The Role of Root Exudates in Rhizosphere Interactions with Plants and Other Organisms

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Abstract

The rhizosphere encompasses the millimeters of soil surrounding a plant root where complex biological and ecological processes occur. This review describes recent advances in elucidating the role of root exudates in interactions between plant roots and other plants, microbes, and nematodes present in the rhizosphere. Evidence indicating that root exudates may take part in the signaling events that initiate the execution of these interactions is also presented. Various positive and negative plant-plant and plant-microbe interactions are highlighted and described from the molecular to the ecosystem scale. Furthermore, methodologies to address these interactions under laboratory conditions are presented.

Contents

INTRODUCTION

Rhizosphere: the soil zone that surrounds and is influenced by the roots of plants

PGPB: plant growth–promoting bacteria

Plant roots exude an enormous range of potentially valuable small molecular weight compounds into the rhizosphere. Some of the most complex chemical, physical, and biological interactions experienced by terrestrial plants are those that occur between roots and their surrounding environment of soil (i.e., the rhizosphere). Interactions involving plants roots in the rhizosphere include root-root, root-insect, and root-microbe interactions. Over the past decade, enormous steps have been taken toward understanding these different types of interactions (79), and recently the field of plant biology has recognized the importance of root exudates in mediating these biological interactions (9, 180, 187).

The rhizosphere represents a highly dynamic front for interactions between roots and pathogenic and beneficial soil microbes, invertebrates, and root systems of competitors (79). However, because plant roots are hidden belowground, many of the interesting phenomena in which they are involved have remained largely unnoticed. In particular, the role of chemical signals in mediating belowground interactions is only beginning to be understood. Chemical signaling between plant roots and other soil organisms, including the roots of neighboring plants, is often based on root-derived chemicals. The same chemical signals may elicit dissimilar responses from different recipients. Chemical components of root exudates may deter one organism while attracting another, or two very different organisms may be attracted with differing consequences to the plant. A concrete example of diverse meanings for a chemical signal is the secretion of isoflavones by soybean roots, which attract a mutualist (*Bradyrhizobium japonicum*) and a pathogen (*Phytopthora sojae*) (122). The mechanisms used by roots to interpret the innumerable signals they receive from other roots, soil microbes, and invertebrates in the rhizosphere are largely unknown.

Root-root, root-microbe, and root-insect interactions may be classified as either positive or negative associations (**Figure 1**). A third category of neutral associations also exists, but is not addressed here. Positive interactions include symbiotic associations with epiphytes and mycorrhizal fungi, and root colonization by bacterial biocontrol agents and plant growth–promoting bacteria (PGPB). Negative interactions include competition or parasitism among plants, pathogenesis by bacteria or fungi, and invertebrate herbivory. The factors that determine whether the chemical signature of a plant's root exudates will be percieved as a negative or a positive signal still require elucidation. However, accumulated

evidence suggests that root exudates have a major role in determining outcomes of interactions in the rhizosphere and, ultimately, plant and soil community dynamics.

WHAT ARE ROOT EXUDATES?

In addition to accumulating biologically active chemicals, plant roots continuously produce and secrete compounds into the rhizosphere (13, 60). Root exudation includes the secretion of ions, free oxygen and water, enzymes, mucilage, and a diverse array of carbon-containing primary and secondary metabolites (17, 172). Root exudation can be broadly divided into two active processes. The first, root excretion, involves gradient-dependent output of waste materials with unknown functions, whereas the second, secretion, involves exudation of compounds with known functions, such as lubrication and defense (8, 172). Roots release compounds via at least two potential mechanisms. Root exudates are transported across the cellular membrane and secreted into the surrounding rhizosphere. Plant products are also released from root border cells and root border-like cells, which separate from roots as they grow (71, 175). Root exudates are often divided into two classes of compounds. Low-molecular weight compounds such as amino acids, organic acids, sugars, phenolics, and other secondary metabolites account for much of the diversity of root exudates, whereas high-molecular weight exudates, such as mucilage (polysaccharides) and proteins, are less diverse but often compose a larger proportion of the root exudates by mass. Root exudation clearly represents a significant carbon cost to the plant (117), and the magnitude of photosynthates secreted as root exudates varies with the type of soil, age, and physiological state of the plant, and nutrient availability (21, 23). Although the functions of most root exudates have not been determined, several compounds present in root exudates play important roles in biological processes (9, 10, 11, 98) (**Figure 2**). The following sections of this

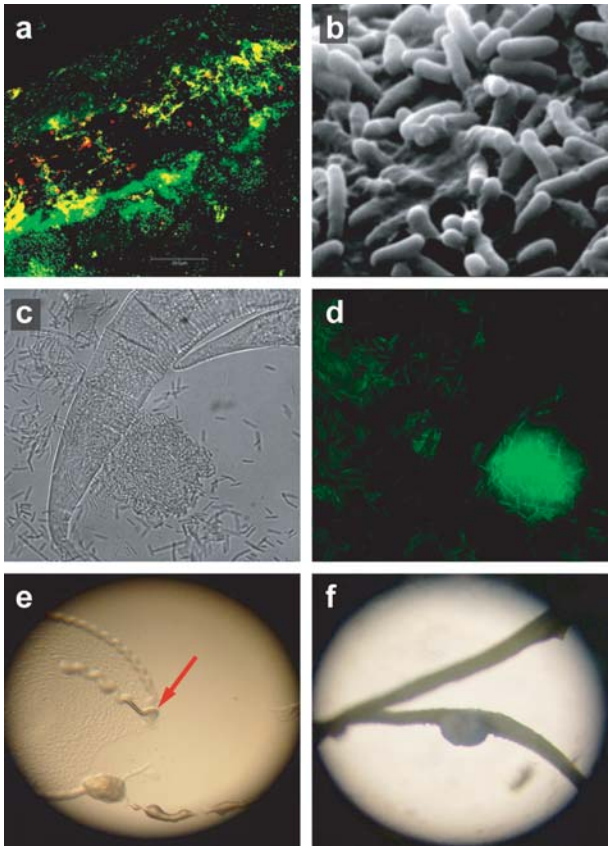


Figure 1

Plant-microbe positive and negative interactions. (*a*) Biocontrol of *Bacillus subtilis* (6051) on *Arabidopsis thaliana* roots by forming protective biofilms against gram-negative bacteria *Pseudomonas syringae* pv. *tomato* DC3000. Panel a shows the formation of aggregates or biofilm by *B. subtilis* on Arabidopsis root surface. Colonization of the root by *B. subtilis* biofilms limits the root space available for *P. syringae* to infection. Additionally, *B. subtilis*, like other gram-positive biocontrols, produces an antibacterial compound, surfactin, against *P. syringae* DC3000. (*b*) Pathogenic biofilm formation by a non-bonafide plant pathogen *Pseudomonas aeruginosa* on *A. thaliana* root surface. Panel b represents a crossover human pathogen, *P. aeruginosa*, which can infect plants under controlled conditions. *P. aeruginosa* forms pathogenic biofilm on Arabidopsis roots to exhibit full pathogenesis in a plant model. (*c–d*) Attachment of symbiont *Sinorhizobium meliloti* on *C. elegans* outer cuticle. In this unique interaction *C. elegans* acts as a vector for *S. meliloti* to transfer rhizobial inoculum to legume roots. (*e–f*) *C. elegans* feeding on the rhizobial lawn and nodule formation on host *Medicago* roots. Panels c–f represent one of the first reports to show a positive tritrophic interaction. *C. elegans*, a soil nematode, uses *S. meliloti* as food but does not digest all the bacteria. Instead the undigested *S. meliloti* and the attached bacteria on the *C. elegans* cuticle are transferred to the host plant root to complete the vector-mediated symbiosis. Additionally, plant roots also trigger *C. elegans* behavioral response by emitting volatile signals inviting nematodes to the root proximity. We kindly thank Dr. Junichiro Horiuchi for providing photos in panels c–f.

review describe the importance of root exudates in positive and negative interactions that determine plant and soil microbe growth and survival.

Allelopathy: the inhibition of growth in one species of plants by chemicals produced by another species

PLANT-PLANT INTERACTIONS MEDIATED BY ROOT EXUDATES

Resource competition, chemical interference, and/or parasitism lead to negative interactions between plants (**Figure 2**). Root exudates have the potential to influence all three mechanisms of interference. For a number of plant species, root exudates play a direct role as phytotoxins in mediating chemical interference (i.e., allelopathy). In addition, root exudates are critical to the development of associations between some parasitic plants and their hosts. Finally, root exudates may play important indirect roles in resource competition by altering soil chemistry, soil processes, and microbial populations.

Positive interactions between plants are also sometimes controlled by root exudates. In particular, some root exudates induce defense responses in neighboring plants. In some cases, the plant defenses induced by root exudates simply reduce susceptibility to pathogen infection, whereas in other cases these defenses initiate production and release of leafy volatiles that attract predators of plant enemies. In addition, effects of root exudates on soil processes and microbial populations can lead to some positive effects on neighboring plants.

