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Plant–microbe interactions: Plant-exuded *myo*-inositol attracts specific bacterial taxa

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Plants exude a plethora of metabolites that transform the microbiome composition. Initiated from genome-wide association studies of either a plant or a bacterium, two new studies dissect the impact of plant-secreted *myo*-inositol on recruitment of certain bacterial taxa by *Arabidopsis*.

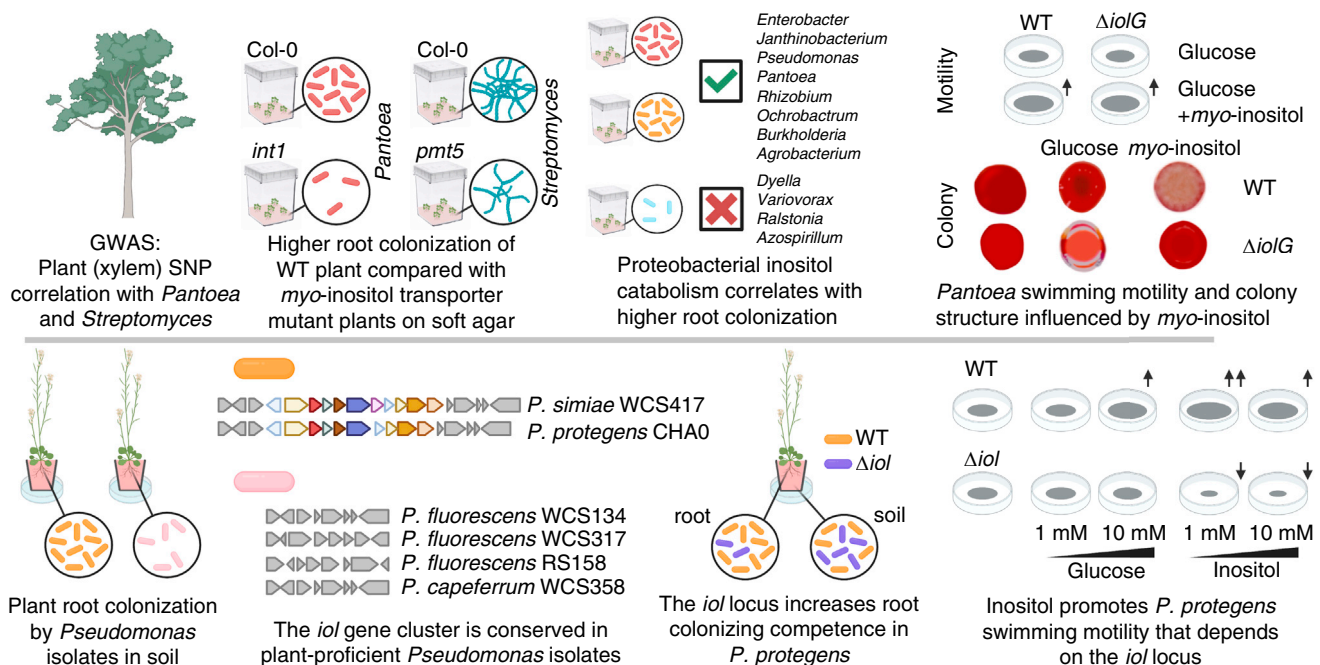
Plants grow in concert with microbes, contributing to the fitness of all interacting species. Plant roots exude a series of metabolites, depending on their developmental stage, in the soil and therefore influence the composition of the surrounding microbes, either specifically attracting distinct microbial species or allowing the catabolism of the metabolites and therefore the presence or growth of microbiome members¹. Therefore, the genetic context of the plant and its microbiome, collectively the plant hologenome, defines the overall fitness of the interacting species. Tracing the molecular and chemical factors behind plant–microbe interactions can be inspired by genome-wide association studies (GWAS) that reveal the genetic context of either the plant or microbes potentially contributing to the intricate interactions between the plant and its microbiome. Two new studies in this issue of *Current Biology* provide vigorous examples of how genetic variability of either a plant host or a microbiome species determines plant–microbe interaction success^{2,3} (Figure 1).

