Plant cell wall component induced bacterial development

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Spotlight

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Plant–microbiome functioning depends on intricate signaling pathways including plant-derived excretions that induce microbial gene expression. Marc Ongena and his team (Boubsi *et al.*) dissect how the pectin backbone homogalacturonan promotes bacterial differentiation programs of *Bacillus velezensis*, potentially facilitating its establishment in the rhizosphere.

Plant-colonizing microorganisms have evolved to recognize plant-derived molecules and therefore optimize the expression of genes required during their establishment in the rhizosphere, the soil layer around the roots that is directly affected by plant exudates. These molecules, either exuded from the plant actively or deposited into the surroundings indirectly during growth, shape the composition and activity of the microbiome in the rhizosphere [1]. In return for the excretions, plants benefit from the microbiome activity that spans from direct growth promotion to indirect plant protection against phytopathogens. By understanding the plant–microbiome feedback processes, we will have higher predictability to develop microbial additives that increase plant health and productivity.

Members of the *Bacillus subtilis* species complex are widely utilized as plant-growth-promoting rhizobacteria (PGPR) supported by ample mechanistic understanding of plant root colonization [2]. *B. subtilis* and closely related species, including *B. velezensis*, are well characterized for their ability to produce a wide range of specialized metabolites with antimicrobial activity that avert plant pathogens. In addition, colonization of the root surface via biofilm formation is proposed to contribute towards the competitive ability of PGPR against phytopathogens by occupying the available rhizosphere niche. Indeed, biofilm development by *Bacilli* has been previously reported to be induced by root-exuded metabolites and plant polysaccharides. These plant excretions can be either metabolized by *Bacilli* promoting growth and the building blocks potentially utilized for biofilm matrix synthesis, or sensed by the bacterial cells using receptors that modulate the activity of transcriptional regulators [2].

In a new publication [3], Boubsi and colleagues dissect how pectic homogalacturonan (HG) induces the establishment and persistence of *B. velezensis* in the rhizosphere (Figure 1). They demonstrate that two conserved pectinolytic enzymes encoded in the genome of *B. velezensis*, PelA and PelB, break down the pectin backbone HG in its low- and high-methylesterified forms, respectively. Indeed, the release of oligogalacturonides (OGs) is detected from native pectin extracted from tomato roots by these enzymes. Nevertheless, the oligomers of galacturonic acid generated from HG degradation do not serve as a carbon source. When the *pelA* and *pelB* genes are deleted, the mutant *B. velezensis* strain exhibits reduced colonization potential on tomato roots compared with the wild type. In contrast to the necessity of pectinolytic enzymes for root colonization, induction of early biofilm development observed in the presence of supplemented HG of high polymerization degree is independent of the Pel enzymes, suggesting that HG, when released from the plant cell wall, directly acts as a cue on the bacterial cells to induce biofilm development. *In vitro* biofilm formation and root surface establishment of the *B. subtilis* group species depend on the operons encoding an amyloid-like fiber protein, TasA, and the exopolysaccharide synthesis apparatus, Eps proteins [4]. Specific reverse transcription (RT)-qPCR and global RNA-sequencing analysis confirmed that the transcription of these operons is induced by HG supplementation [3]. A previous study from the same laboratory revealed that HG also enhances the production of the lipopeptide surfactin in *B. velezensis* [5] that prompted Boubsi *et al.* to assay the role of surfactin in HG-triggered biofilm induction. While surfactin influences the gene expression programs in *Bacilli*, including enhancement of biofilm development in *B. velezensis*, deletion of the biosynthetic gene cluster for the specialized metabolite surfactin still retained HG-induced biofilm promotion, demonstrating a surfactin-independent sensory pathway [3]. Intriguingly, DNA release from the cells – which contributes to the 3D architecture of the early biofilms – is also enhanced in the presence of HG [3].

These results strengthen the role of plant-derived molecules in inducing biofilm formation in the *B. subtilis* group. Indeed, both root exudate (e.g., L-malic acid) and plant-derived polysaccharides (e.g., arabinogalactan, pectin, and xylan) have been previously reported to induce the expression of genes for biofilm development in *B. subtilis* [4]. Intriguingly, adaptive evolution of *B. subtilis* on the roots of Arabidopsis (*Arabidopsis thaliana*). selects for clones that increase biofilm formation in the presence of xylan, the major component of plant hemicellulose, under the conditions where the ancestor strain unable to respond to this plant polysaccharide [6]. This suggests an intricate evolution between signaling by and metabolism of the plant-derived