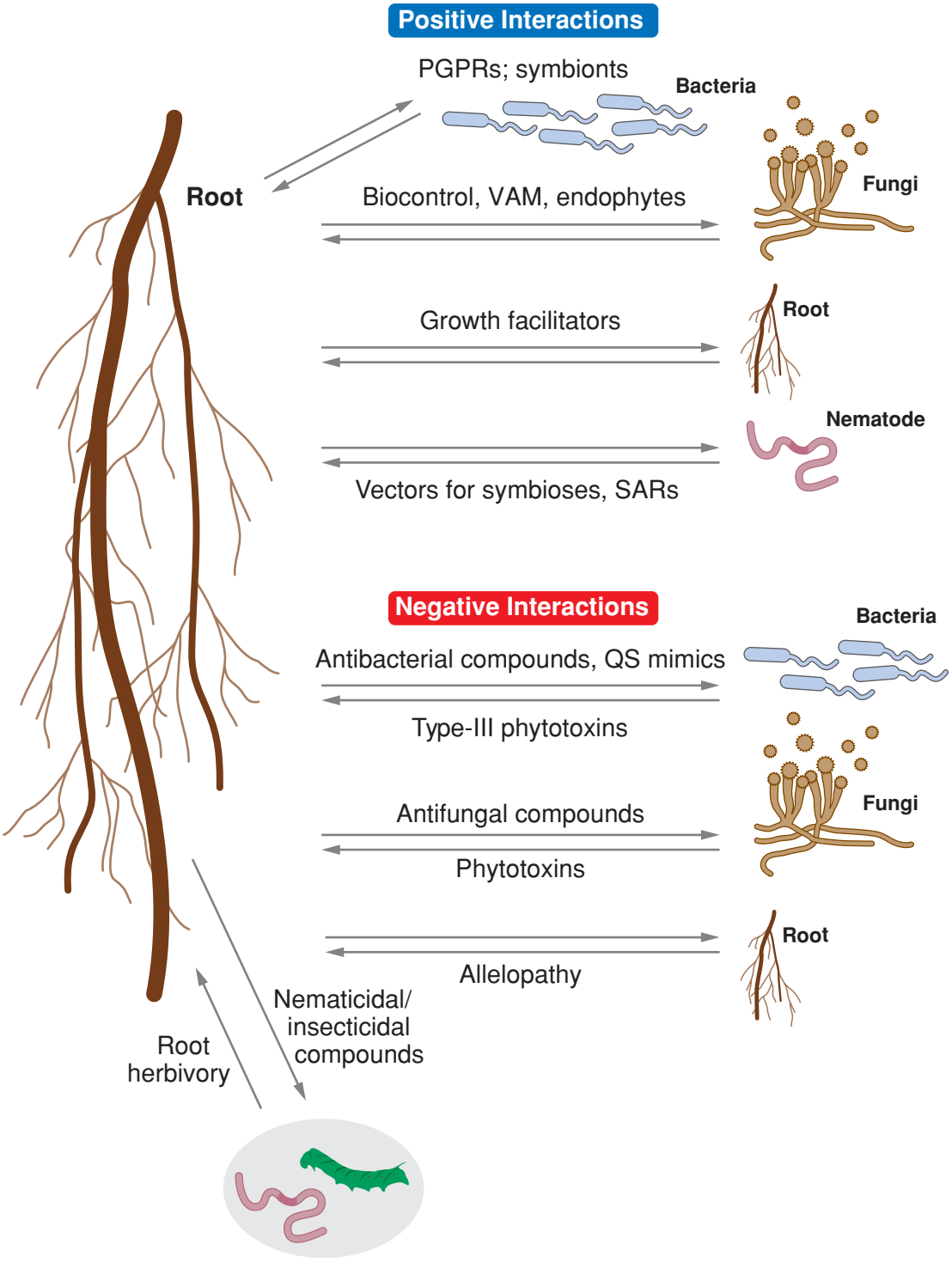
Negative Plant-Plant Interactions

Allelopathy. Chemical-mediated plant-plant interference, or allelopathy, is one mechanism by which plants may gain an advantage over their competitors. Plants that produce and release potent phytotoxins can reduce the establishment, growth, or survival of susceptible plant neighbors, thus reducing competition and increasing resource availability. Plants release phytotoxins in decomposing leaf and root tissue, in leachates from live tissue, in green leafy volatiles, and in root exudates (17, 187). Plant-produced phytotoxins vary considerably in chemical structure, mode of action, and effects on plants. Different phytotoxins in root exudates affect metabolite production, photosynthesis, respiration, membrane transport, germination, root growth, shoot growth, and cell mortality in susceptible plants (47, 187). These effects on plant physiology, growth, and survival may in turn influence plant and soil community composition and dynamics.

A number of phytotoxic compounds in plant root exudates have been identified, including but not limited to 7,8-benzoflavone (*Acroptilon repens*, Russian knapweed) (164), (±)-catechin (*Centaurea maculosa*, spotted knapweed) (12), DIMBOA and DIBOA (*Triticum aestivum*, wheat) (190), juglone (*Juglans nigra*, black walnut) (89), 8-hydroxyquinoline (*Centaurea diffusa*, diffuse knapweed) (176), sorgoleone (*Sorghum* spp.) (133), and 5,7,4′-trihydroxy-3′,5′-dimethoxyflavone (*Oryza sativa*, rice) (101). These compounds share some structural

Figure 2

Rhizospheric chemical warfare: schematic representation of possible rhizospheric interactions mediated by root exudates. Root-mediated rhizospheric interactions are broadly classified into two categories, positive and negative interactions. Positive interactions involve root exudate-mediated interactions with plant growth–promoting Rhizobacteria (PGPR). Roots produce chemical signals that attract bacteria and induce chemotaxis. Positive interactions mediated by root exudates also include growth facilitators or growth regulator mimics that support growth of other plants and also perform cross-species signaling with rhizospheric invertebrates. Contrastingly, negative interactions mediated by root exudates involve secretion of antimicrobials, phytotoxins, nematicidal, and insecticidal compounds. The arrows in the panels indicate chemical exchange. VAM, vesicular arbuscular mycorrhizas; SARs, systemic acquired resistance.



Autoinhibition: autotoxicity that is beneficial to some plants within a population

components, such as aromaticity (with the exception of sorgoleone), and the presence of hydroxyl and/or ketone groups. However, the structures of the compounds also vary considerably, and include flavonoids [7,8-benzoflavone, (±)-catechin, and 5,7,4′-trihydroxy-3′,5′-dimethoxyflavone], quinones (juglone and sorgoleone), quinolines (8-hydroxyquinoline), and hydroxamic acids (DIMBOA, DIBOA).

Phytotoxic root exudates can mediate negative plant-plant interactions only if present at sufficient concentrations to affect plant growth and survival. *Centaurea maculosa*, *C. diffusa*, and *Sorghum* spp. produce their phytotoxins at high concentrations, whereas *Juglans nigra* appears to produce lower concentrations of juglone. Young *C. maculosa* plants grown together in liquid culture can produce >80 μg ml^{-1} under standard conditions and >180 μg ml^{-1} in the presence of fungal cell wall materials (12). Soil (±)-catechin concentrations averaged 2.24 mg g^{-1} in one *C. maculosa* population (9) and 1.55 mg g^{-1} in another population (144). 8-Hydroxyquinoline soil concentrations in a *C. diffusa* population were lower than reported catechin concentrations, but still relatively high: 0.25 mg g^{-1} (176). Variation in (±)-catechin and 8-hydroxyquinoline concentrations among seasons, years, and soil types has not yet been examined. *Sorghum* spp. rhizosecrete more sorgoleone than any other compound in their root exudates (36). Agricultural species such as *S. bicolor* (sorghum) and *S. sudanese* (sudangrass) produce between 1.3 and 1.9 mg g^{-1} of sorgoleone, whereas the invasive weed *S. halepense* (johnsongrass) can rhizosecrete up to 14.8 mg g^{-1}. Sorgoleone concentrations in *Sorghum* spp. soils have not yet been reported. Juglone concentrations in soil beneath *J. nigra* trees rarely exceed 3 ug g^{-1} of soil (89), suggesting that production of juglone may be much lower than production of (±)-catechin, 8-hydroxyquinoline, and sorgoleone. However, both chemical stability and production rates determine phytotoxin concentrations in the rhizosphere. Juglone is relatively stable in soil and shows little seasonal variation in concentration (89). In contrast, sorgoleone degrades quickly in soil (35), suggesting that continuously high production rates may be necessary to maintain phytotoxic concentrations of sorgoleone in soil. Degradation rates of (±)-catechin and 8-hydroxyquinoline in soil have not yet been determined.

The ecological relevance of phytotoxic root exudates also depends on the susceptibility of the plants with which the allelopathic plants coexist. (±)-Catechin and 8-hydroxyquinoline inhibit the growth of native North American plants in communities invaded by *Centaurea maculosa* (9, 186) and *C. diffusa* (176), respectively. In particular, (±)-catechin inhibits root growth of more than 20 North American grassland species (143). Likewise, sorgoleone, DIBOA, and 5,7,4′-trihydroxy-3′,5′-dimethoxyflavone limit the growth of weeds that coexist in agricultural systems with *Sorghum bicolor* (133), *Triticum aestivum* (114), and *Oryza sativa* (101), respectively. However, most of these experiments were conducted under laboratory, and not field, conditions. Tests applying typical soil phytotoxin concentrations under realistic conditions are necessary to evaluate with more certainty the importance of phytotoxin production to outcomes of plant-plant interference (83). An even more informative approach would involve comparisons with mutants or transgenic plants that do not produce phytotoxins. Recently, a gene involved in sorgoleone production was identified in *Sorghum bicolor* (192), perhaps providing an opportunity for a clear test of the importance of allelopathy in one species.

Many plants also produce secondary metabolites that inhibit the growth of conspecific plants (i.e., autotoxicity). Autotoxicity has been widely observed in agricultural crops and weeds, as well as in some plants that inhabit natural systems (160). Phytotoxic root exudates appear to mediate autoinhibition in at least some of these species, including *Asparagus officinalis* (garden asparagus) (131), *Cucumis sativa* (garden cucumber) (195),

and *Centaurea maculosa* (spotted knapweed) (144). In many cases, plants that are allelopathic also exhibit signs of autotoxicity (160). However, only one study has identified that the same root exudate is responsible for both allelopathy and autotoxicity in a plant species. Perry et al. (144) demonstrated that (±)-catechin, the phytotoxin produced by *C. maculosa*, also inhibits *C. maculosa* seedling establishment at high concentrations. Autotoxicity may be a simple consequence of producing an allelochemical for which complete resistance is energetically expensive. Alternatively, autotoxicity may be beneficial to some plants within the population, a phenomenon termed autoinhibition. Autoinhibition may benefit adult plants or seedlings that produce autoinhibitors by reducing the establishment of intraspecific competitors in dense populations (44), or may benefit ungerminated seeds by delaying germination in areas with intense intraspecific competition, if the autoinhibitor induces seed dormancy (146).

