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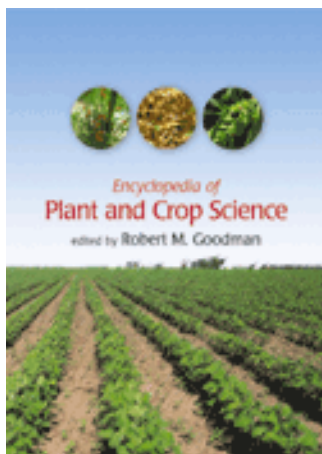
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# Root Communication: The Role of Root Exudates

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## Abstract

Plants communicate with neighboring plants and other organisms surrounding them. Aboveground communication is articulated through stems, leaves, or flowers while below-ground communication is mediated by roots. The plant root is capable of secreting chemicals into the rhizosphere through root exudates. The chemical constituents of the root exudates are characteristic of a particular plant species and also depend on the surrounding biotic and abiotic environment. Recent research suggests that the root exudates act as a sort of chemical 'language' between the secreting plant and other organisms in the rhizosphere.

## INTRODUCTION

Plant embryos germinate to form two meristematic primordia—one geotropic that differentiates to form the root system and the other negatively geotropic that develops into the shoot. A plant's root system anchors it to the soil and absorbs water and nutrients for growth and development. Plants are mostly sessile and therefore cannot move in response to biotic or abiotic insults. However, plants respond to these cues by triggering appropriate responses—usually by secreting a mixture of chemical compounds. Plants communicate with neighboring plants and other organisms by secreting compounds or a bouquet of volatile organic compounds. For example, floral scents attract insects that aid in pollination<sup>[1]</sup> while plants attacked by herbivores emit a cocktail of volatiles that attract enemies of the herbivores.<sup>[2]</sup>

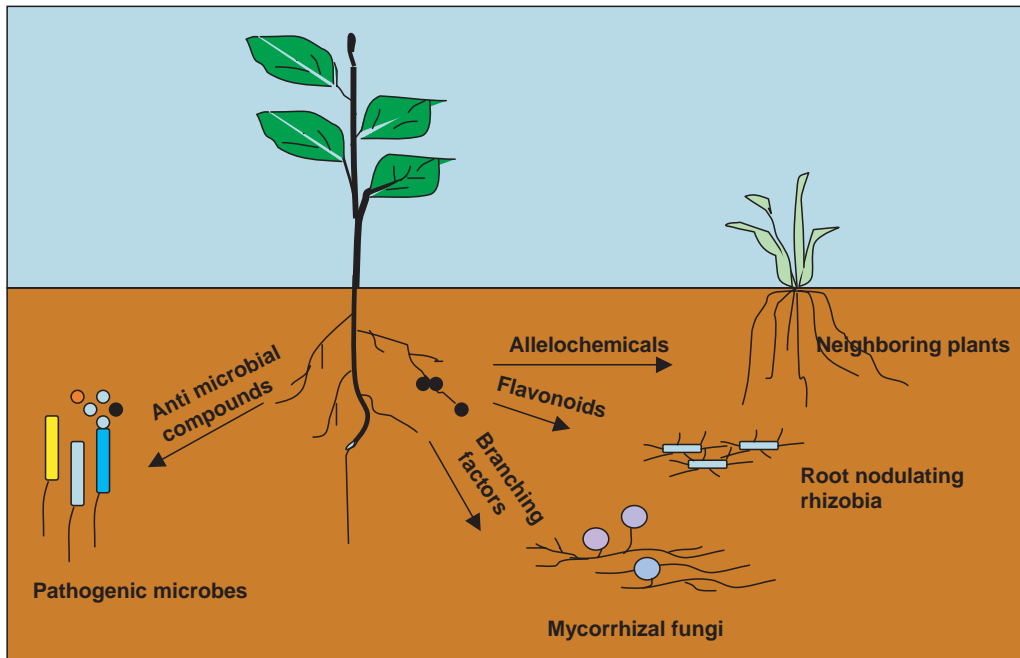
Communication between plants has not been studied in detail. The best known example of aboveground plant–plant communication is that mediated by the volatile compound methyl salicylate.<sup>[3]</sup> Tobacco plants infected by the tobacco mosaic virus (TMV) release methyl salicylate and its perception by neighboring plants results in the induction of resistance genes in the receiver plant that confer resistance. Plant hormones, such as ethylene and jasmonic acid, play an important role in plant–plant communication and the communication between plants and other organisms.<sup>[4,5]</sup> Below-ground communication is orchestrated by roots through the secretion of root exudates.

