growth. Among the compounds released from germinating seeds and from roots of both angiosperms and gymnosperms are a

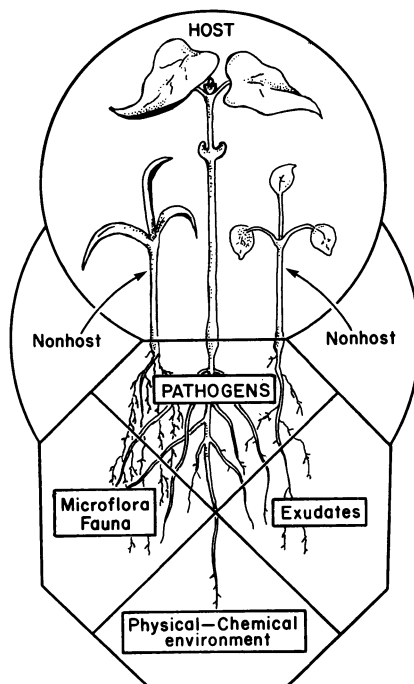


Fig. 1. Interacting environmental components that affect the growth and health of plants.

# Pathogen Behavior and Root Disease

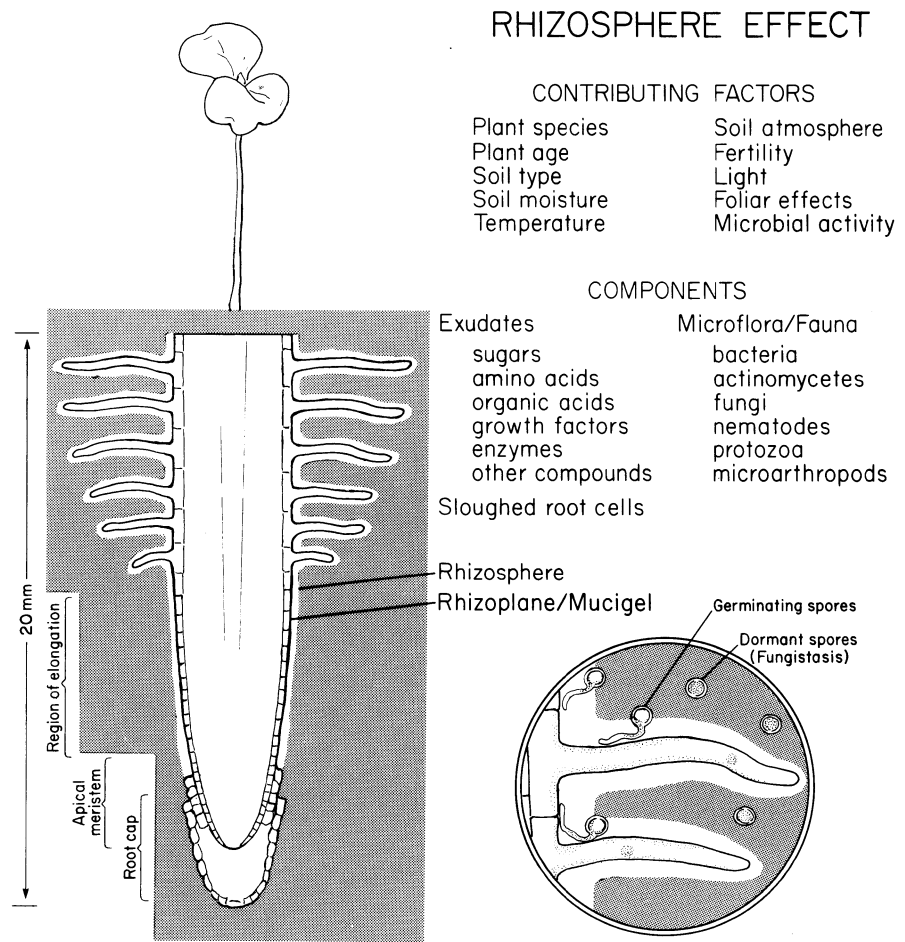
number of volatiles, including alcohols, aldehydes, olefins, volatile organic acids, ethylene, and propylene (21).

Radioactive labeling techniques have facilitated the precise location of exudation sites along roots (15). The region of meristematic cells behind the root tip is a site of major exudation of sugars and amino acids. Significant amounts also are released from germinating seeds and from the region of root elongation. Exudation is greater from poor-quality seeds and at sites where lateral roots emerge from primary roots.

Many plant and environmental factors influence the amount and composition of root exudate released into the rhizosphere (6). Some of these are the plant species, stage of plant development, soil type and physical factors, soil fertility, light, foliar treatments or injury, and microbial activity at the root surface. Generally, any kind of stress on plant growth may induce increased exudation.