Many allelopathic plants, however, appear to be relatively resistant to the phytotoxins they produce. Furthermore, some nonallelopathic plants are also relatively resistant to phytotoxins produced by other plants. For example, in a study of grassland species resistant to *Centaurea maculosa*'s phytotoxin, 8 of 23 species examined were more resistant to (±)-catechin than *C. maculosa* (143). Plants employ various methods to resist phytotoxins in the rhizosphere. Some plants may avoid effects of phytotoxins by sequestering the toxins in vacuoles or specialized tissues, or by secreting the phytotoxins as they are taken up (189). Other plants avoid inhibition from phytotoxins by altering the chemical structure of the toxins. For example, *Polygonella myriophylla* (Small's jointweed) avoids the effects of its own phytotoxins, hydroquinone and benzoquinone, by instead producing and releasing arbutin, a glycoside of hydroquinone (185). Microbial degradation of the glycoside allows the phytotoxins to be produced in the rhizosphere rather than in the plant. Similarly, *Zea mays* (corn) relies on *N*-glucosylation to avoid the effects of DIMBOA, DIBOA, and BOA, phytotoxins secreted into the rhizosphere by *Triticum aestivum* (wheat) and several other grasses. BOA glucosylation occurs in incubations with *Z. mays*, forming a substantially less toxic compound (158). *Zea mays* possesses two glucosyltransferases, *BX8* and *BX9*, that act specifically on DIBOA and DIMBOA, and confer resistance to DIBOA and DIMBOA in transgenic *Arabidopsis thaliana* plants, demonstrating the importance of *BX8* and *BX9* to *Z. mays* phytotoxin resistance (179).

Autotoxicity: a form of allelopathy that refers to a plant's ability to ward off competition from new growth within its own species

Nevertheless, the sensitivity of many plants to a range of plant-produced phytotoxins suggests that resistance may be energetically expensive and limited to a subset of species. Thus, negative biochemical interactions among plants may be an important factor shaping plant community structure.

Community-scale interactions: biological invasions. Over evolutionary time, plants frequently encountering allelopathic species are likely to acquire resistance to root-secreted phytotoxins. However, because phytotoxin resistance probably involves some energetic cost, plants that do not frequently encounter a phytotoxin may be unlikely to possess resistance to the toxin. Thus, transient plant species might be more sensitive to phytotoxins produced by other plants. By the same logic, phytotoxins produced by transient plants might be expected to affect a wider array of plant species than those that persist for long periods in particular plant communities. Among species that frequently associate with one another, coevolution might lead to an arms race of increasingly sophisticated allelochemicals with increasingly expensive requirements for resistance. Alternatively, coevolution in plant communities might decrease the ecological importance of direct chemical interference.

Biological invasions by exotic allelopathic plants present a unique case, in which native species in the invaded range have most likely never encountered the phytotoxins produced by the invader. As a result, these

"novel weapons" (29) would have much larger negative effects on "naïve" native species in an invaded range than the "experienced" species in the invader's native range. The greater success of some exotic plants in their invaded ranges may be partially explained by the sensitivity of native species to the phytotoxins of the invader (9, 29, 77, 176). To date, the novel weapons hypothesis for invasion has been tested for only a few species, although the available evidence suggests that numerous other exotic invaders may also be allelopathic (36, 61, 164). The strongest evidence for the novel weapons hypothesis comes from experiments on two invaders of North American grasslands, *Centaurea diffusa* (diffuse knapweed) and *C. maculosa* (spotted knapweed). Callaway & Aschehoug (29) found that adding activated carbon to adsorb organic compounds (i.e., root exudates) in *C. diffusa* soils alleviated phytotoxic effects on neighboring grass species. Their experiments indicated that North American grassland species were significantly more inhibited by *C. diffusa* root exudates than the European grassland species with which *C. diffusa* naturally coexists. Vivanco et al. (176) applied 8-hydroxyquinoline, a phytotoxin identified in *C. diffusa* root exudates, to North American and European grassland species and also found that the North American species were significantly more susceptible to the phytotoxin, suggesting an important role of 8-hydroxyquinoline in *C. diffusa* invasions in North America. In a similar experiment, Bais et al. (9) found that North American grassland species are also more sensitive than European congeners to (±)-catechin, the phytotoxin identified in *C. maculosa* root exudates, suggesting a similar role of (±)-catechin in *C. maculosa* invasions. Finally, Prati & Bossdorf (148) found that root exudates from *Allium petiolata*, another invasive species in North America, had a significantly greater negative effect on a North American species, *Geum laciniatum*, than on a European congener, *Geum urbanum*, supporting the novel weapons hypothesis for *A. petiolata* invasion. However, root exudates from European *A. petiolata* populations had similar negative effects on the two congeners, indicating that *A. petiolata* phytotoxins may have important ecological effects in both the native and the invaded range.

Biological invasions may result from phytochemical effects on soil chemistry and soil microbial communities as well as from direct chemical interference (184). For example, secondary metabolites from one invasive plant, *Carduus nutans* (musk thistle), appear to inhibit nodulation and nitrogen fixation in leguminous species such as *Trifolium repens* (white clover) (182). Perhaps as a result, *T. repens* growth and survival is strongly reduced in field patches invaded by *C. nutans* (183). *C. nutans* appears to tolerate the resulting low-nitrogen conditions and benefit from the absence of competitors, re-establishing in previously invaded patches (182). In another example, secondary metabolites from *Empetrum hermaphroditum* (crowberry) inhibit symbiotic associations between *Pinus sylvestris* (Scots pine) trees and mycorrhizal fungi, thus reducing *P. sylvestris* nitrogen uptake (132). Moreover, secondary metabolites in *E. hermaphroditum* litter inhibit soil microbial and macrofaunal activity, thus reducing decomposition rates and further reducing soil nutrient availability (181). The effects of *E. hermaphroditum* secondary metabolites on soil processes, perhaps in conjunction with phytotoxic effects on forest plants (196), appear to facilitate *E. hermaphroditum* dominance and reduce tree productivity (184). Despite the strong evidence that plant secondary metabolites can affect soil processes that in turn alter plant-plant interactions, the effects of invasive plants' root exudates on soil processes in their native and invaded ranges have received little attention. More research is needed to evaluate the importance of interactions between root exudates and soil processes as mechanisms of biological invasion.

Parasitic plant-host interactions. Root exudates are essential in the development of

associations between parasitic plants and their plant hosts, an association that is negative for the host and positive for the parasite. More than 4000 facultative and obligate parasitic plants have been identified to date (194). The chemical cross talk that controls the location of parasite germination and the development of physical connections between the parasite and the host is well understood for several obligate parasites, including *Striga* spp. (witchweed) and *Orobanche* spp. (broomrape) (137). Most current knowledge of the role of root exudates in parastic plants has been obtained from research on *Striga asiatica* and *S. hermonthica* (hereafter *Striga*) infestations of *Sorghum* spp.

Striga have very small seeds that can survive for only a few days after germination before forming an association with a host (137). The limited carbohydrate reserves in *Striga* seeds restrict seedling root elongation before host attachment. Thus, arranging for germination to coincide with proximity of an appropriate host root is critical to *Striga* seedling survival. To ensure that germination occurs near host roots, *Striga* seeds germinate only in the presence of sustained (10–12 h) high concentrations of germination inducers exuded into the soil by host roots (31). Germination inducers vary between different *Striga* hosts. To date, the only plant-produced *Striga* germination inducer that has been identified and characterized is sorghum xenognosin (SXSg). SXSg is highly unstable in aqueous solution (49), a useful trait for a *Striga* germination inducer because it is unlikely to persist in the soil and falsely indicate the presence of a host. However, SXSg is so unstable that it initially seemed difficult to explain how SXSg persisted and traveled in the soil in quantities sufficient to affect nearby *Striga* seeds (49). Fate & Lynn (49) provided an explanation for SXSg activity in soil by demonstrating that a compound structurally similar to SXSg, recorcinol, is released in small quantities with SXSg in sorghum root exudates and stabilizes SXSg enough to allow it to induce *Striga* germination.

Root exudates also play an integral role in *Striga* haustorial formation. Haustoria are specialized root structures in plant parasites that allow the parasites to infect host roots and form connections with host vascular tissue. The most recent evidence suggests that the chemical cross talk between *Striga* seedlings and host roots that results in haustorial formation begins with the constitutive release of hydrogen peroxide from *Striga* seedling root tips into the rhizosphere (94). Hydrogen peroxide activates host, and perhaps parasite, peroxidases that degrade host cell wall pectins, oxidatively releasing benzoquinones into the rhizosphere (92). The host benzoquinones are detected by the *Striga* seedling root, perhaps by redox activation of a receptor, and initiate haustorial formation (161). The mechanisms through which host benzoquinones induce haustorial development are not yet fully understood, but involve downregulation of a gene for one *Striga* expansin protein, and upregulation of genes for two unusual expansins, saExp1 and saExp2 (135). Expansins enable cell expansion by disrupting hydrogen bonds in cell walls (120). saExp1 and saExp2 may be important factors in the development and expansion of the unusual root cells in *Striga* haustoria.