Root exudation has long been viewed as a passive leaching process. However, recent research has proved that roots synthesize, accumulate, and actively secrete diverse compounds. Further, root exudation is part of the larger process of rhizodeposition, which is a major source of soil organic carbon released by plant roots.<sup>[6,7]</sup> The root exudates form the basis of inter- and intra-organismal communication in the rhizosphere (Fig. 1). The quantity and quality of root exudates differ between plant species and by age within a single plant species. Typically, young seedlings exude about 30%–40% of their fixed carbon as root exudates,<sup>[8]</sup> while older plants exude about 21%. External factors like biotic and abiotic stress can influence the composition of root exudates. Organic compounds (ranging from high molecular weight mucilage, polysaccharides, and proteins to low molecular weight compounds like organic acids, amino acids, simple sugars, and a suite of secondary metabolites) form the majority of root exudates while minor components include nonorganic compounds like H<sup>+</sup>, inorganic acids, and water (from Bais et al. and references therein).<sup>[9]</sup>

## Root–Root Communication

The most widely studied underground plant–plant interaction is intraspecific chemical signaling known as allelopathy. Allelopathy, which benefits the producer and are detrimental to the receiver, are the most commonly described form of allelochemicals. There are numerous examples of plant allelopathy: juglone (5-hydroxy-1,1-naphthoquinone), is a potent allelopathy produced by black walnut (*Juglans nigra*) trees, which inhibits the growth of tomatoes, peas, and potatoes as well as ornamental

*Keywords:* Allelopathy; Antimicrobial compounds; Root exudates; Root-microbe communication; Root–root communication.



**Fig. 1** Schematic representation of inter- and intra- organismal communication mediated by root exudate.

plants.<sup>[10]</sup> Juglone acts as an electron donor and acceptor in photosynthesis and respiration reactions, affecting the photosynthesis and respiration of sensitive plant species.<sup>[11]</sup> The highest concentration of juglone is present in actively growing roots and is secreted into the rhizosphere. Another classical example of an allelochemical is sorgoleone (2-hydroxy-5-methoxy-3-[(8'*Z*, 11'*Z*)-8',11',14'-pentadecatriene]-*p*-benzoquinone).<sup>[12]</sup> Sorgoleone is a strong growth inhibitor of a number of plants, even at a concentration as low as 10  $\mu$ M.

Recently, the potential role of allelochemicals in the invasive behavior of weeds has been identified. For example, the roots of the invasive spotted knapweed *Centaurea maculosa* secrete a racemic mixture of a flavonal (+)-catechin and (–)-catechin (13), and both of these enantiomers (although at different levels) exhibit strong inhibitory effect on a number of plant species.<sup>[13,14]</sup> The addition of activated charcoal (which adsorbs secondary metabolites) to the soil in which *C. maculosa* is growing diminishes its allelopathic effect on other plants. Using the model plant *Arabidopsis thaliana*, the molecular mechanism of this negative interaction has been elucidated. Catechin causes a signal transduction cascade that starts with the induction of reactive oxygen species, follows with a calcium spike, and finally results in a wave of cell death in *A. thaliana* roots.<sup>[13]</sup> Although these findings put forward a novel “weapons hypothesis” of plant invasion mediated by a root-secreted chemical, more research is needed to understand allelochemistry under natural field conditions. Collaboration between plant ecologists, plant biologists, and soil biochemists will be crucial to achieving this goal.