**Microflora and fauna.** Populations of organisms in the rhizosphere include species of both the microflora (bacteria, fungi, algae) and the microfauna or meiofauna (protozoa, nematodes, microarthropods). The kinds and numbers of these organisms at the soil-root interface are related either directly or indirectly to root exudates and thus vary according to the same environmental factors that influence exudation. Populations of the microflora in rhizosphere soil can be estimated by dilution-plating procedures with selective culture media and expressed as a numerical value, the R:S ratio, which compares the rhizosphere (R) population with the root-free soil (S) population. Differences are usually very distinct (Fig. 3). Direct microscope counts and measurements of soil respiration also are useful for determining microbial distribution and activity. Though less attention has been given to rhizosphere effect on faunal populations, it is generally recognized that nematodes and some microarthropods are favored by the root zone and often can be observed to accumulate around root tips.

The majority of microorganisms in the rhizosphere, and in soil generally, are saprophytes, unable to induce disease



**Fig. 2. Diagrammatic representation of the rhizosphere of a small cotton root, with lists of exudate and microbial components and influencing factors. Fungal spores within the rhizosphere (inset) are stimulated to germinate.**

under conditions favorable to plant growth. Root-infecting agents include fungi, bacteria, nematodes, and viruses, but most investigations of rhizosphere influence have concentrated on fungal pathogens. The root-infecting fungi may be categorized generally as: 1) specialized, host-dependent parasites with low competitive ability for saprophytic growth and 2) unspecialized parasites, endowed with some of the competitive characteristics of true saprophytes. The first group consists of the vascular wilt species of *Fusarium* and *Verticillium* and

certain fungal pathogens with ectotrophic growth habits, eg, those which grow extensively over the root surface prior to infection, such as *Gaeumannomyces graminis* on wheat, *Phymatotrichum omnivorum* on cotton, and *Heterobasidion annosum* (*Fomes annosus*) on pine. Root exudates are essential to promoting ectotrophic growth. The most highly specialized and efficient of the root-infecting fungi are the symbiotic mycorrhizal forms; these usually are not pathogenic but may influence the parasitic activity of other fungi or of

nematodes. The unspecialized parasitic fungi are exemplified by *Rhizoctonia solani*, *Pythium* spp., *Phytophthora* spp., *Fusarium solani* f. sp. *phaseoli*, and others that can grow and reproduce on organic matter in the absence of host plants. Both of these ecological groups can persist in soil in an inactive state as resistant spores, sclerotia, or quiescent mycelia until activated by living roots.

### The Rhizosphere Effect

Any chemical or physical influence of living roots on microbial activity and the subsequent effect on plant health and vigor is referred to as the rhizosphere effect. The primary contributing factor is root exudate. Depending on the exudate chemicals involved and the physiological nature of the organism responding, the net effect may be one of stimulating or inhibiting a pathogen or other organisms in the associated microflora and fauna. Figure 4 depicts the effects of exudates on a pathogen as either direct, ie, a specific pathogen responding to specific exudate compounds, or indirect, ie, a pathogen responding to nutrients released from organic matter decomposition and growth factors synthesized or to antagonistic phenomena imposed by the general microbial population. Both the direct effects and the interaction effects on a pathogen are further governed by the physical nature of the rhizosphere soil.

**Direct effects of roots on pathogens.** It should be understood at the outset that much of the information about the direct effects of roots and exudates on pathogen behavior comes from highly controlled experiments in axenic liquid or soil culture. This is often necessary in order to exclude microbial metabolites that may be confused with exudate materials. Such studies have established that components of root exudates can directly affect propagule germination, mycelial growth, and reproduction of a pathogen, thus influencing the inoculum potential necessary for infection (Fig. 4). Inoculum potential refers to the capacity of a pathogen population to infect a susceptible plant under a given set of environmental conditions. The population, or inoculum density, is the mass or number of viable propagative units of a pathogen per unit of soil.

A number of cases could be cited in which amino acids, sugars, or other exudate components have directly stimulated pathogen activities (11,17). Stimulation of chlamydo-spore germination of *F. solani* f. sp. *phaseoli* (18) and *Thielaviopsis basicola* (12) occurs at the surface of bean seeds and roots but not in soil distant from the host. The pathogenic Oomycetes, such as species of *Phytophthora*, *Pythium*, and *Aphanomyces*, have the advantage of motile zoospores that accumulate around roots in chemotactic or electrotactic responses to exudates (23). Germ tubes from spores of

