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Special Issue: Unraveling the Secrets of the Rhizosphere

Review

Beneficial Microbes Affect Endogenous Mechanisms Controlling Root Development

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Plants have incredible developmental plasticity, enabling them to respond to a wide range of environmental conditions. Among these conditions is the presence of plant growth-promoting rhizobacteria (PGPR) in the soil. Recent studies show that PGPR affect *Arabidopsis thaliana* root growth and development by modulating cell division and differentiation in the primary root and influencing lateral root development. These effects lead to dramatic changes in root system architecture that significantly impact aboveground plant growth. Thus, PGPR may promote shoot growth via their effect on root developmental programs. This review focuses on contextualizing root developmental changes elicited by PGPR in light of our understanding of plant–microbe interactions and root developmental biology.

Trends

Interaction between plant roots and the beneficial bacteria within their rhizosphere shapes the bacteria community composition, and enhances plant growth and plant pathogen defense.

Plant growth-promoting rhizobacteria (PGPR) affect cell division and differentiation leading to changes in root system architecture, which contributes to enhanced shoot growth. These modifications are established by changing plant endogenous signaling pathways.

While several PGPR can produce phytohormones, many effects on plant developmental pathways are exerted by other molecules.

Several fungi have the same effects on root system architecture as PGPR, indicating that growth-promoting mechanisms might be conserved across kingdoms.

Beneficial Microbes Can Induce Plant Growth by Modifying Root Development

In the early 1900s, Hiltner made the key observation that the soil around the plant root contains more microorganisms than the surrounding soil [1]. Soil has since been documented to have exceptional microbial diversity [2], containing fungi, invertebrates, archaea, and bacteria [3]. Among the soil bacteria are **PGPR** (see Glossary) [4,5]. Unlike obligate symbionts, these bacteria can interact with numerous host plants and improve plant growth and health via various mechanisms that can be direct, such as nitrogen fixation [6,7], or indirect, including competition with pathogens [8,9]. PGPR are capable of modulating the root system architecture (i.e., the spatial configuration of the root system), which is a significant determinant of crop yield [10–12]. The potential of PGPR to affect plant growth and root architecture was excellently addressed in two recent reviews [13,14]. By contrast, the mechanisms by which PGPR influence cell division, and alter the balance between proliferation and differentiation in the primary root and lateral root initiation sites, remain largely unknown.

In this review, we focus on the ability of PGPR to affect post-embryonic root development. It has become clear that PGPR affect post-embryonic root development by altering cell division and differentiation within the primary root as well as affecting root hair formation and lateral root development. We highlight recent findings demonstrating that bacteria modulate endogenous root developmental mechanisms to establish these effects. This review has three main sections, describing root–bacterial interactions in progressive detail. We begin by describing root–bacterial interactions in the **rhizosphere** and the determinants of microbial community structure in association with plant roots. Subsequently, we describe the current knowledge of the effects of soil bacteria on root development at the cellular level. Finally, we discuss the current understanding of bacteria on plant regulatory mechanisms. We have selected a few bacterial

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species to highlight those that alter cell division and differentiation in the Arabidopsis root. While our focus is on PGPR, we conclude our review by addressing how fungi affect root development to draw attention to the similarities between these two plant–microbe interactions.

Future studies integrating the fields of plant–microbe interactions and plant developmental biology will lend insight into how soil microbes affect root development. This work will enhance our understanding of these complex cross-kingdom interactions and increase our knowledge of root developmental biology and bacterial signaling. Ultimately, this knowledge will foster development of sustainable plant growth-promoting technologies that have the potential to dramatically increase crop yield and food security.

Plant–Microbe Interactions in the Rhizosphere

When Hiltner observed the increased number of microorganisms around roots compared with bulk soil in the 1900s, he assumed that this increase was due to nutrient secretion by the plant and termed it 'the rhizosphere effect' [1]. Since then, the rhizosphere has been defined as the soil around plant roots influenced by the root and its exudates, whereas the rest of the soil is referred to as bulk soil (Figure 1) [15]. Soil properties themselves are exceptionally diverse, with abiotic factors that influence the bacteria in the bulk soil including pH, moisture, and nutrient content [2,16]. The extent to which plants and soil characteristics influence the microbial communities in the soil has been elegantly reviewed [17–20]. Recently, studies using deep-sequencing techniques found that soil type has a more dramatic effect on rhizosphere microbial communities than plant genotype [21–23]. These results suggest that the soil composition plays a pivotal role in shaping the bacterial communities in the soil and rhizosphere.