SXSg: sorghum xenognosin

Haustorium: a specialized absorbing structure of a parasitic plant, such as the rootlike outgrowth of the dodder, that obtains food from a host plant

Positive Plant-Plant Interactions

Induced herbivore resistance. Root exudates can also have positive effects in plant-plant interactions, although these have been less frequently reported. In particular, some root exudates increase herbivore resistance in neighboring plants. For example, *Elytrigia repens* (couch-grass) produces several phytotoxic compounds in its root exudates, of which one, carboline, has been identified (61). *Hordeum vulgare* (barley) treated with either *E. repens* root exudates or with carboline alone was significantly less likely to be chosen as a host by aphids than control *H. vulgare* plants. Carboline in the absence of *H. vulgare* did not repel aphids, indicating that *H. vulgare*

responses to *E. repens* root exudates are necessary for aphid repulsion. The induction of *H. vulgare* defense responses by *E. repens* exudates may be a consequence of secondary metabolite production resulting from exposure to *E. repens* phytotoxins. Alternatively, *E. repens* may produce carboline in part for induction of its own defense responses, and has unintended effects on neighboring plants such as *H. vulgare*.

Induced herbivore defense via predator attraction. In addition to having direct effects on herbivore behavior, some root exudates induce defense responses in neighboring plants that reduce herbivore populations indirectly by attracting predators and parasites of the offending herbivore (30). For example, *V. faba* plants under attack release root exudates that induce green leafy volatile production in undamaged *V. faba* plants, which in turn attracts aphid parasitoids (42a). Similarly, *Phaseolus lunatus* (lima bean) plants under attack by spider mites produce root exudates that induce volatile production in undamaged *P. lunatus* plants, attracting predatory mites (66). Green leafy volatiles produced by plants under herbivore attack have also been shown to induce volatile production in neighboring plants, increasing the predator attraction signal (24). Thus, both root exudates and leafy volatiles can serve as signals to inform plants of herbivores nearby. Plants that have developed the ability to "eavesdrop" on the chemical status of their neighbors are more likely to be prepared for herbivore attacks, and can participate in coordinated biocontrol efforts that may substantially reduce herbivore populations. Most research on induced herbivore defense responses within plant communities has focused on volatile signals and predator behavior aboveground. Further research is needed to identify and characterize the root exudates that initiate volatile production in neighboring, undamaged plants.

Mechanisms That Influence Soil Resources

Some effects of root exudates on both positive and negative plant-plant interactions may also be mediated by indirect effects on soil resources (84, 184). Root exudation can increase or decrease soil nutrient availability by altering soil chemistry and soil biological processes. These effects can in turn influence outcomes of resource competition between plants, particularly if the root exudates alter the limiting resources. Effects of root exudates on soil resource availability may most often be strongest in the rhizosphere of the plants that produce them, providing a competitive advantage over neighboring plants that lack the same abilities. However, in some systems, root exudates may influence soil properties on a larger scale, with the potential for positive or negative effects on soil resource availability to neighboring plants. Here, we discuss two of the mechanisms through which root exudation of plant secondary metabolites can influence soil resource availability: phytosiderophore secretion and organic acid secretion.

Phytosiderophores and micronutrient availability. Some root exudates that act as metal chelators in the rhizosphere can increase the availability of metallic soil micronutrients, including iron, manganese, copper, and zinc (37). Metal chelators form complexes with soil metals, thus releasing metals that are bound to soil particles and increasing metal solubility and mobility. The best evidence that plants use chelators in root exudates to increase micronutrient availability comes from research on the effects of graminoid phytosiderophores on iron (Fe) availability. Although Fe is often relatively abundant in soil, it is also often present as insoluble Fe(III) precipitates, particularly in soils with high or neutral pH. Graminoid-secreted phytosiderophores bind to Fe(III) to form Fe(III)-phytosiderophores,

which grasses can take up with substantially greater efficiency than other chelated forms of Fe (153). Phytosiderophores that have been identified include nonproteinogenic amino acids such as mugenoic and avenic acid (165). Graminoid secretion of phytosiderophores is markedly greater in Fe-deficient than Fe-sufficient plants, indicating an important role of the compounds in mitigating Fe stress. Different grasses efficiently take up Fe(III) bound to phytosiderophores produced by other species (153), suggesting that phytosiderophore secretion may increase Fe availability across graminoid communities. The evidence that rhizosecreted chelators play a similarly important role in micronutrient availability to dicots is less strong than for graminoids (88). However, many phenolics produced by dicots have the potential to form complexes with metallic micronutrients and may also increase metal availability (37).

Organic acids and phosphorus availability. Organic acids can also act as metal chelators in the rhizosphere, but are thought to have more important effects on phosphorus availability than on micronutrient availability (37). Phosphorus, like iron, is often relatively abundant in soils, but in unavailable forms. In particular, phosphorus is often bound in insoluble ferric, aluminum, and calcium phosphates, especially in soils with high pH. Organic acids such as citric, malic, and oxalic acid can form complexes with the iron or aluminum in ferric and aluminum phosphates, thus releasing plant-available phosphates into the soil (37, 118). Organic acids may also increase phosphorus availability by blocking phosphorus absorption sites on soil particles or by forming complexes with cations on soil mineral surfaces (88). Several plants increase organic acid rhizosecretion substantially in response to phosphorus deficiencies, including *Lupinus alba* (white lupine) (87, 129), *Brassica napus* (rape) (80), and *Medicago sativa* (alfalfa) (108). Among species examined for organic acid production in response to phosphorus stress, lupines exhibit the strongest trends (37). Lupines form clusters of specialized root structures, termed proteoid roots, in response to phosphorus deficiency. Mature proteoid roots appear to both increase organic acid production and decrease organic acid metabolism compared to nonproteoid roots, resulting in much higher levels of organic acid exudation (1.16 compared to 0.09 μmol h^{-1} g^{-1} in one study) (91, 129, 171). Perhaps as a result, phosphorus uptake can be as much as 50% greater in proteoid than nonproteoid lupine roots (129). However, to date, research on effects of organic acids on phosphorus availability and uptake has been conducted mainly under relatively unrealistic laboratory conditions. Further studies to determine rhizosphere concentrations of organic acids in live soil and to examine the effects of those concentrations on phosphorus solubility and uptake are needed to confirm the role of organic acids in plant responses to phosphorus stress (88). In addition, it has not yet been determined whether the high rates of organic acid secretion by lupines also increase phosphorus availability to neighboring plants.

Plant-Plant Molecular Interactions

The molecular targets of root exudates remain poorly defined. For allelochemicals, a range of cellular effects have been reported, from loss of plasma membrane integrity and ion leakage (54) to inhibition of photosynthetic and respiratory electron transport (1, 54, 141) and inhibition of cell division (3). There are very few cases where the effects of allelochemicals are proposed to be more or less direct. For example, sorgoloene likely interferes with mitochondrial electron transport by inhibiting the reduction of cytochrome c_1 by cytochrome *b*, a site inhibited by several hydroxyquinone analogus (178), and the photosynthetic electron transport chain by blocking oxidation of the PSII-reduced primary electron acceptor, by binding to Q_B (62). Similarly, juglone and sorgoleone inhibit plasma membrane proton pumping (72, 73), likely

ROS: reactive oxygen species

contributing directly to loss of membrane integrity and ion leakage. One other potential direct allelochemical effect contributing to cell death is through generation of reactive oxygen species (ROS) and subsequent oxidative damage to the target plant. Bais et al. (9) reported that catechin produced from *Centaurea maculosa* could elicit root toxicity associated with an increase in ROS production by the susceptible root. Scavenging the ROS change reduced catechin's toxicity, leading to the idea that ROS might be part of the phytoxic cascade elicited by this root exudate. Indeed, an increase in oxidative stress has been proposed as a widespread phenomenon in such allelopathic responses (9, 34, 152). Environmental stress is often linked to oxidative stress, which is countered by a plant antioxidant system including ascorbate, superoxide dismutase, catalase, and the glutathione system (4). ROS can have wide-ranging damaging effects on biology through directly modifying cellular components. One such action that may be highly relevant to allelochemical-induced toxicity is ROS-related effects on the lipid bilayer, such as lipid peroxiadation. Lipid peroxidation leads to the destruction of the polyunsaturated fatty acids that are integral to membrane integrity and transport activities across the plasma membrane. Increase in lipid peroxidation accompanies addition of aqueous allelochemical in tomato and cucumber roots (34, 147) and, as noted above, electrolyte leakage from cells is often associated with allelopathic response. It is interesting that a range of antioxidant system-related genes are induced in *Arabidopsis* treated with catechin (9). Thus, although a major pathway to plant resistance to allelochemical action is thought to be through chemical detoxification and sequestration (187), the relationship between antioxidant system and allelochemical resistance is worthy of a more in-depth study.

However, in addition to a direct role in cell mortality, ROS is also well characterized as a signaling molecule (4). For example, ROS gates signal-related ion channels (e.g., 52, 100, 140) and has critical roles in mediating hormone responses (105). These observations highlight the possibility that root exudates could act via triggering a host of signaling events within the susceptible plant. Thus, flavanoids are well characterized in animal cells as being signaling molecules (188), and in plants they act in many signaling and regulatory pathways. For example, they modulate auxin transport either directly through interactions with the transport system (26, 124) or possibly indirectly via regulating the vesicular trafficking responsible for targeting this system to the correct membrane surface (139). Similarly, flavanoids play roles in pollen germination (121), perhaps via a protein kinase signaling cascade (67). However, the molecular sites of action and signaling cascades triggered by flavanoids in general, and especially by the varied components of root exudates, are unknown. Defining potential receptors and the associated signaling systems for these exudates is an area with great potential to help elucidate how exudates yield such highly specific and yet varied responses in susceptible plants.