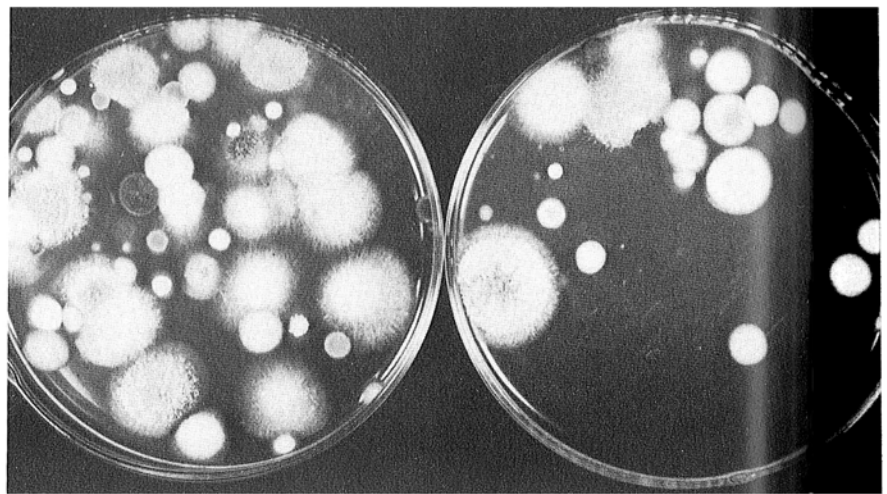


Fig. 3. Dilution plates of fungal colonies from rhizosphere soil (left) and nonrhizosphere soil (right) of wheat, representing an R:S ratio of 2:2.

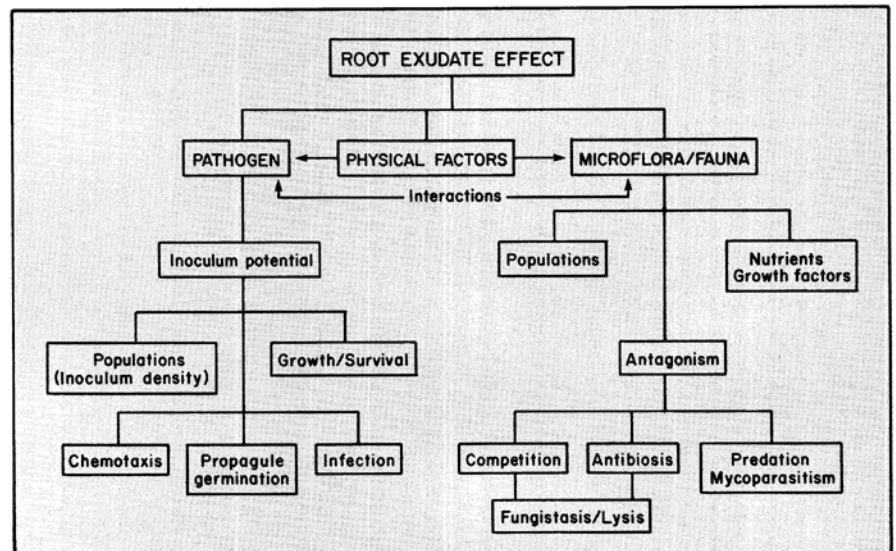


Fig. 4. Direct and indirect effects of root exudate on pathogen activity.

*Phytophthora cinnamomi* also exhibit chemotropism, as they become oriented toward the region of elongation of susceptible roots.

**Microbial interactions.** While there is no longer doubt that fungal propagules requiring exogenous carbon or other nutrients are stimulated to germinate by root exudate components, this fact may not readily translate to a natural soil environment where myriad populations compete for the same nutrients and synthesize biostatic substances. Figure 4 indicates how the indirect effects of root exudates on pathogens are mediated through responses of the general microflora and fauna.

Rhizosphere populations of microorganisms are composed of species affecting both plant growth and pathogen behavior. Primarily, two kinds of interaction occur in mixed populations: 1) those promoting growth of individuals (commensalism and nutritional mutualism) and 2) those in which organisms are inhibited (antagonism: competition, antibiosis, and predation or parasitism).

Both the microflora and fauna are involved in these interactions, since they can occupy the same microhabitat and are affected by the same food chain. Exudate-fed microorganisms decompose organic matter in the rhizosphere, releasing ammonia, nitrates, sulfates, and phosphates, and bacteria synthesize growth factors required by some pathogens.

Exudate-induced interactions unfavorable to propagule germination, growth, and colonization of roots by pathogens are grouped under the term "antagonism." Two of these interactions—competition for limited nutrients and antibiosis from toxic microbial metabolites—contribute to the natural phenomenon of soil fungistasis that holds fungal propagules in a state of exogenous dormancy. Both volatile and nonvolatile compounds from plant roots, plant residues, and microbial activity affect survival and germination of spores and sclerotia of pathogenic fungi. Adding to the natural suppression of pathogens in the rhizosphere are mycoparasites and small soil fauna.

