

Interactions between Soil Microbial Communities and Plant Roots: A Minireview.

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ABSTRACT

Plant roots in the soil represent a rich source of diverse, abundant, and somewhat reliable substrates through the secretion of root border cells and root exudates, in an environment (the soil) that is otherwise extremely heterogeneous in nutrient and water supply through time and space. These exudates consist of a wide array of compounds and simple substrates from low molecular weight compounds such as sugars, phenolics, amino acids, organic acids, and other secondary metabolites, to higher molecular weight compounds such as proteins and mucilage.

Depending on the exact nature of the compound in the root exudates, they may play a role in activation of microbial genes responsible for recognition and initiation of symbiotic association, act as an antimicrobial plant defense, activate or disrupt key microbial genes responsible for biofilm formation, or they may simply act as an easy source of moisture, nutrients, and energy.

Although the processes that are mediated by roots and root exudate molecular activity on the microbial community are only beginning to be understood, data collected on the peripheral issues suggests that this rhizosphere effect on soil microbes is highly reciprocal and dynamic. The effect is even highly specific to the plant species, morphological and phenological stage of development, as well as the microbial species present. Primarily in the past, the thought has been that the plant community exerts control over the microbial community. However, some researchers have begun to explore the idea

that it is actually the microbial community that acts as a driver of plant community structure and dynamics. This review will address some of these arising issues as well as the established facts of root exudates effects on the soil microbial community.

INTRODUCTION

Plant roots in the soil represent a four dimensional region, in space and time, of profuse activity relative to the bulk soil, revolving around pH, nutrient, redox potential, and exudate gradients changing as distance from the root increases (Marschner, 1995). This region of gradients in chemical and physical factors strongly influenced by the presence of plant roots and characterized by high rates of microbial population and activity is increasingly referred to as the rhizosphere. In fact, in 1904, Hiltner first defined the rhizosphere as "... that zone of soil in which the microflora are influenced by plant roots." However, for the sake of practical investigation, the rhizosphere is most often defined as the soil adhering to plant roots when they are rigorously shaken, throughout which the rhizosphere effect must be observed to some extent (Kang and Mills, 2004).

This rhizosphere effect is primarily due to the influx of mineral nutrients to the plant roots through mass flow and diffusion, alongside the efflux and accumulation of plant root exudates. Plant root exudates are a complex mixture of chemicals and organic compounds secreted into the soil by the roots that drive underground interactions (Bias, et al. 2004). The exact composition of the exudates is determined by many factors, including species and nutritional status of the plant, soil structure and micronutrient status (Marschner, 1995). Depending on the composition of the exudates secreted by a given plants' roots, that plant may be able to alter the physical and chemical properties of the soil, inhibit the propagation or growth of another plant species, withstand underground herbivory, enhance the possibilities and success of symbiotic relationships, and dictate, to

some extent, the soil microbial community in the rhizosphere. In fact, most rhizosphere bacteria and fungi are highly dependent on associations with plants that are clearly regulated by root exudates (Bais, et al. 2004), and in the rhizosphere numbers of microorganisms can reach 10^{10} to 10^{12} organisms g^{-1} soil (Foster, 1988). This review will examine some of the chemicals that make up plant root exudates, their known functions, and the possibility that the microbial community may in some cases actively influence the composition and success of the plant community.

DISCUSSION

I. EXUDATE COMPOSITION.

Root exudates are a plants' only means of communicating with the rhizosphere and the microbes residing there, so the plant must make use of a wide array of compounds and signal molecules to accomplish this communication (Phillips, et al. 2003). In fact, one of the most amazing metabolic components of plant roots is this ability to exude such a complex and broad assortment of chemical compounds into the rhizosphere. Anywhere from 5% (Walker, et al. 2003) to 60% (Marschner, 1995) of the entirety of photosynthetic carbon fixed by the plant can be transferred to the rhizosphere by exudation through its root system.

Root exudates may consist of water soluble compounds such as amino acids, sugars, hormones, and vitamins that leak from the root surfaces, or actively secreted polymeric carbohydrates and enzymes. The products of the roots may also include gasses such as CO_2 and ethylene, lysates released when cells autolyse, solid materials including cell walls, sloughed cells and root border cells, and eventually parts as large as root hairs or roots themselves (Kang and Mills, 2004). Plants collectively produce a diverse array of

>100,000 compositionally different secondary metabolites, each with different functions in the rhizosphere (Bais, et al. 2004). Some of these exudate compounds have been clearly identified and the general purposes of each of the different classes elucidated; a partial list may be found in Table 1.