PLANT-MICROBE INTERACTIONS MEDIATED BY ROOT EXUDATES

Plant-microbe interactions can positively influence plant growth through a variety of mechanisms, including fixation of atmospheric nitrogen by different classes of proteobacteria (123), increased biotic and abiotic stress tolerance imparted by the presence of endophytic microbes (157), and direct and indirect advantages imparted by plant growth–promoting rhizobacteria (63) (**Figure 2**). Bacteria can also positively interact with plants by producing protective biofilms or antibiotics operating as biocontrols against potential pathogens (7), or by degrading plant- and microbe-produced compounds in the soil that would otherwise be allelopathic or even autotoxic. However, rhizosphere bacteria can also have detrimental effects on plant health and survival through pathogen or parasite

infection. Secreted chemical signals from both plants and microbes mediate these complex exchanges and determine whether an interaction will be malevolent or benign.

Root colonization is important as the first step in infection by soil-borne pathogens and beneficial associations with microorganisms. The "rhizosphere effect," first described by Hiltner in 1904 (78), assumes that many microorganisms are attracted to nutrients exuded by plant roots. Hiltner observed that the number and activity of microorganisms increased in the vicinity of plant roots. However, in addition to providing a carbon-rich environment, plant roots initiate cross talk with soil microbes by producing signals that are recognized by the microbes, which in turn produce signals that initiate colonization. Motility is an important trait for competitive pathogens and beneficial microbes and enables participation in this cross talk (39, 112, 113). Chemical attraction of soil microbes to plant roots, or chemotaxis, is a well understood mechanism involved in initiating cross talk between plant roots and microbes (8). Another recently discovered mechanism involves the use of electric potentials in plant roots, produced by electrogenic ion transport at the root surface, to attract swimming zoospores of oomycete plant pathogens to plant root surfaces (174). These data also suggest that electrical signals may mask the chemical signals in mediating short-range responses of oomycete zoospores to root surfaces. It is not known whether the perception of chemotaxis or electrotaxis signals may affect the likelihood that soil microbes will act as pathogens or symbionts. Below, we describe in depth the direct and indirect positive and negative roles of root exudates in mediating plant-microbe interactions in the rhizosphere.

Positive Plant-Microbe Interactions

Nodulation of legumes by rhizobia. Rhizobia form symbiotic associations with leguminous plants by fixing atmospheric nitrogen in root nodules. Scientists have always wondered whether plants outside the Fabaceae family might be manipulated to form associations with rhizobia (109). However, rhizobia-legume interactions are very specific, allowing specific rhizobial strains to nodulate with specific host legumes. *Sinorhizobium meliloti* effectively nodulates species of the *Medicago*, *Melilotus*, and *Trigonella* genera, whereas *Rhizobium leguminosarum bv viciae* induces nodules in the *Pisum*, *Vicia*, *Lens*, and *Lathyrus* genera. However, not all rhizobia-legume associations are this limited. For example, Rhizobium strain NGR234 nodulates with 232 species of legumes from 112 genera tested and even nodulates with the nonlegume *Parasponia andersonii*, a member of the elm family (149). Conversely, not all members of the legume family form nodules. Of the three subfamilies of legumes, *Caesalpinoideae*, *Mimosoideae*, and *Papilionoideae*, members of the basal subfamily *Caesalpinoideae* are mainly non-nodulating. Thus, nodulation and presumably nitrogen fixation are not ubiquitous within the legume family.

The signal components largely responsible for these specific host-microbe relationships belong to a class of compounds termed flavonoids (145). More than 4000 different flavonoids have been identified in vascular plants, and a particular subset of them is involved in mediating host specificity in legumes (142). Isoflavonoids are only found in members of the legume family. Daidzein and genistein, isoflavonoids produced by soybean (*Glycine max*), effectively induce *Bradyrhizobium japonicum nod* genes, but inhibit *S. meliloti nod* gene expression. *S. meliloti nod* genes are instead induced by luteolin (145). This specificity enables rhizobia to distinguish their hosts from other legumes. The specific flavonoid not only induces *nod* gene expression, but also rhizobial chemotaxis. Nevertheless, other than the isoflavones, most flavonoids are not unique to legumes. How do soil rhizobia recognize their host and initiate the symbiosis when nonlegume plant species growing in the same area are also sources of flavonoids? Apparently,

AMF: arbuscular mycorrhizal fungi

GUS: β-glucuronidase

CHS: chalcone synthase

once the flavonoids are perceived, another level of specificity comes into play. Flavonoids are perceived as aglycones, which induce rhizobial *nod* genes by interacting with the gene product of *nodD*, a LysR-type regulator. This interaction results in a conformational change in the NodD protein that allows it to bind to *nod* box elements in the promoters of the *nod* genes (142). The concerted expression of these genes leads to the synthesis of Nod factor molecules, lipochitooligosaccharides, that usually consist of four or five β-1,4 *N*-acetylglucosamines, with the terminal nonreducing sugar *N*-acylated by a 16–18 carbon fatty acid. Nod factors can be chemically modified with acetate, sulfate, or carbamoyl groups, or can have different sugars, such as arabinose, fructose, and substituted fructose. The degree of saturation of the acyl tail may also vary (142). The assemblage of these substitutions results in a specific Nod factor that is recognized by the host legume.

Mycorrhizal associations. Unlike the selective legume-rhizobial associations, arbuscular mycorrhizal fungi (AMF) and plant roots form associations in more than 80% of terrestrial plants. This symbiotic relationship increases nutrient uptake, improving plant fitness, and in turn, the associated fungi extract lipids and carbohydrates from the host root (5, 130). Both AMF and rhizobial associations with plants derive from a common ancestral plant-microbe interaction, likely of fungal origin. This position is supported by the fact that AMF and rhizobia share conserved proteins that regulate both AMF and rhizobial associations with plants (107). AMF may recognize the presence of a compatible host through root exudates, similar to recognition by rhizobia (125, 166). Evidence for a fungal signaling molecule that induces plant gene activation was obtained from experiments by Kosuta et al. (102), in which fungal hyphae and host roots were grown in close proximity but physically separated by impenetrable membranes. In this system, a *Medicago EARLY NODULATION11* (*ENOD11*)-promoter::β-glucuronidase (GUS) fusion, which is responsive to both AMF and a rhizobial Nod-factor (90), was activated at a distance from the fungal hyphae (102). This was the first experimental evidence for a postulated fungally derived, diffusible signaling molecule.

The critical developmental step in the life cycle of mycorrhizal fungi is hyphal branching, which ensures contact with the host root and establishment of symbiosis (38). The branch-inducing factor is a plant signaling molecule that triggers hyphal morphogenesis preceding successful root colonization (25, 58). The development of an in vitro bioassay for hyphal branching in germinating spores from the genus *Gigaspora* (126) facilitated the analysis of the chemical characteristics and distribution of branching factor in the plant kingdom. Branch-inducing factor was present in root exudates of all the mycotrophic plants tested, but absent in those of nonhost plants. Flavonoids have been ruled out as branching factor candidates because root exudates of maize mutants deficient in chalcone synthase (CHS) show comparable activity to those of the wild type (25). Root exudates from phosphate (P)-limited plants are more active than those from plants with sufficient P, suggesting that the production and/or exudation of branching factor in roots is regulated by P availability (126). Recently, a sesquiterpene, which triggers hyphal branching in dormant mycorrhizal fungi, was identified from *Lotus japonicus* root exudates (2), establishing a novel role for root exudates in plant root-mycorrhizal cross talk.

As described above, mycorrhizal fungi extensively invade host root tissues upon perceiving a chemical response from the host roots. However, the spread of mycorrhizal mycelium occurs only in the root cortex, suggesting that host plants exert control over fungal proliferation, confining it to specific root tissues. Defense processes, which are triggered in response to microbial invasion, are modulated in mycorrhizal roots (56). Most host plants show remarkably little cytological reaction to appressorium formation

or the first steps of root colonization (57). Some elements of plant defense response such as phenylpropanoid biosynthesis, oxidative stress-induced enzymes, and pathogenesis-related (PR) genes are activated in mycorrhizal roots. In most cases, however, these defense responses are weak, transient, or strictly localized, differing from those in plant-pathogen interactions (57). Transcripts encoding enzymes of the flavonoid biosynthetic pathway, phenylalanine ammonia lyase (PAL), and chalcone synthase (CHS), but not the defense-specific enzyme isoflavone reductase (IFR), are induced specifically in cells containing arbuscules in *M. truncatula*. This induction may reflect biosynthesis of flavonoid compounds that stimulate the growth of mycorrhizal fungi rather than production of antimicrobial phytoalexins (68, 69). Changes in the profiles of antioxidative enzymes such as superoxide dismutase (SOD), catalases, and peroxidases have also been observed in mycorrhizal roots (19, 136). A recent study by Lanfranco et al. (106) describes the cloning and characterization of a *CuZnSOD* gene from *Gigaspora margarita* and presents evidence that this gene is differentially expressed during the fungal life cycle. The study also showed that the expression levels of *G. margarita CuZnSOD* are enhanced following exposure to plant root exudates.

Plant growth–promoting bacteria. Bacteria thrive on abundant nutrients in the rhizosphere and some of these rhizobacteria provide benefits to the plant, resulting in plant growth stimulation (63). Bacteria are likely to locate plant roots through cues exuded from the root, and root exudates such as carbohydrates and amino acids stimulate PGPB chemotaxis on root surfaces (162). Root exudates also influence flagellar motility in some rhizospheric bacteria (39). To test the hypothesis that motility was induced by chemotaxis toward exudate components, *cheA* mutants, motile but defective in flagella-driven chemotaxis, were constructed in four strains of *Pseudomonas fluorescens*, a known PGPB (112, 113). Relative to wild-type bacteria, mutants had a strongly reduced ability to competitively colonize roots (39). Thus, chemotaxis appears to be important for competitive colonization by extracellular PGPB. The bacterial Major Outer Membrane Protein (MOMP) also plays an important role in early host recognition. MOMPs from *Azospirillum brasilense* bind to membrane-immobilized root extracts from several plant species with differing affinities. The *A. brasilense* MOMP showed stronger adhesion to extracts of cereals than extracts of legumes and tomatoes, and may act as an adhesin involved in root adsorption and cell aggregation of the bacterium (27).