The salient features of the combined direct and indirect effects of root exudates and rhizosphere on pathogen activity can be summarized from the life cycle of *F. solani* f. sp. *phaseoli* (17), based largely on work of Snyder, Schroth, and associates in California in the 1960s. Chlamydospores provide the primary inoculum in field soil. The fate of these spores and their potential for establishing infections (inoculum potential) are determined by their energy level, which is influenced by energy sources both within and beyond the rhizosphere (2). A propagule in the soil may: 1) die of aging degeneration in the absence of a stimulant; 2) germinate in response to nutrients from dead organic matter or from root exudates of a nonhost plant, then either lyse or grow and produce new spores; 3) germinate in response to root exudates of a susceptible plant, followed by new spore production or death by lysis owing to microbial antibiosis or insufficient energy source for infection; or 4) germinate at the host surface in response to exudates, followed by infection or a period of ectotrophic growth before penetration.

**Physical factors.** Indicated in Figure 4 is the fact that both direct effects of root exudates on pathogen behavior and indirect effects from microbial interactions are further governed by a third major principle, the physical characteristics of rhizosphere soil. A growing root and associated microbial activity release CO<sub>2</sub> into the soil while O<sub>2</sub> is consumed. The mechanical force of the root displaces soil particles, altering the bulk density and the diffusion rate of gases, exudates, and water. Many studies have shown that increasing CO<sub>2</sub> concentrations are inhibitory to a number of soilborne fungal pathogens, affecting spore production, spore germination, mycelial growth, saprophytic colonization of organic matter, and pathogenesis. Pathogens with high tolerance to CO<sub>2</sub> may have a competitive advantage over less tolerant microorganisms for colonization of food bases in soil. This seems to be the case for *P. omnivorum*, which is favored in poorly aerated soils and is induced to form sclerotia in an environment of high CO<sub>2</sub> content or in the presence of the bicarbonate ion (10). Hydrogen ion concentration at the root surface can be expected to vary with production of CO<sub>2</sub> and other microbial metabolites, and pathogens are affected according to their tolerance of pH extremes. Forms of soil nitrogen (NH<sub>4</sub>-N or NO<sub>3</sub>-N) influence root exudates and the rhizosphere pH (9). Biological control of take-all disease of wheat, caused by *G. graminis*, in soil of high NH<sub>4</sub>:NO<sub>3</sub> ratios in the root zone has been attributed to suppression of ectotrophic hyphal growth of the pathogen by acidity in the rhizosphere coupled with microbial antagonisms (19).

The influence of soil moisture and temperature on pathogen behavior is well known. These fluctuating environmental factors also impose stress conditions on plant growth, resulting in increased root exudation and potential for infection. Periods of desiccation followed by rewetting often increase exudation, leading to higher microbial populations in the rhizosphere. Plant stress from either high or low temperatures may induce increases (or decreases) of specific carbohydrates, amino acids, cofactors, or other exudate constituents and thus affect pathogen activity. For example, cottonseed germinating at low temperatures (12 and 18 C) exudes more carbohydrate, and consequently damping-off of seedlings by *R. solani* is increased (7).

### Regional Research

Soil scientists and plant pathologists internationally have contributed to our knowledge of rhizosphere ecology-plant disease relationships. In some areas, such work is highly organized. A multidisciplinary regional project (S-90) was organized in the United States to direct the collective efforts of cooperating state and federal researchers specifically to rhizosphere phenomena in relation to plant health and vigor. Active contributing projects are largely within the southern region, but participation is not limited to the South (Fig. 5). Current objectives of the S-90 project deal with: 1) rhizosphere components, 2) microbial interactions, 3) research techniques, and 4) implementation of research results. Project

leaders from participating states or agencies comprise a technical committee that holds annual meetings to review research progress and to plan for future coordinated effort. Other regional and independent projects on root pathogens also have contributed greatly to our knowledge of the rhizosphere.

Overall, the collective efforts of S-90 and related projects have provided a better understanding of root exudates and microbial interactions in the rhizosphere and have shown potential for practical application to agricultural systems. Of special interest is the Texas A&M University multiadversity resistance (TAM-MAR) research program (3) to develop cotton cultivars with resistance to root rot (*P. omnivorum*) and to other major diseases and insects. The TAM-MAR procedure identifies genotypes that have seed and root exudates differing in quantity and quality of carbohydrates, calcium, potassium, sodium, and magnesium. Certain combinations of these nutrients are believed to favor seed- and root-colonizing microorganisms that compete with root-infecting organisms and provide a natural biological protective system. Cultivars selected from annual field-test performance trials show levels of resistance sufficient to reduce root-rot losses when used in conjunction with crop management practices that reduce the inoculum density of the pathogen.