Table 1. Components of root exudates, functions in the rhizosphere, and examples identified in root exudates of different plant species, including knapweeds, flax, tomatoes, turnip, peanut, lupine, pine, rape, and other agronomically significant species.

Exudate Component	Rhizosphere Functions	Specific Compounds Identified in Root Exudates	
Organic Acids	nutrient source chemoattractant signals to microbes chelators of poorly soluble mineral nutrients acidifiers of soil detoxifiers of Al <i>nod</i> gene inducers	citric oxalic malic fumaric succinic acetic butyric valeric glycolic piscidic formic aconitic lactic pyruvic	glutaric malonic aldonic erythronic ferulic butanoic syringic rosmarinic <i>trans</i> -cinnamic vanillic tetronic
Amino Acids	nutrient source chelators of poorly soluble mineral nutrients chemoattractant signals to microbes	α - and β -alanine asparagine aspartate cystein cystine glutamate glycine isoleucine leucine lysine methionine serine threonine	proline valine tryptophan ornithine histidine arginine homoserine phenylalanine ?-Aminobutyric acid α -Aminoadipic acid
Sugars & Vitamins	promoters of plant and microbial growth nutrient source	glucose fructose galactose maltose ribose xylose rhamnose arabinose raffinose	desoxyribose oligosaccharides biotin thiamin niacin pantothenate riboflavin

Enzymes	catalysts for P release from organic molecules biocatalysts for organic matter transformations	acid/alkaline phosphatase invertase amylase protease	
Purines	nutrient source	adenine guanine cytidine uridine	
Inorganic Ions and Gases	chemoattractant signals to microbes	HCO ₃ ⁻ OH ⁻ H ⁺ CO ₂ H ₂	
Phenolics	nutrient source chemoattractant signals to microbes microbial growth promoters <i>nod</i> gene inducers in rhizobia <i>nod</i> gene inhibitors in rhizobia resistance inducers against phytoalexins chelators of poorly soluble mineral nutrients detoxifiers of Al phytoalexins against soil pathogens	liquiritigenin daidzein genistein coumetrol eriodictyol naringenin isoliquiritigenin umbelliferone formononetin quercetin	luteolin 4',7-dihydroxyflavanone 4',7-dihydroxyflavone 4,4'-dihydroxy-2'-methoxychalcone 4'-7-dihydroxyflavone 3,5,7,3'-tetrahydroxy-4'-methoxyflavone 7,3'-dihydroxy-4'-methoxyflavone (+)- and (-)- catechin
Root Border Cells	produce signals that control mitosis produce signals controlling gene expression stimulate microbial growth release chemoattractant synthesize defense molecules for the rhizosphere act as decoys that keep root cap infection-free release mucilage and proteins		

Compiled from Dakora (2003), Dakora and Phillips (2002), and Bais, et al. (2004).

II. EXUDATES' ROLES IN THE RHIZOSPHERE.

a. Direct Effects.

i. Antimicrobials.

Because of the diversity of the compounds and secondary metabolites contained in root exudates, plants can send an equally diverse number of signals to surrounding soil biota. One of the most studied root-microbe interactions is that of the antimicrobial compound production and accumulation in and around the roots (Bais, et al. 2004).

In general, it has been discovered that plant families will employ similar secondary metabolites for similar purposes. For instance, most of the family Leguminosae use isoflavonoids as antimicrobials, while Solanaceae members typically use sesquiterpenes. For example, the leguminous *Glycine max* produces glyceollin, *Vigna unguiculata* produces medicarpin, *Mundulea seica* produces munduserone, *Phaseolus vulgaris* produces coumestrol, and *Cajanus cajan* produces cajanin; all of which are isoflavonoids that function as phytoalexins (defensive antimicrobial proteins) in the rhizosphere (Dakora, 2003). Many of the different compounds that make up root exudates can have both antibacterial as well as antifungal properties, but most often, the compounds work synergistically to achieve general antimicrobial results (Bais, et al. 2004). In an effort to reproduce these antibiotics in other organisms and in search of new therapies to battle human pathogens, identification of the genes responsible for the rich production of the antimicrobial indoles, terpenoids, benzoxazinones, flavanoids and isoflavanoids in different plant species such as rice, corn, soybean and various legumes, these species have been subjected to intensive gene-sequencing efforts (Bais, et al. 2004).

ii. AHL Interference.