Some PGPB produce phytostimulators, which directly enhance plant growth. In addition to fixing atmospheric nitrogen, *Azospirillum* spp. secrete phytohormones such as auxins, cytokinins, and gibberellins (163). There is the exciting possibility that most PGPB are capable of producing growth regulators continuously, provided that precursors of phytohormones are available in the rhizosphere. Root exudates could supply the pool of precursors for PGPBs to biotransform. An interesting report describes the mapping of sugar and amino acid availability in the root exudates of *Avena barbata* (85). The study showed the availability of tryptophan mainly near the root tip region. Tryptophan is the precursor for a major auxin, indole 3-acetic acid (33), suggesting that PGPB could exploit root exudate pools for various precursors of growth regulators.

Other rhizobacteria create "suppressive soils" by controlling plant diseases caused by soil fungi and bacteria. The mechanisms responsible for this biocontrol activity include competition for nutrients, niche exclusion, induced systemic resistance (ISR), and the production of antifungal metabolites. The biocontrol agents that are best characterized at the molecular level belong to the genus *Pseudomonas*. Most of the identified *Pseudomonas* biocontrol strains produce antifungal metabolites, of which phenazines, pyrrolnitrin,

PAL: phenylalanine ammonia lyase

IFR: isoflavone reductase

Phytoalexins: toxic compounds produced by higher plants in response to attack by pathogens and to other stresses; sometimes referred to as plant antibiotics, but rather nonspecific, having a general fungicidal and bacteriocidal action

SOD: superoxide dismutase

MOMP: Major Outer Membrane Protein

Biotransform: the transformation of a material by microbial action

ISR: induced systemic resistance

DAPG: 2,4-diacetylphloroglucinol

CMV: Cucumber mosaic virus

RA: rosmarinic acid

2,4-diacetylphloroglucinol (DAPG), and pyoluteorin are most frequently detected. However, antifungal metabolites belonging to the class of cyclic lipopeptides, such as viscosinamide (127) and tensin (128), have also been discovered. Viscosinamide prevents infection of *Beta vulgaris* L. (sugarbeet) by *Pythium ultimum* (170). *Arabidopsis thaliana* ecotype Columbia plants (Col-0) treated with the PGPBs *Serattia marcescens* strain 90–166 and *Bacillus pumilus* strain SE34 developed minor disease symptoms upon infection with the Cucumber mosaic virus (CMV) (156). The study also showed that the acquired resistance in *Arabidopsis* plants to CMV by *B. pumilus* strain 90–166 is caused by adapting a signaling pathway for virus protection that is independent of salicylic acid (156). Finally, it was reported that some of the known gram-positive biocontrol PGPBs (such as *B. subtilis* 6051 strain) assist plants in evading a gram-negative plant pathogen, *Pseudomonas syringae pv. tomato* DC3000, by forming a protective biofilm on *A. thaliana* roots limiting pathogen access to the root surface and by producing an antimicrobial cyclic lipopeptide surfactin (7).

Negative Plant-Microbe Interactions

Antimicrobial effects. Plant root exudates substantially increase microbial activity in the rhizosphere (134). The role root exudates play in pathogenesis of root-infecting bacteria and fungi, however, has not been fully appreciated, in part because of inadequate methods available for analysis. Just as symbiotic root-microbe interactions depend on secondary metabolites in root exudates for initiation and development of beneficial associations, the survival of physically vulnerable root cells under continuous attack from pathogenic microorganisms depends on "underground chemical warfare" mediated by plant secretion of phytoalexins, defense proteins, and other as yet unknown chemicals (8, 9, 50). *Arabidopsis*, rice, corn, soybean, and the model legume *Medicago truncatula*, which have been subject to intensive sequencing efforts, are, collectively, rich sources of antimicrobial indole, terpenoid, benzoxazinone, and flavonoid/isoflavonoid natural products. The unexplored chemodiversity of root exudates in all these genetically tractable species is an obvious place to search for novel biologically active compounds, including antimicrobials.

Bais et al. (11) identified rosmarinic acid (RA), a caffeic acid ester, in the root exudates of hairy root cultures of sweet basil (*Ocimum basilicum*) elicited using fungal cell wall extracts from *Phytophthora cinnamoni*. Basil roots also exuded RA by fungal in situ challenge with *Pythium ultimum*, and RA demonstrated potent antimicrobial activity against an array of soil-borne microorganisms, including an opportunistic plant pathogen *Pseudomonas aeruginosa* (11). Brigham et al. (22) reported that *Lithospermum erythrorhizon* hairy roots showed elicited, cell-specific production of pigmented naphthoquinones that had biological activity against soil-borne bacteria and fungi. These findings strongly suggest the importance of root exudates in defending the rhizosphere against pathogenic microorganisms.

Distinguishing between phytoalexins, which are produced in response to pathogen attack, and phytoanticipins, which are produced constitutively and prior to attack, can be difficult, because the terms describe in vivo antimicrobial activity. In most cases, local concentrations of phytoalexins have not been measured in cells that are in direct contact with invading microorganisms. One exception is a careful study of the cellular- and organ-level concentrations of different classes of phenylpropanoids in the root exudates of *A. thaliana*. Phenylpropanoid levels were significantly higher in roots that were challenged by nonhost bacterial pathogens (nonhost *Pseudomonas syringae* strains) compared to host bacterial pathogens (*P. syringae* pv. *tomato* DC3000). Bacterial pathogens capable of infecting roots and causing disease were resistant to these compounds, suggesting an important role of these compounds in defense against nonhost pathogens (6). In contrast, a recent study

revealed that concentrations of indolic and phenylpropanoid secondary metabolites in *A. thaliana* roots increased upon infection with the root-pathogenic oomycete *Pythium sylvaticum* (15, 167). These results indicate that roots differ greatly from root exudates with regard to the nature and relative abundance of major soluble phenylpropanoid constituents and with regard to responses to applied biological stress. To date, only a few studies have been undertaken to gain insights into the diverse metabolic realm of antimicrobial root exudates. These recent findings outline the current direction of this field, which may lead to the discovery of novel antimicrobial compounds and to unraveling as yet unknown root-microbe interactions in the rhizosphere.

Quorum-sensing inhibitors and signal mimics. A number of studies have shown overlap in the virulence factors that are required for bacterial pathogenesis in both mammalian and plant systems (86, 150, 151). In a large number of pathogenic bacteria, initiation of the production and secretion of these virulence factors is controlled by a phenomenon described as quorum-sensing (QS). Briefly, QS is a density-dependent regulatory mechanism that was first described in the aquatic bacteria *Vibrio fischeri* as the signal-mediated induction of the *lux* genes responsible for bioluminescence (45). QS activation is mediated by small autoinducer (AI) molecules, which are responsible for cell-cell communication, and the coordinated action of many bacteria, including plant-associated bacteria. The most commonly reported type of autoinducer signals are N-acyl homoserine lactones (AHLs) (177), although half a dozen other molecules, including diketopiperazines in several gram-negative bacteria (81), a furanosyl borate diester in *Vibrio harveyi* (32), and γ-butyrolactone in *Streptomyces* (191), have also been implicated in density-dependent signaling. Typically, a basal level of AHLs are constitutively synthesized until a threshold population of bacteria has been achieved, at which point these molecules serve as ligands to a global transcription regulator (LuxR or LuxR-like proteins) that activates many QS-controlled genes, including virulence factors. The rhizosphere contains a higher proportion of AHL-producing bacteria as compared to bulk soil, suggesting that they play a role in colonization (48). This leads to the speculation that plants could be using root-exuded compounds in the rhizosphere to take advantage of this bacterial communication system and influence colonizing communities. Discovery and characterization of these plant-secreted compounds could have important biological implications in both agriculture and medicine.

Quorum-sensing (QS): the density-dependent mechanism used by many bacteria to regulate gene expression in a coordinated manner

AI: autoinducer molecules

AHL: N-acyl homoserine lactones

Since the discovery of penicillin, only a limited selection of new antibiotics have been discovered or synthesized for treating bacterial infections. These antibiotics work by interfering with specific metabolic events that ultimately culminate in the death of the bacteria. However, selective pressure exerted by this approach has resulted in the survival of antibiotic-resistant bacterial strains. This has created an urgent need for new strategies to control bacterial infections (74). A recent trend in drug discovery has been to search for compounds that are capable of inhibiting or interfering with QS in pathogenic bacteria. QS inhibitors may prove to be valuable treatments for bacterial infections because they decrease selective pressure by having little effect on bacterial growth and survival, while downregulating the production of antibiotic-resistant biofilms and bacterial toxins (75, 76). Because most bacteria are naturally present in soil, yet only a handful of these bacteria have become successful plant pathogens, it stands to reason that plants, using their staggering array of root-secreted phytochemicals, may have evolved the ability to interfere with bacteria via their QS systems.