Much has been learned also about the factors affecting root exudation and soil fungistasis, the relation of inoculum density to root infection, interactions between mycorrhizal fungi and fungal or

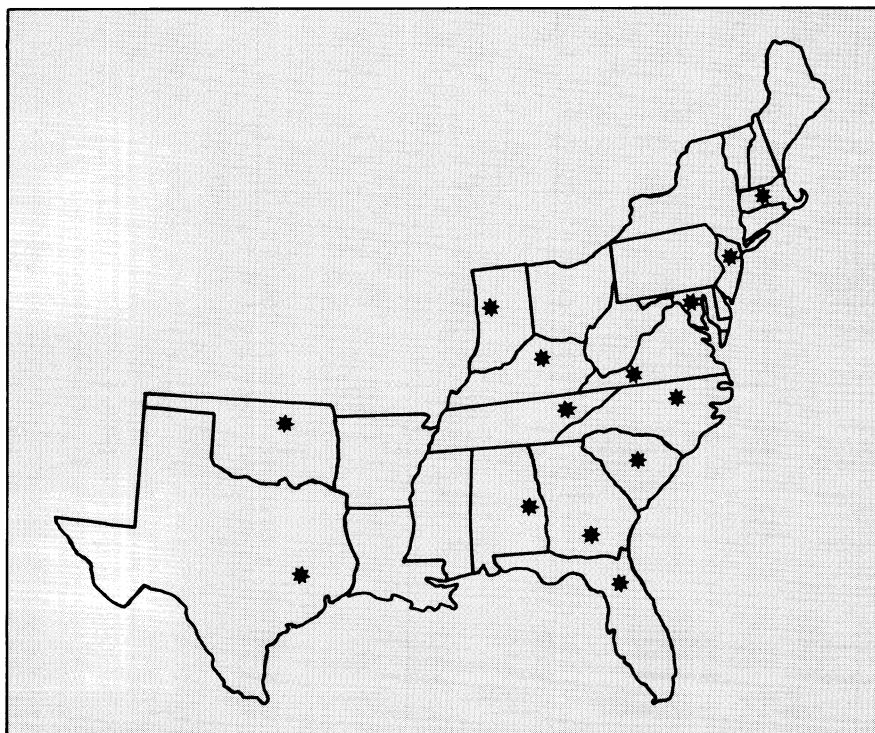


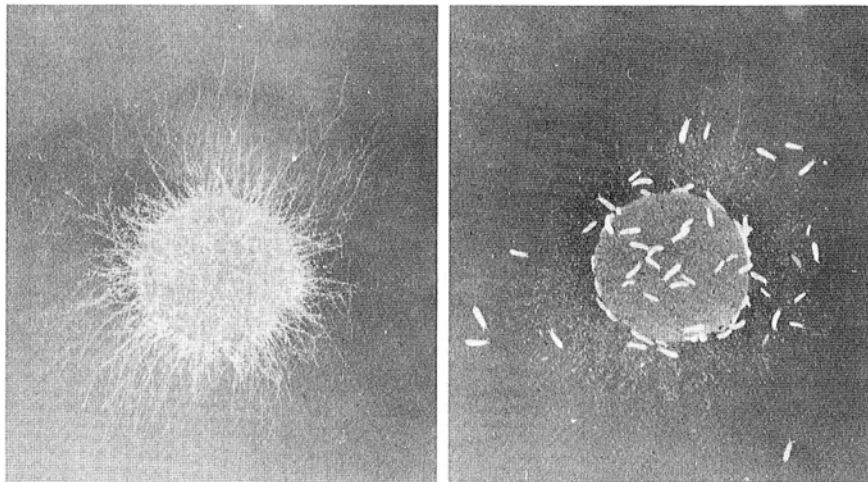
Fig. 5. State and USDA participation in a regional research effort on rhizosphere relation to plant health and vigor.

**Table 1.** Effect of trifluralin on chlamydospores of *Fusarium oxysporum* f. sp. *vasinfectum* in the rhizosphere of cotton seedlings grown in unsterilized soil<sup>y,z</sup>

Herbicide treatment ( $\mu\text{g/g}$ )	Dry root weight (mg)	Chlamydospore germination (%)	Germ tubes lysed (%)
0 (control)	44.8 a	23.5 a	15.8 a
1	26.6 b	25.6 a	27.6 b
5	12.7 c	37.4 b	27.0 b
10	11.7 c	48.9 c	25.3 b

<sup>y</sup>From the dissertation of G. L. Benson, Auburn University, 1976.

<sup>z</sup>Values in columns followed by a common letter are not significantly different at the 5% level of probability.



**Fig. 6.** Destructive feeding of mixed species of Collembola extracted from cotton root systems and placed on a young potato-dextrose agar culture of *Rhizoctonia solani* (right).

nematode parasites, *Phytophthora* toxins, biological control agents, and other rhizosphere-related phenomena.