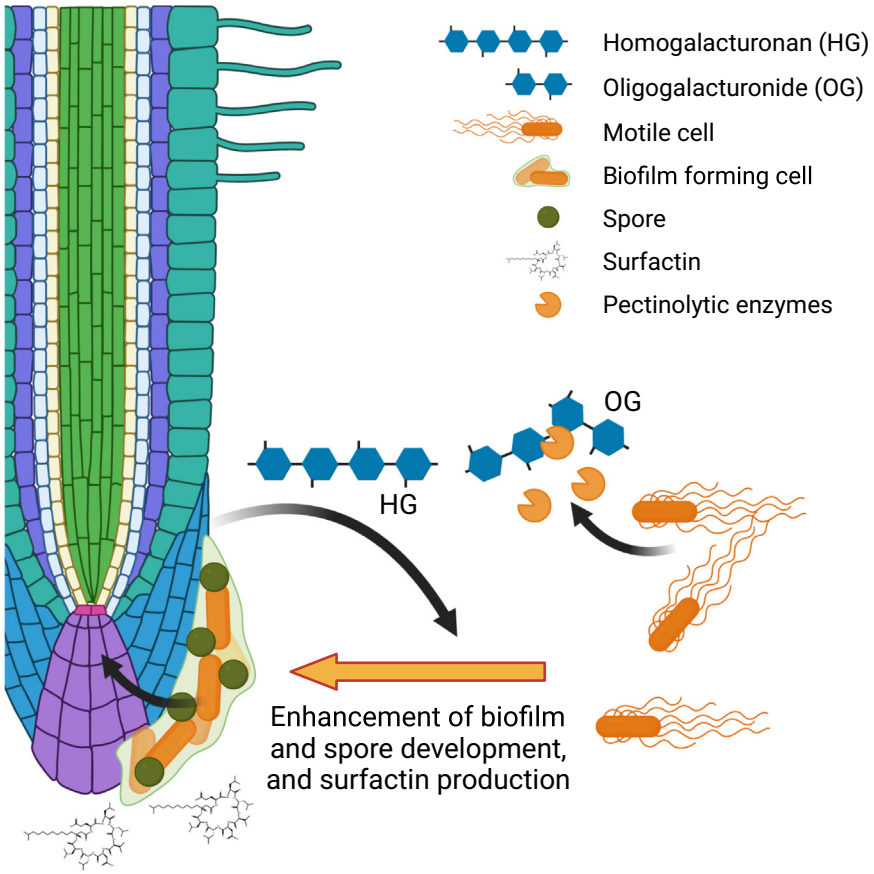

Figure 1. Depiction of plant-cell-wall-derived homogalacturonan-(HG)-promoted differentiation of *Bacillus velezensis* cells to secrete the lipopeptide surfactin, produce the biofilm matrix, and initiate spore development. Additionally, pectinolytic enzymes contribute to the release of HG from the cell wall and subsequent lysis to oligogalacturonide (OG). Figure created with BioRender.com.

polysaccharides that induce plant colonization traits in bacteria contributing to their establishment in the rhizosphere. Importantly, Boubsi and colleagues propose that the Pel enzymes of *B. velezensis* do not majorly impair the plant cell wall integrity, as they do not observe any adverse impact on the plant health and growth [3]. This suggests a gentle balance between plant and its beneficial microbiome, where the microbe-derived benefit exceeds the costs of plant polysaccharide deposition.

Interaction between the plant and microbes is dynamic. Root exudate composition shifts with the development stage of plants and therefore the rhizosphere microbiome also changes over time [1]. Plant cell wall biosynthesis is similarly dynamic during plant growth [7]. In addition to these plant development phase-dependent changes, both root exudates and growth, and perhaps plant polysaccharide deposition, follow a 24 h pattern [8,9]. Following the plant circadian programs, the plant-derived molecular cues within the rhizosphere might display a 24 h pattern, potentially influencing the microbial responses depending on the time of the day. In the future, it will be important to follow the transcriptional changes in plant-colonizing bacteria to clearly depict the dynamic response of the plant microbiome at a finer time scale.

Finally, Boubsi and colleagues also demonstrate that HG enhances the sporulation dynamics of *B. velezensis*, increasing the spore-forming cell fraction in the population both in the wild type and *pelA-pelB* mutant, once again highlighting the primary stimulating role of undegraded HG. Indeed, enhancement of *B. subtilis* sporulation has been previously observed on arabidopsis roots [10].

In summary, the work of Boubsi and colleagues provides an excellent example of the intricate function of plant polysaccharides as a cue stimulating the differentiation programs in bacteria that contribute to persistence of PGPR in the rhizosphere and therefore plant growth promotion. Although currently challenging, it would be fascinating to reveal the global developmental programs present in complex multispecies communities at high spatial and temporal resolution to systematically understand the plant–microbiome functioning that contributes to plant growth promotion and biocontrol.

Declaration of interests

The author has no interests to declare.

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