A key mechanism to the virulence of many bacterial pathogens such as *Erwinia* spp., *Pseudomonas* spp., and *Agrobacterium* spp. in a given system is their ability to communicate amongst themselves, cell to cell, and to form biofilms. This cell-cell communication is called quorum sensing and is mediated by “small diffusible signaling molecules (autoinducers)” that bacteria not only produce, but can perceive in the environment (Walker, et al. 2003). In Gram-negative bacteria these autoinducers are most often in the form of *N*-acylhomoserine lactones or AHLs, which allow the bacteria to

control population densities and gene expression. To date, the roots of several plant species have been found to produce compounds that exhibit clearly AHL inhibitory activity, suggesting that these species have evolved means to deal with biofilms, something humans have not yet successfully accomplished. One example is the root exudates of pea (*Pisum sativum*) seedlings which were found to secrete compounds that exactly mimicked AHL signals in bacterial reporter strains (Fray, 2002). The disruption of the AHLs by plant root exudates may be substances that mimic bacterial signals, block bacterial signals, or enzymatically degrade signals, but full characterization of the exact compounds is still underway (Walker, et al. 2003).

iii. Symbiosis.

Many of the phenolic and flavonoid compounds that are released by plant roots have very specific roles in the formation of symbiotic relationships in the rhizosphere. As signal molecules to microbial symbionts, legumes exude flavonoids, aldonic acids, and betaines from seeds and roots in the rhizosphere. These very specialized signals induce the microbial genes involved in nodule formation (*nod* gene), inhibit the *nod* gene, promote fungal hyphal growth, or inhibit spore germination, depending on the species of the host, the compounds in its exudates, and the symbiont. For instance, biochanin A and formononetin, when produced by white clover have been reported to promote hyphal growth, but when produced by soybean and alfalfa, they have been reported to inhibit the *nod* gene and spore germination (Dakora, 2003). These signals are highly specific between host and symbiont, to assure that only very specific associations will form.

iv. Poor Adaptations?

However, some data suggests not all plants have developed effective strategies to successfully reduce or inhibit pathogenic microbes and encourage beneficial microbes. One example of some work on such compounds is the examination of yellow lupine by Kneer, et al. (1999). They reported the rhizosecretion of isoflavonoid genistein being elicited by salicylic acid, potassium cyanide, and chitosan, and acting as a significant attractant to pathogenic fungi.

Additionally, a recent study has proven that root exudates of certain plants may significantly enhance the growth specific pathogens. Nicol, et al. (2003) found that ginsenosides, saponins exuded by the roots of American ginseng, isolated from the soil as well as a root exudate trapping system resulted in significantly enhanced growth of two common fungal pathogens of the ginseng plants, *Phytophthora cactorum* and *Pythium irregulare*, in culture. These ginsenosides may be acting as feeding and growth stimulants and could be contributing to the susceptibility of the American ginseng to these pathogens. However the ecological relevance of this study may be questionable considering the dynamic interactions and indirect consequences of other factors in the rhizosphere.

b. Indirect Effects.

i. Bacterial Biocontrol.

Above and beyond the direct consequences of the exudates on pathogens and symbionts, the effects of chemotactic signals in the exudates that encourage beneficial symbiotic or mutualistic microorganisms and generate enhanced microbial growth may be yielding *indirectly* pathogen deterrent consequences as well. In recent years there have been several interesting studies performed to determine the effect of bacteria-bacterial

pathogen interactions in the rhizosphere that have found certain species or strains of non-pathogenic bacteria can act as biocontrol agents on pathogenic bacteria. One such example is the use of inoculation with non-pathogenic strains of *Streptomyces* to control scab of potato which is caused by the pathogenic *Streptomyces scabies*. In this particular interaction, competition for space and nutrients in the rhizosphere is thought to be the controlling factor (Ryan and Kinkel, 1997; Neeno-Eckwal and Schottel, 1999). Another example is the control that *Pseudomonas fluorescens* F113 exerts over the soft rot potato pathogen *Erwinia carotovora* subsp. *atroseptica* by production of the antibiotic 2,4-diacetylphloroglucinol (Cronin, et al. 1997). Other *Pseudomonas* species may also control crown gall disease caused by *Agrobacterium tumefaciens* (Whipps, 2001).

ii. Fungal Biocontrol.