### Pesticides and the Rhizosphere

A wide variety of specific and nonspecific fungicides, nematicides, and insecticides applied to field soils annually act on many organisms for which the chemicals were not primarily intended. Such nontarget effects may shift the balance within a microhabitat of microbial activity to favor one organism over another. Affected are populations of specific microorganisms, antagonistic relationships (competition and antibiosis), symbiosis (mycorrhizae and rhizobia), and pathogenesis of root-infecting fungi and nematodes.

Pertinent to the rhizosphere are the effects of herbicides on pathogen activities. Specific compounds, or degradation products, either directly inhibit or stimulate fungal growth and reproduction or indirectly affect the pathogen through induced action of the associated microflora. These activities, along with altered resistance in the herbicide-stressed host plant, often lead to increased disease severity. The effect depends on the chemical nature of the compound, its concentration, and the physical-chemical nature of the soil environment.

The herbicide trifluralin has been cited frequently for its suppressive effects on crop-plant growth, sometimes accompanied by increased root disease. The percentage germination of *F. oxysporum* f. sp. *vasinfectum* chlamydospores increased in the rhizosphere of cotton seedlings as root weight decreased in unsterilized soil treated with increasing concentrations of trifluralin (Table 1). Another herbicide, fluometuron, had little effect on root growth or spore germination in the rhizosphere. After spore germination, the amount of germ-tube lysis around roots increased in the presence of either herbicide.

Herbicide-induced exudation from weed plants also may influence chlamydospore germination. Sicklegod (*Cassia obtusifolia* L.) foliar-treated with linuron released 19.8% more root exudate than did untreated plants (S. L. Brown, unpublished). Germination of chlamydospores in unsterilized rhizosphere soil from the herbicide-stressed weed plants was inhibited beyond the natural fungistatic effect. Nutrients from exudates often negate fungistasis and allow spore germination, but in this case the exudate probably enhanced microbial antagonism and exogenous dormancy.

Alteration of rhizosphere ecology by pesticides can have practical implications. Sumner et al (20) found that field

treatments with the herbicide DCPA increased root disease severity in turnip, while root growth and crop yield decreased; at the same time, populations of *Pythium* spp. increased in the rhizosphere. Aside from the direct effects of pesticides on disease, the general health of plants can be disturbed by interference with mycorrhizal relationships, particularly by broad-spectrum fumigants (13).

### Role of Small Animals

We need not dwell on the well-recognized relation of plant-parasitic nematodes to roots and their synergistic activities with root-infecting fungi. Other small animals most likely to be influenced by the environment of the root sphere are the microarthropods, ie, the mites (Acarina) and the springtails (Collembola), that abound in soils of high organic matter content. They are generally unspecialized feeders, but many species are mycophagous and congregate where fungi are available. Rhizosphere studies with these animals in relation to plant pathogens are rare indeed. However, recent investigations in Alabama have shown a favorable cotton-rhizosphere effect on populations of fungus-feeding Collembola. The very common *Proisotoma minuta* and a species of *Onychiurus* feed destructively on a number of plant pathogens, including *R. solani* (Fig. 6); *Trichoderma*, however, is not a favored food source. The bristled bodies of these animals are uniquely suited for collecting fungal spores and bacteria, which can be transported through sterilized soil to cotton roots leading to microbial colonization of the rhizosphere. Pure cultures of *F. oxysporum* f. sp. *vasinfectum* were isolated from cotton seedling roots after Collembola, which had fed on the pathogen, were introduced into large tubes of sterile soil with the plants (22). In other laboratory experiments, Collembola have shown a potential for protecting cotton roots from infection by *R. solani*. Roots growing in previously sterile soil infested with a chopped, oat-grain inoculum of *Rhizoctonia* (0.05 g/kg of soil) suffered a high degree of mortality, whereas Collembola added at 1,600–4,800/kg of soil to the same kind of plant culture provided significant protection (Fig. 7).

These studies suggested the possibility of a dual disease-related role for Collembola: 1) transmission of both pathogenic and saprophytic sporulating fungi to the soil-root interface, thus determining to some extent the nature of the competitive microbial community, and 2) reduction of inoculum density (and therefore inoculum potential) by destructive feeding on pathogen mycelia. The logic of the second part of this hypothesis was revealed in a series of greenhouse tests with cotton plants in unsterilized field soil naturally infested

and supplemented with *R. solani* (5). Effective biological control of pre-emergence and postemergence damping-off was obtained by adding Collembola to the soil in numbers of 1,000–2,000/kg (Fig. 8). The disease index value was reduced by nearly 50%.

### Digest and Outlook

Plant development is controlled largely by the soil environment in the root region, an environment the plant itself helps to create and where microbial life constitutes a major influential force. The effect of living roots on microbial behavior reveals true significance to agriculture when we turn the topic around and view the effects of microorganisms on plants.