### Root-Microbe Communication

The rhizosphere soil that surrounds plant roots is rich in microorganisms. There is constant communication between plants and microbes in the rhizosphere that is mediated by the chemicals present in root exudates. The interaction can have positive or negative effects on the plant or the microbe. The interaction between legume roots and *Rhizobia* bacteria, which are capable of forming dinitrogen-fixing nodules in the roots of legumes, has been widely studied. The composition of flavonoids present in the root exudates of a particular legume seems to influence the plant-rhizobia interaction. For example, soybean roots (*Glycine max*) secrete the flavonoids daidzein and genistein, which specifically attract the compatible rhizobium *Bradyrhizobium japonicum*. Further, the presence of compatible rhizobia in the rhizosphere enhances the synthesis and secretion of flavonoids from legume roots, resulting in accumulation of a high concentration of flavonoids in the rhizosphere.<sup>[15]</sup> The flavonoid is perceived by bacteria through a sensor protein NodD, which in turn activates the transcription of nod box genes that synthesize the nod factors (lipo-chitooligosaccharides) that aid in the early development of nodules.<sup>[16]</sup> Such perception suggests that flavonoids in root exudates help mediate host specificity. Although less understood, similar processes are thought to control symbioses between dinitrogen-fixing *Frankia* bacteria and their actinorhizal plant hosts. Root exudate modulates the interaction between plants and plant growth-promoting rhizobacteria (PGPR), and as such the chemical

components present in the exudates of tomato plants attracts a major PGPR, *P. fluorescens*.<sup>[17]</sup> Recent evidence suggests such behavioral changes in the bacteria are a result of altered gene expression elicited by the compounds present in the root exudates.<sup>[18]</sup>

Similarly, chemicals present in root exudates play an important role in the establishment of symbiotic associations between mycorrhizal fungi and plants. More than 80% of all land plants form symbiotic mycorrhizal associations, which enhance phosphorous uptake and impart biotic and abiotic stress tolerance in plants. Hyphal branching of fungi is an important precursor of root colonization and is mediated by branching factors (BF) present in host plant root exudates.<sup>[19]</sup> These BF are absent in plants that are not colonized by mycorrhizal fungi. Recently, Akiyama et al.<sup>[20]</sup> isolated a sesquiterpene, strigolactone, in the root exudates of *Lotus japonicus* that induces the hyphal branching of the mycorrhizal fungus *Gigaspora margarita*.

Communication between plants and soil-borne pathogens is also mediated by root-secreted compounds, as root exudates and exudates of root border cells<sup>[21]</sup> may attract or repel pathogens. Those allelochemicals, which benefit the receiver rather than the producer, are referred to as kairomones. For example, flavonoids in soybean exudates attract the soybean pathogen *Phytophthora sojae*.<sup>[22]</sup> The presence of a number of phenolic compounds<sup>[23]</sup> and antimicrobial proteins<sup>[24]</sup> in the root exudates may help guard the root against potential pathogens. Recently, Bais et al.<sup>[23]</sup> showed that the secretion of antimicrobial compounds by roots of *A. thaliana* is responsible for its resistance to many nonhost pathogens present in the rhizosphere. The addition of activated charcoal to the rhizosphere resulted in the conversion of nonpathogenic strains to potent pathogens.

### Benefits of Studying Root Communication Mediated by Root Exudates

A better understanding of root-mediated communication between plants and other organisms will result in enhanced agricultural production and will potentially aid in the reclamation of land infested with invasive weeds. For example, several plant species, including *Gaillardia grandiflora* and *Matricaria recutita*, have been found to be resistant to high concentrations of the allelochemical catechin.<sup>[14]</sup> Planting these resistant species may help restore infested areas. Using the strategy of genetically engineering plants to overproduce secondary metabolites, it may be possible to develop legumes that are capable of secreting higher levels of flavonoids in their root exudates, resulting in "super-nodulating" varieties. Similarly, plants that are capable of producing higher levels of antimicrobials in their root exudates will be more resistant to soil-borne pathogens. It might also be possible to control plant community composition by introducing key plant species

that produce allelochemicals targeting particular competing species.

### CONCLUSION

Root communication in the rhizosphere is mediated by root exudates. It has been shown that the secondary metabolites in the root exudates aid in the root-root communication<sup>[13]</sup> as well as in the communication between the root and beneficial and pathogenic organisms in the rhizosphere.<sup>[9,15,23]</sup> This type of information exchange is critical for the survival of the plant.

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