Bacteria-fungal pathogen interactions have also been well documented with a significant increase of interest in the area of biocontrol. Many of the anti-fungal interactions documented have involved *Pseudomonas* species (Whipps, 2001). However, other species of bacteria that are typically referred to as plant growth promoting rhizobia that live in the rhizosphere dependent on plant root exudates, specifically *Bradyrhizobium* spp., and 49 different strains of *Sinorhizobium meliloti*, have also been proven to reduce a wide range of plant pathogens. In some cases these rhizobia can decrease fungal pathogen sporulation up to 75% and inhibit growth up to 50% (Dakora, 2003). Some further examples of bacteria-fungal pathogen interactions is found in Table 2.

Table 2. A few examples of bacteria on seeds or roots providing control of fungal plant pathogens in the soil environment.

Bacteria	Fungal pathogen	Plant
<i>Actinoplanes</i> spp.	<i>Pythium ultimum</i>	table beet

<i>Bacillus</i> spp.	<i>Rhizoctonia solani</i> ;	wheat
<i>Bacillus subtilis</i> GB03	<i>Gaeumannomyces graminis</i> var. <i>tritici</i>	chickpea
<i>B. subtilis</i> BACT-D	<i>Fusarium oxysporum</i> sp. <i>ciceris</i>	tomato
<i>Burkholderia cepacia</i> A3R	<i>Pythium aphanidermatum</i>	wheat
	<i>Fusarium graminearum</i>	
	<i>Fusarium</i> spp.	
<i>B. cepacia</i> PHQM 100	<i>Pythium</i> spp.	maize
<i>Comamonas acidovorans</i> HF42	<i>Magnaporthe poae</i>	Kentucky bluegrass
<i>Enterobacter</i> sp BF14	<i>Magnaporthe poae</i>	Kentucky bluegrass
<i>Pseudomonas chloroaphis</i> MA342	<i>Drechslera graminea</i>	barley
	<i>D. teres</i>	barley
	<i>D. avenae</i>	oats
	<i>Ustilago avenae</i>	oats
	<i>U. hordei</i>	barley
	<i>Tilletia caries</i>	wheat
<i>P. chloroaphis</i> PCL 1391	<i>Fusarium oxysporum</i> sp. <i>radicis-lycopersici</i>	tomato
<i>Pseudomonas fluorescens</i>	<i>Fusarium oxysporum</i> sp. <i>raphani</i>	radish
<i>P. fluorescens</i> Q8r1-96	<i>Gaeumannomyces graminis</i>	wheat
<i>P. fluorescens</i> VO61	<i>Pythium ultimum</i>	<i>Lotus corniculatus</i>
	<i>Rhizoctonia solani</i>	rice
<i>Pseudomonas putida</i>	<i>Fusarium oxysporum</i> sp. <i>raphani</i>	radish
<i>Stenotrophomonas maltophilia</i> C3	<i>Rhizoctonia solani</i>	tall fescue

Edited and adapted from Whipps (2001).

The effect of these beneficial microbes being stimulated by root exudates, and, in turn, decreasing the incidence of plant pathogens is so well recognized that inoculation of plants in the field and greenhouse is becoming a cheap and effective pathogen biocontrol method.

III. RECIPROCITY.

The rhizosphere effect, with rhizodeposition of root exudates, is well established, solidifying the fact that the rhizosphere is a strictly confined zone of mutualistic and commensal interactions between not only symbiotic organisms with plants, but free-living microorganisms as well (Kang and Mills, 2004). Up to this point, the molecular aspects of root exudates and effects on individual microbial species have been discussed, but how can

this be applied at an ecosystem level? How might these interactions affect ecosystem processes, and which factors are controlling or guiding what goes on?

A. Plant Domination.

Previously, the dogma has been that because microorganisms in the rhizosphere are so dependent on root exudates, that plants largely control the interactions, microbes, and processes that exist in the rhizosphere, exemplified by studies like Kourtev, et al. (2003), an examination of how exotic and native plant species may alter the structure and function of soil microbial communities. Exotic plant species often are suspect for allelopathy and can frequently exert significant changes on ecosystem levels, however, little is known about the effects these non-native plants may have on the soil microbial community.