To the plant physiologist, the rhizosphere is important for processes relating to nutrient uptake, O<sub>2</sub> and CO<sub>2</sub> exchange, soil moisture gradients, and other factors affecting plant growth. Agronomists and soil scientists deal with the beneficial processes of mineralization, ammonification, nitrification, and symbiosis in the root zone. Plant pathologists have demonstrated significant effects of root exudates and microbial interactions on pathogen populations, propagule germination, and infection. Clearly, a coordinated interdisciplinary effort is essential if rhizosphere research is to provide the kind of information needed for eventual application to cropping practices.

Much of our present knowledge of rhizosphere biology is derived from in vitro experimentation under conditions bearing little resemblance to those in natural soil. This has invited certain misconceptions (4) regarding applicability to plants growing in the field. Such information has been useful, however, in differentiating between the direct effects of exudates on pathogen behavior and the indirect effects of exudate-induced microbial activity. Knowing the major factors contributing to root exudation and knowing the components of exudate and the rhizosphere microflora/fauna, the stage is set for building conceptual models aimed at manipulating specific rhizosphere phenomena for plant disease control.

Genetic research, like that of the TAMMAR program for cotton disease control (3) and the genetic management of wheat rhizosphere flora for root rot (*Cochliobolus sativus*) control (1), may offer the best opportunity for altering the host rhizosphere in favor of biological control agents. Foliar treatment with translocatable nutrients or other chemicals that induce specific microbial activity at the root surface deserves more attention. Relatively little is known about the influence of conventional agronomic practices on microbial activity in the rhizosphere. Pesticides, whether foliar or soil-applied, can be expected to affect

some physiological processes of plants, the quantity or quality of root exudate, and the activities of pathogenic or antagonistic organisms. Elucidation of the direct and indirect effects of specific

pesticides on specific nontarget organisms (mycorrhizal fungi, rhizobia, secondary pathogens, etc.) can aid in developing criteria for evaluating chemicals used in integrated pest management. Intensive

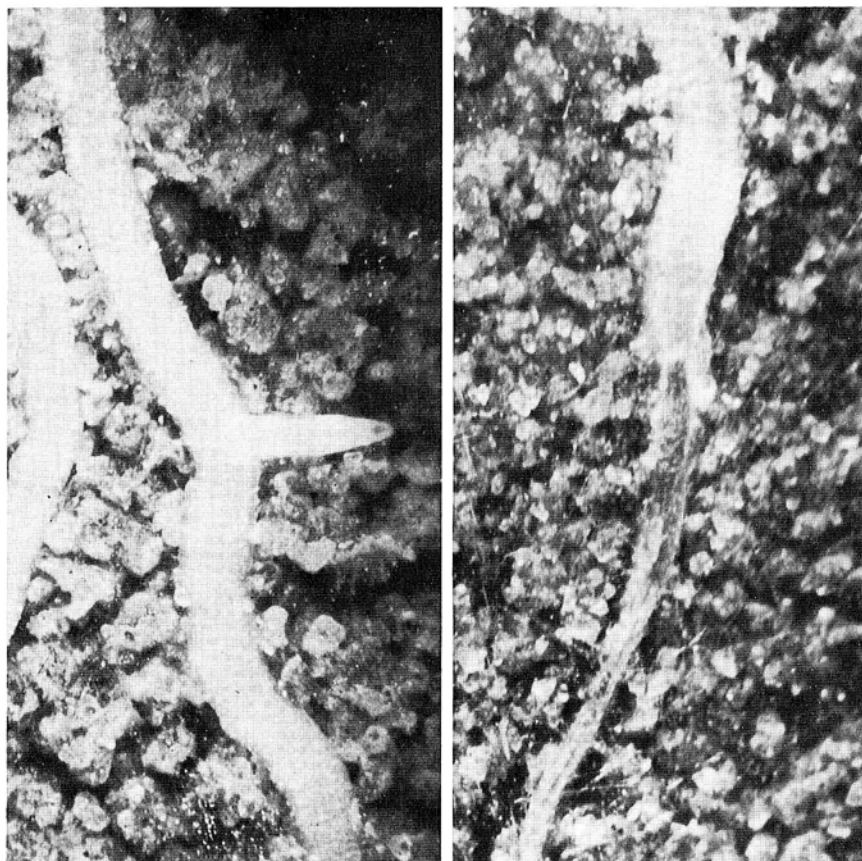


Fig. 7. Collembolan protection of roots from infection by *Rhizoctonia solani*: (Left) Root system from pathogen-infested soil with Collembola and (right) diseased root from pathogen-infested soil without Collembola.