As Hiltner speculated in addition to soil type, bacterial communities in the rhizosphere are likely dependent on the type and composition of root exudates secreted by the plant [24,25]. Root exudates include sugars, amino acids, organic acids, fatty acids, phenolics, enzymes, and flavonoids [26]. The ability of bacteria to thrive in the rhizosphere depends on their ability to move toward these plant-derived carbon sources (for more on chemotaxis, see [27,28]) and to use them and other root-derived rhizodeposits such as sloughed-off root cells or lysates as energy sources [29–31]. The rhizosphere effect has been documented by numerous groups since Hiltner's initial observations [32]. Correlated with differences in root exudates, Arabidopsis accessions, or natural variants, differ in their root-associated microbial community [33]. Additionally, a single mutation in the gene encoding an ATP-binding cassette transporter in Arabidopsis changes the microbial community around the plant root [34]. Plant-derived compounds, including polysaccharides and, rosmarinic acid, affect **quorum sensing** in soil bacteria [35,36], suggesting that plants excrete certain compounds to influence bacteria in the rhizosphere. Microbes within the rhizosphere can in turn modify root exudate composition [37–40], enhance growth [41–43], and induce systemic resistance to subsequent pathogen attack [44–47]. These examples reveal a rich language of chemical communication between plants and rhizosphere-inhabiting microbes resulting in altered microbial community structure and plant growth and health.

Bacteria found within plant roots are referred to as **endophytic** bacteria and comprise a much less diverse community than what is found in either the rhizosphere or the bulk soil [21,22,48,49]. The plant immune system [50] likely mediates the decreased bacterial diversity. **Phytohormones** used in plant defense, including jasmonic acid, **ethylene**, and salicylic acid, have been shown to influence rhizosphere composition in certain soils [51]. Salicylic acid was recently shown to alter the colonization of certain bacterial families within roots [52]. Additionally, mutant plants defective in multiple phytohormone signaling pathways had lower survival rates and distinct endophytic microbial colonization compared with wild-type plants [52]. These results reflect the importance of plant defense mechanisms in regulating bacterial colonization within the root.

Glossary

Auxin: phytohormone that, among other plant processes, is involved in cell division and specification in the root meristem as well as formation of lateral root primordia.
Casparian strip: a waxy cell-wall thickening in the root endodermis that restricts the flow of solutes and water into and out of the central vasculature. This barrier also restricts bacteria and fungi from entering these cells. The Casparian strip is a hallmark of differentiated endodermis.
Cytokinin: phytohormone that often functions antagonistically of auxin. In root development, cytokinin induces differentiation of cells as the move shootward.
Endophytes: microorganisms living within plant tissue without causing harm to the plant.
Ethylene: phytohormone involved in regulation of cell size, aging, and fruit ripening.
Phytohormone: signaling molecule produced by the plant that regulates a broad range of cellular processes from cell division and plant defense to aging. Examples include auxin, cytokinin, and ethylene.
Plant growth-promoting rhizobacteria (PGPR): bacteria found in the rhizosphere that promote plant growth or health either directly or indirectly.
Quorum sensing: a process by which bacteria measure their density and modify their behavior accordingly, i.e., to form biofilms, produce antibiotics, or coordinate virulence.
Rhizosphere: the thin layer of soil around plant roots that is influenced by the root and its exudates. The rhizosphere harbors a more numerous, but less diverse, group of microorganisms than the surrounding bulk soil.
Stem cell niche: the group of cells near the root tip that contains the initials, or stem cells, and quiescent cells. Together these cells supply cells that enable primary root elongation and root topology. A stem cell niche is established in the tip of lateral roots during their formation.