Indeed, a fair body of evidence suggests that cross talk between plants and bacteria may occur through QS signal mimics. QS mediates several plant-microbe interactions, both pathogenic and beneficial. The first

described examples of plant-secreted QS mimics were halogenated furanones produced by the marine red algae, *Delisea pulchra* (59). These compounds are structurally similar to bacterial AHLs and are capable of interfering with QS-controlled processes such as swarming and bioluminescence (59), as well as production of virulence factors and biofilm formation in *Pseudomonas aeruginosa* (76). These particular compounds displaced tritiated AHLs from *E. coli* cells engineered to overproduce LuxR receptors (116), leading to reduced LuxR activity by destabilizing this protein, and resulting in accelerated proteolytic degradation (115). Furthermore, halogenated furanone concentrations found on the algal surface were sufficient to prevent gram-negative bacteria from colonizing algal thalli (43, 97).

AHL signal mimics have also been found in secretions of higher plants and in the unicellular green algae, *Chlamydomonas reinhardtii*, but their exact chemical nature has not been identified (55, 168, 169). Limited studies have shown that several higher plants, including *Pisum sativum* (pea), *Coronilla varia* (crown vetch), *Medicago truncatula*, *Oryza sativa* (rice), *Glycine max* (soybean), and *Lycopersicum lycopersicon* (tomato), all contain components in their exudates that are capable of activating bioluminescence in several QS reporter strains (169). These compounds partitioned into polar solvents, suggesting that they are not structurally similar to the AHLs, and probably interact with bacterial QS systems differently than structural analogues such as the halogenated furanones. These signal mimics appear to stimulate QS-controlled processes in most cases. For instance, swarming in *Serratia liquefaciens* appeared to be specifically induced by *P. sativum* exudates as well as several other plant compounds, as indicated by parallel induction of both swarming and *swr*A gene expression and synthesis of serrawettin, a lipopeptide surfactant required for surface swimming (46). In addition, exudates of several other plants activated bioluminescence in LuxRI', AhyRI', and LasRI' plasmid reporters. On the other hand, pea seedling exudates inhibited AHL-controlled behaviors in *Chromobacterium violaceum* (169), and a purified AHL mimic from *C. reinhardtii* specifically stimulated the LasR receptor in *P. aeruginosa*; however, the effect on *Sinorhizobium meliloti* was ambiguous, with some QS-related proteins being stimulated and others being suppressed (168). These data hint that QS signal mimics may be widespread in the plant kingdom, and suggest that these mimic compounds interact specifically with different QS receptors from bacteria, leading to either the activation of transcription of QS-controlled genes or the destabilization and degradation of the receptor protein (14).

Although QS signal mimics have been found in a range of plant species, they appear to be particularly prevalent among nodulating plants, such as *P. sativum*, *C. varia*, and *M. truncatula*. As previously discussed, an intricate two-way signaling between nitrogen-fixing rhizobia and leguminous host plants is required to form a symbiotic relationship. The nodulating plant *M. truncatula* has the ability to detect and respond to nanomolar concentrations of bacterial AHLs from both *S. meliloti* and *P. aeruginosa* (119). Proteome analysis revealed significant changes in the accumulation of more than 150 proteins in response to these bacterial AHLs, with about one third of those proteins showing distinct differences in terms of direction or magnitude of change in accumulation, or timing of the response to the different AHLs. This suggests that a general set of genes is activated in response to bacterial AHLs, but that the plant can also differentiate between AHLs to activate specific genes. Exposure to C_6-HL, the principal AHL produced by several bacterial species, including some *Rhizobium* strains, also led to increased secretion of AHL mimics in exudates of *M. truncatula* (119). Although direct proof remains elusive, indirect lines of evidence suggest that leguminous plants may have evolved the ability to secrete AHL mimics as a means of increasing the efficiency of their nitrogen-fixing symbionts while possibly

confusing would-be pathogens by causing them to activate QS-controlled genes before there is a sufficiently large number of bacteria to overcome host defenses.

Ecological Plant-Microbe Interactions

Plant-microbe interactions in the rhizosphere are responsible for a number of intrinsic processes such as carbon sequestration, ecosystem functioning, and nutrient cycling (159). The composition and quantity of microbes in the soil influence the ability of a plant to obtain nitrogen and other nutrients. Plants can influence these net ecosystem changes through deposition of secondary metabolites into the rhizosphere that attract or inhibit the growth of specific microorganisms. This rhizodeposition, made up of small-molecular weight metabolites, amino acids, secreted enzymes, mucilage, and cell lysates, can range from less than 10% of the net carbon assimilation by a plant to as much as 44% of a nutrient-stressed plant's total carbon (64, 138). Soil microbes utilize this abundant carbon source, thereby implying that selective secretion of specific compounds may encourage beneficial symbiotic and protective relationships whereas secretion of other compounds inhibit pathogenic associations (6, 80, 81).

Fons et al. (51) demonstrated that they could change the microbial population dynamics in the rhizosphere of *Trifolium subterraneum* (clover) by adding 1% saponin from *Gypsophila paniculata*. *Aquaspirrillum* spp., typically found in *G. paniculata* rhizospheres, became the dominant microbe in the *T. subterraneum* rhizosphere. Furthermore, *Chryseomonas* spp. and *Acinetobacter* spp., the two previously dominant bacteria found in the *T. subterraneum* rhizosphere, were significantly decreased (51). Although there were no apparent negative effects on *T. subterraneum* colonized by *Aquaspirillium* spp., other studies have shown that changes in the microbial populations colonizing a plant's rhizosphere can have detrimental or beneficial effects. Callaway et al. (28) showed that fungicide treatments affected the interactions between the invasive weed *Centaurea maculosa* and neighboring plant species. For instance, *C. maculosa* biomass was increased in untreated soils when growing with two native grass species, *Festuca idahoensis* and *Koelaria cristata*; however, this effect was not seen when *C. maculosa* was grown alone or with these two grasses in Benomyl-treated soils. This indirectly suggests that mycorrhizal fungi associated with these grasses favor the growth of *C. maculosa*. However, when the same experiment was conducted using *C. maculosa* and the forb, *Gaillardia aristata*, the opposite effect was observed, with *G. aristata*-associated fungi apparently having detrimental effects on *C. maculosa* growth. None of the beneficial or detrimental effects were seen when *C. maculosa* was grown in the presence of different soil microbial communities when competing plants were absent, indicating that these effects are not direct, but part of more complex ecosystem-level interactions.

Plant root exudates also affect the level of contamination found in soil and ground water from various environmental pollutants. This rhizoremediation results from root exudate-mediated stimulation of bacterial growth and survival, resulting in more efficient degradation of environmental pollutants (103). In addition, root colonization of pollutant-degrading bacteria allows penetration and spread of these beneficial bacteria to other areas of the soil. This naturally occurring process is effective for degradation of a variety of environmental pollutants. For example, *Pseudomonas putida* strains associated with root systems of *Zea mays* (corn) and *Triticum aestivum* (wheat) effectively rhizoremediate soils containing 3-methyl benzoate and 2,4-D, respectively (95, 154). To enhance this process, select pairings of specific plant species and bacterial species or communities that would allow even more efficient and targeted degradation of environmental contaminants are being sought (103, 104).

Rhizoremediation: the contribution of rhizosphere microbes to the degradation of environmental pollutants

Direct and Indirect Effects of Root Exudates on Rhizosphere Nematodes

As described above, root exudates provide a source of organic carbon to soil microbes, leading to abundant microbial populations in the rhizosphere (53). Microbial-feeding nematodes take advantage of these dense microbial populations as a food source and increase microbial turnover, and thus nutrient supply, to the plant when digesting microbes (65). Plant species and environmental conditions greatly affect the quality and quantity of carbon and nutrient sources secreted into the rhizosphere and the structure of the microbial community around roots, but the influence of these factors on microbe-nematode interactions is still unknown.

Root-feeding nematodes may participate in complex interactions with roots and soil microbes. Rovira et al. (155) estimated that, despite the large microbial populations in the rhizosphere, bacteria occupy <10% of the root surface and that fungal hyphal densities are only 12–14 mm m^{-2} root. At such densities, mobile nematodes may readily avoid nematode microbial pathogens and select uncolonized sections of root on which to feed. In addition, the accumulation of root-secreted nematicidal compounds may be avoided by parasitic nematodes. Until recently, there was little work on the impact of root exudates on rhizosphere interactions between plant roots, microbes, and nematodes. Using a ^{14}C pulse-labeling technique, Yeates et al. (193) demonstrated that infection of white clover (*Trifolium repens*) roots by *Heterodera trifolii* and various other nematodes leads to a significant increase in photosynthetically fixed ^{14}C in soil microbial biomass. These results indicate that white clover plants infected by plant-parasitic nematodes generally release more organic compounds into the rhizosphere. Thus, increasing carbon translocation to the soil microbial biomass as a consequence of the activity of root-feeding nematodes may be another mechanism by which microfaunal grazing enhances microbial turnover. In addition, the effects of rhizosphere nematodes on the quality and quantity of root exudates in turn influence the activity of both plant pathogenic and beneficial microorganisms in the rhizosphere (20, 93). Roots infected with *Meloidogyne incognita* act as metabolic sinks, and symplastic transport of nutrients from the phloem to the feeding cell, and ultimately the nematode, results in increased leakage into the rhizosphere compared to healthy plants (42). Exudates from tomato roots infected with *M. incognita* contain more water-soluble ^{14}C and larger concentrations of several metal ions than those from healthy roots (173). Associated changes in the rhizospheric carbon:nitrogen (C:N) ratio alter the trophic state of *Rhizoctonia solani*, making the fungus a pathogen. The importance of nematode-associated increases in root exudate concentrations and altered nutrient ratios to interactions between nematodes and microbial pathogens are not yet known.