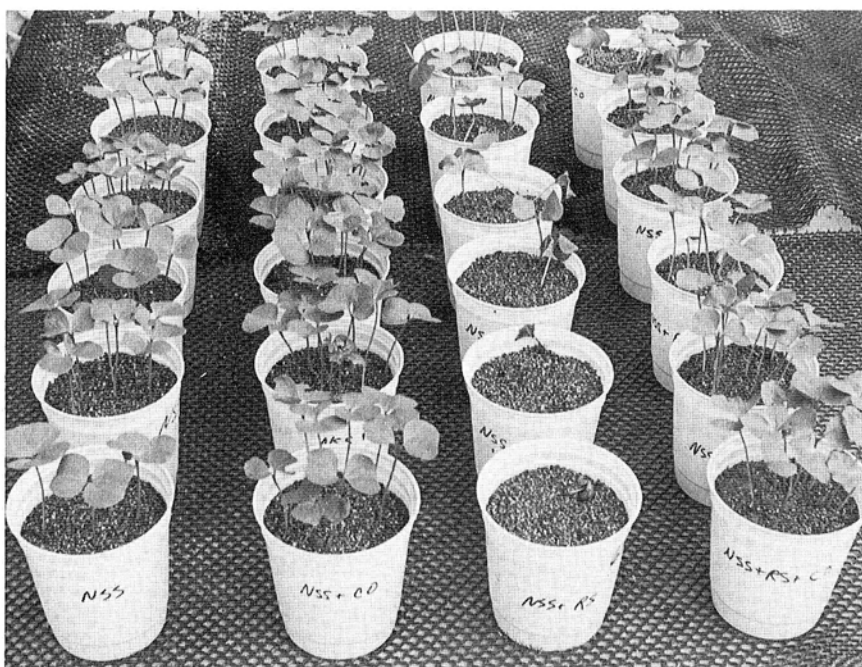


Fig. 8. Control of cotton-seedling disease by Collembola in unsterilized soil: (Left to right) Unamended field soil, 75% seedling emergence; field soil with Collembola (2,000/kg), 99% emergence; field soil with *Rhizoctonia* inoculum but without Collembola, 48% emergence; field soil with both *Rhizoctonia* inoculum and Collembola, 88% emergence.

use of herbicides and reduced mechanical cultivation in minimal tillage or no-till agriculture can alter the root environment and probably affect pathogenic or symbiotic associations.

Allelopathy (the harmful effects of plants on contiguous plants) is currently undergoing a revival of interest primarily in relation to weed vs. crop-plant associations. Understanding the influence of these merging rhizospheres on pathogen population (inoculum density) and the potential for crop-plant infection could contribute to our perception of the relationships between weed control and plant pathology. Effects of multiple cropping systems and fertilization regimes on plant disease have been recorded for many years, but little of this work has been focused specifically on the rhizosphere, where pathogens must establish competitively before host penetration.

Most plants gain nutritional benefit from association with mycorrhizal fungi. In addition, both ectomycorrhizae and endomycorrhizae may affect the susceptibility of plant roots to infection by pathogenic fungi or nematodes (16). The potential for commercial production of mycorrhizal fungi and their establishment in the rhizosphere of field and forest plants is under serious investigation at several research centers. Coating of seeds with rhizosphere-inhabiting species of *Pseudomonas*, *Bacillus*, and *Azotobacter* also offers promise of enhanced plant growth and some protection against pathogens.

Except for nematodes, the role of the microfauna in rhizosphere ecology has been largely ignored. The transmission of bacteria and fungal spores from more distant soil microhabitats into the rhizosphere on the bristled bodies of small arthropods, and the mycophagous habits of many species of these animals,

must determine to some extent the qualitative nature of the rhizosphere flora and the competitive capacity of root-colonizing pathogens.

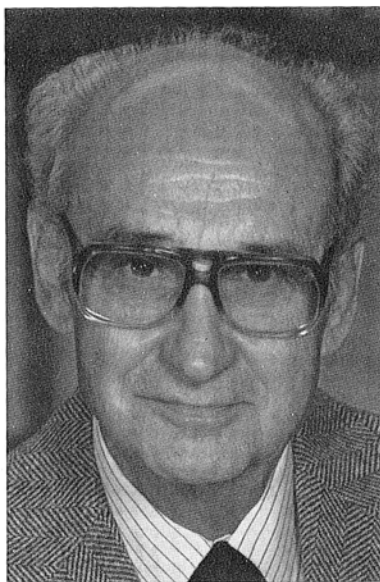
Answers are needed to many questions about rhizosphere-pathogen relationships under conditions more nearly simulating field environments. Through such experiments and the expected advances in genetic research, the components of the rhizosphere could become tools for inducing biological control or enhancing pesticide effectiveness. Rovira and Davey (15) stated appropriately: "We cannot visualize a quick and easy path toward this goal of controlling the biology of the rhizosphere, but the rewards of success should be high in terms of the ultimate effects upon food production."

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