Kourtev, et al. (2003) compared soil microorganisms under two introduced species from Japan to those of native plant species and found a shift towards more bacterially dominated systems and decreases in beneficial arbuscular mycorrhizal (AM) fungi under the non-natives. They concluded that plant species were significantly altering soil microbial community structure *and* function within a short period of time, and that these changes were accompanied by ecosystem-level process (nitrogen fixation, etc.) changes.

Söderberg, et al. (2004) also looked at the rhizosphere effect and how it might differ along the root and between different species of grasses and a legume. Using physiological profiles (an indirect measure of activity and substrate utilization abilities of a microbial community) as well as different types of phospholipids fatty acid profiles, they found that not only did the microbial community of the bulk soil differ significantly from that of rhizosphere soil in both structure *and* function, but that the effect was significantly different along the axis of the root, and between different plant species.

Some might argue that these methods are somewhat inconclusive as to actual species present or absent in the rhizosphere, however, other studies have addressed this question as well. Smalla, et al (2001) used polymerase chain reaction (PCR) amplification of 16S rDNA fragments and analyzed them by denaturing gradient gel electrophoresis (DGGE) to assess soil microbial community shifts from bulk to rhizosphere soil and between strawberries, potatoes, and oilseed rape. They found significant differences in dominant bacterial species, as represented by and sequenced from dominant bands on the gels, between bulk and rhizosphere soil as well as between plant species.

B. Microbial Domination

However, many rhizosphere bacteria are plant growth promoters stimulating seedling growth and development (Dakora, 2003), while mycorrhizal fungi provide vegetation with increased efficiency of nutrient uptake, increased productivity (Johnson, et al. 2003), drought stress (Figueiredo, et al. 1999), and may contribute to plant diversity (Klironomos, et al. 2000). These facts, among others are leading to a possible paradigm shift to a more microbially dominated, or at least highly reciprocal view of the relationship between plant and associated microbiota.

Dobbelaere, et al. (2001) reported an exhaustive review that detailed plant responses to inoculation with *Azospirillum* spp., from basic plant physiological responses due to the growth regulation by the *Azospirillum*, to plant respiration, mineral, and water uptake changes. Experiments were carried out in over 7 different countries across the world, including field trials and commercial utilization, and the overwhelming result was a significant increase in yield.

A more specific example of soil microbial community control on vegetation is found in Klironomos (2003), where a large number of plant and fungal species were crossed to determine the range of responses. In some cases, exotic fungal species were grown with native plant species to determine if responses varied according to genotype. The findings were that plant growth responses to mycorrhizal inoculation can range from highly mutualistic to highly parasitic. Plant response was best with native combinations and turned deleterious or parasitic when exotic fungi were introduced to native plant species. Klironomos concluded that this control of plant growth is likely a significant contributor to plant species coexistence by affecting competition and influences the overall structure of the plant community.

However, a somewhat comprehensive synopsis of this new paradigm in which plant-microbe interactions are discussed as drivers of plant community structure and dynamics is found in Reynolds, et al. (2003). This review discusses many aspects of the plant-microorganism relationship, including the fact that this relationship is highly dependent on the soil environment pH, moisture availability, nutrient availability, presence or absence of other microbes, and many other factors, which makes study of community dynamics a challenge, and highly variable within itself. In spite of this fact, compartmentalized studies of aspects of these relationships have yielded the knowledge that pathogenic and mutualistic (microbe-plant) associations are often highly specific, the effects of these associations can be recognized at ecosystem proportions through resource partitioning, and resource partitioning is a key mechanism to preventing competitive dominance or causing exclusions. Through spatial and temporal feedback systems, soil microbial communities may be limiting or growth promoting, and may provide the edge or utilize the last resource necessary to shift the ecosystem forward or back. Recognizing the

fact that soil microorganisms influence many important ecological processes, Reynolds, et al. (2003) concluded with a challenge to subsequent research with newly available methods to delve into the question of bottom-up regulation of above-ground dynamics with greater intensity.

CONCLUSION

Undoubtedly there are numerous and complicated interactions that occur in the rhizosphere. High degrees of activity by both the plant roots and the microbial community are often difficult to conclusively characterize. Does the microbial community drive the structure and function of the plant community, or vice versa? Is there a constant co-evolution and simultaneous succession of both communities? Further research is clearly necessary.

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