Most knowledge of microbe-nematode interactions in the rhizosphere has been derived from research with rhizobia, mycorrhizal fungi, and plant pathogens (93). Such research has clearly demonstrated complex tritrophic webs, in which nematodes and microorganisms act in competitive, additive, or synergistic associations to affect the plant host. In addition, a recent study has redefined the beneficial association of the tritrophic interactions between plant roots, microbes, and nematodes. This new study shows that soil-dwelling nematodes, such as *Caenorhabditis elegans*, may mediate interactions between roots and rhizobia in a positive way, leading to nodulation (82). Horiuchi et al. (82) found that *C. elegans* transfers the rhizobium species *Sinorhizobium meliloti* to the roots of the legume *Medicago truncatula* in response to plant root-released volatiles that attract the nematode. Thus, root-secreted volatiles, in addition to other root-secreted chemicals, may also play an important role in multitrophic interactions. Research on the tritrophic interactions between plants,

nematodes, and microbial pathogens will contribute much to our understanding of the signaling systems mediated by root exudates in the rhizosphere.

METHODS TO STUDY INTERACTIONS MEDIATED BY ROOT EXUDATES

The biggest hurdle to the study of plant-plant and plant-microbe interactions mediated by root exudates is the underground nature of the roots. The study of root exudation requires knowledge of both the structure and function of a root system, as well as a meaningful assessment of the rhizospheric community. One must consider the abundance and distribution of plant species and the functional diversity and redundancy present in microbial communities. Some striking studies have used the exudation of fluorescent compounds as a marker for such interactions (10). The majority of conventional methods used in studying plant-plant and plant-microbe interactions involve in vitro tissue culture techniques (7, 10). Briefly, to study plant-plant interactions mediated by root exudates, plants are regrown in vitro in an aerated liquid media, root exudates are harvested, and concentrated exudates are tested for phytotoxicity on seedlings that share the rhizosphere of the tested plant (**Figure 3**). This methodological partitioning of root exudates has led to the isolation of a number of phytotoxins secreted by invasive plants. However, the full complexity of interactions occurring in a natural rhizosphere is eliminated in this system, and thus results should be viewed with caution (12, 16, 164, 176). There are two different ways to extract phytochemicals from root exudates: One involves extraction specifically for polar compounds, usually with methanol, whereas the second method targets nonpolar compounds using nonpolar solvents. This differential partitioning of root exudates results in isolation of various classes of chemical compounds, such as flavonoids, quinalones, carbolines, and terpenes (12, 16, 164, 176).

Identifying plant-produced antimicrobials, profiling rhizosphere microbes, and studying microbial colonization requires several methodologies. The diversity of metabolic functions possessed by microbial communities is often examined using BIOLOG GN substrate utilization assays (41), which assess the ability of the community as a whole to utilize select carbon substrates. A DNA microarray technique for the simultaneous identification of ecological function and phylogenetic affiliation of microbial populations has also been developed (96). This approach permits the assessment of growth rate and substrate utilization of individual microbial populations within a community. Advances in microscopy have also greatly facilitated study of root-microbe interactions. Confocal laser scanning microscopy (CLSM), in combination with various other fluorescent markers and reporter gene systems, is used to observe and monitor rhizosphere bacterial populations on the root surface. Most of these studies have been conducted with biocontrol microbes, specifically gram-negative *Pseudomonas* spp. (112). Using a combination of immunofluorescence and an rRNA-targeting probe that monitors the presence and metabolic activity of *P. fluorecens* DR54, Lubeck et al. (111) showed that bacteria at the root tip are the most metabolically active and that endogenous bacteria enter the rhizosphere two days after inoculation. Visualization of interactions among carrot roots, mycorrhizal mycelium, and *P. fluorescens* CHA0 showed that mucoid mutant strains of CHA0 adhere much better to the root, indicating that acidic extracellular polysaccharides can enhance root colonization (18). Also by using microscopy, it was shown that a gram-positive biocontrol bacteria *B. subtilis* competes for space against a pathogenic gram-negative bacteria *P. syringae* on *Arabidopsis* root surfaces (7).

CLSM: confocal laser scanning microscopy

The screening and functional identification of the diverse array of natural compounds present in root exudates that affect

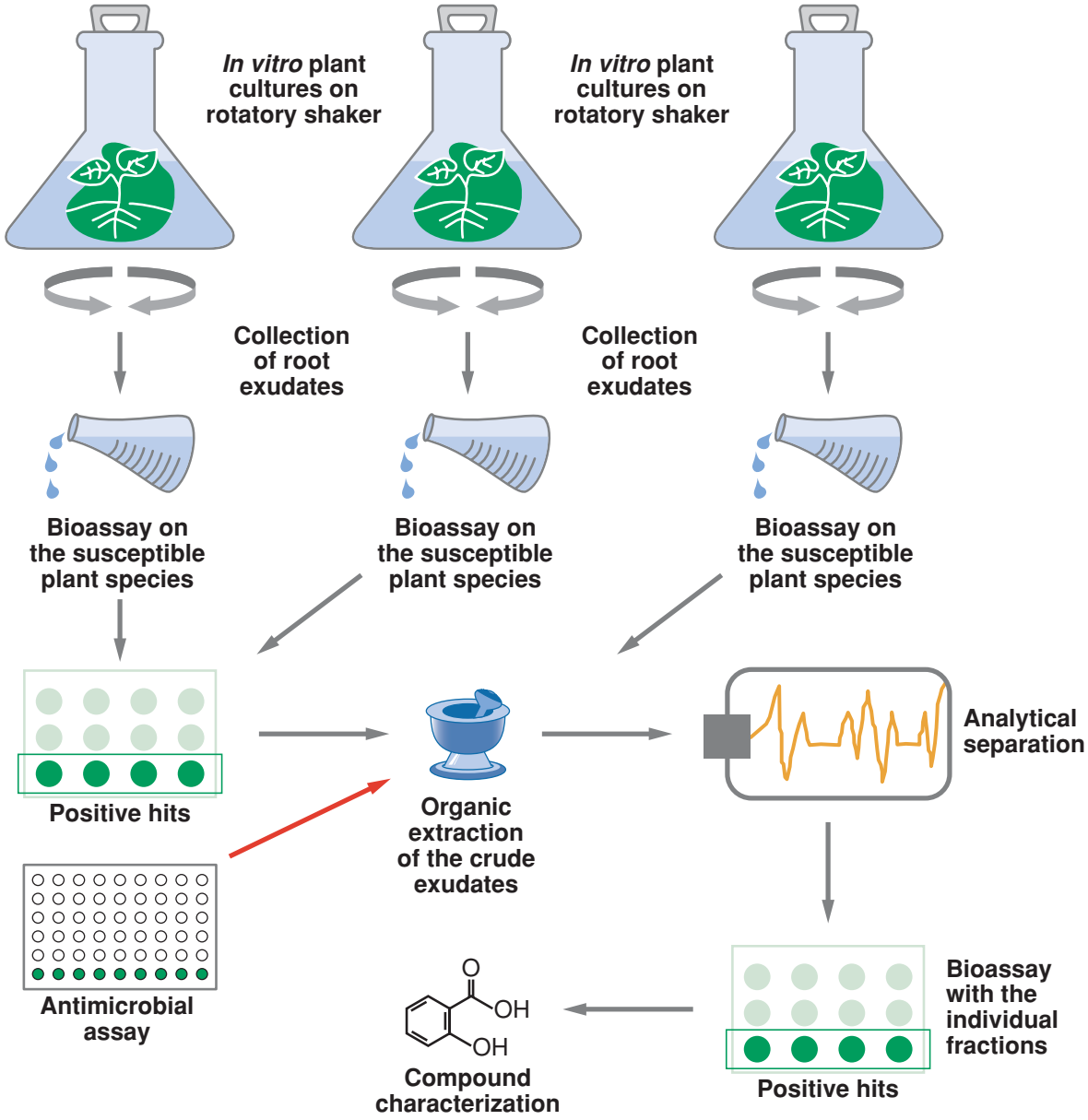


Figure 3

A flow chart representation of methods involved in collection, separation, bioassay, and candid compound characterization from plant root exudates.

rhizospheric microbes is a daunting task. Until recently, only traditional in planta extraction and subsequent testing of crude extracts directly on microbes was available. A caveat of this method is the inability to observe direct interactions between plant roots and microbes. To bypass this shortfall, one could grow plants and microbes together under in vitro conditions and observe the effect either component exerts on the other. This method

could also be used to identify antimicrobials or QS mimics from plant root exudates. Studies to observe global gene-expression levels in rhizospheric microbes upon interacting with roots and root exudates are also possible using a number of microbes whose genomes have been sequenced. These studies would highlight the physiological functioning of microbial cells in a specific environment.

CONCLUSION

We presented a partial picture of the interactions that occur in the rhizosphere and the role of root exudates in mediating some of these processes. However, our understanding of these interactions is incomplete due to the difficulty of studying underground processes under controlled yet realistic conditions. Thus, developing novel methodologies to study rhizosphere ecology under natural conditions is needed and will require collaboration between plant biologists, ecologists, and soil scientists to develop rhizotron systems where biochemical and molecular biology studies could be performed on site. It is clear that our understanding of root-mediated processes has moved beyond the classical belief that the sole functions of roots are anchorage and uptake of water and nutrients. It is now understood that roots are rhizosphere ambassadors, facilitating communication between the plant and other organisms in the soil. Ecological knowledge indicates that aboveground interactions could potentially be translated to belowground responses in plants. What does this mean at the rhizosphere level? What is the effect of aboveground herbivory on the ability of roots to initiate microbial symbiosis or to fight microbial attack? A clear understanding of the molecular process involved in the actual secretion of phytochemicals by roots is also needed in order to develop molecular markers for this process. Finally, synthesis of the knowledge of root exudation from the molecular to the ecosystem scale will potentially lead to the development of better plants capable of absorbing more nutrients, detoxifying soils more efficiently, or more effectively warding off invasive weeds and pathogenic microbes.

Rhizotron: a device used to view and manipulate organisms in a natural rhizosphere

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