In one of the new studies, O'Banion and colleagues² dissect a previously generated (holo)metatranscriptome dataset on developing xylem and mature leaf tissues of poplar trees and its

microbiome⁴ to identify the single nucleotide polymorphisms (SNPs) of the plant that correlate with the abundance of two bacterial genera, *Pantoea* and *Streptomyces*. Thorough analysis of the xylem-based GWAS dataset revealed that genes with SNPs encoding distinct transporters of *myo*-inositol correlate with these two bacterial genera. *Pantoea* was associated with the *INT1* gene, which encodes a tonoplast-localized transporter of *myo*-inositol, while the *Streptomyces* network correlated with the *PMT5* gene, encoding a transporter of various polyols and monosaccharides, including *myo*-inositol, across the plasma membrane. Motivated by these correlations detected in field-grown plants and microbiomes, the authors tested isolates of *Pantoea* and *Streptomyces* for their root colonization abilities using axenic soft-agar grown *Arabidopsis* seedlings harboring specific mutations for *myo*-inositol transport. As expected, *Pantoea* displayed reduced root colonization of *Arabidopsis* plants with *int1* disruption, while *Streptomyces* exhibited reduced establishment on the roots of *pmt5* mutant plant seedlings. Reassuringly, supplementation of *myo*-inositol rescued the mutant root colonization deficit of the bacterial strains but did not increase root colonization levels when wild-type Col-0 plants were used.

In the other new study, Sánchez-Gil and colleagues³ employed a microbe-centered genetic trait analysis in which they identified that *Pseudomonas* isolates that display the highest colonization of *Arabidopsis* roots grown in an axenic soil system carry the *iol* gene cluster, encoding inositol catabolism in bacteria. Specifically, *Pseudomonas simiae* WCS417 and *Pseudomonas protegens* CHA0 displayed the strongest colonization of the root fraction without the soil (i.e., a combination of root and rhizoplane, the root's inner part and the surface zone, respectively), while the other *Pseudomonas* isolates (*Pseudomonas capeferrum* WCS358, *Pseudomonas fluorescens* RS158, and *Pseudomonas* sp. WCS317) that lacked the complete *iol* gene cluster had reduced colonization of the root structures, in spite of comparable abundance in the rhizosphere and bulk soil compartments. In addition to the *iol* gene cluster, the two *Pseudomonas* isolates were also enriched for genetic traits related to siderophore biosynthesis. Subsequently, the authors tested a *P. protegens* mutant lacking the *iol* gene cluster, which demonstrated significantly diminished *Arabidopsis* root colonization in the axenic soil system when initially mixed with the wild-type strain, but displayed comparable root colonization when either





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Figure 1. Inositol-mediated interaction between plant and bacteria.

Schematic representation of key experiments in the studies by O'Banion *et al.*² (above) and Sánchez-Gil *et al.*³ (below). GWAS: genome-wide association studies, SNP: single nucleotide polymorphism, WT: wild type. The figure was created with BioRender.com. The author acknowledges his daughter, Alba Manon Kovács, for drawing the colony artwork used in the figure.

strain was inoculated individually. Importantly, soil colonization was unaffected by the *iol* mutation in both individual and co-inoculated settings. Consequently, both O'Banion *et al.* and Sánchez-Gil *et al.* highlight the pivotal role of *myo*-inositol during plant colonization. Indeed, *myo*-inositol is required for the mutualism between the beneficial *Priestia megaterium* (formerly *Bacillus megaterium*) and the *Arabidopsis* or tomato plants⁵, suggesting a general role for *myo*-inositol in bacterial recruitment to plant roots.

Importantly, disrupting the *iol* genes prevented the *in vitro* growth of both *Pantoea* and *Pseudomonas* in minimal medium containing inositol as the sole carbon source^{2,3}. However, while *Pseudomonas* motility enhancement in the presence of inositol required the *iol* gene cluster³, inositol catabolism was not necessary for inositol-promoted motility augmentation of *Pantoea*². Another contradicting *iol*-dependent phenotype between *Pseudomonas* and *Pantoea* was plant root colonization. Plant root colonization by *iol*-disrupted *Pseudomonas* was diminished in the axenic soil system when the mutant was

co-inoculated with the wild-type ancestor³. In contrast, plant root abundance of the *Pantoea* strain lacking inositol catabolism was comparable to the wild-type strain both when inoculated individually or when in competition within the plant cultivation setup on soft agar². The differences might have arisen from the differences in either the plant cultivation setup or the way in which these two distinct species interact with *Arabidopsis*. Nevertheless, O'Banion and colleagues also identified that architecturally complex colony development, which associates with biofilm development ability, by *Pantoea* was promoted by inositol and was dependent on the *iol* genes², suggesting that inositol catabolism might be more relevant in persistence of the bacterium under more adverse conditions. While *Streptomyces* do not generally harbor single-cell motility, an easily testable trait for both *Pantoea* and *Pseudomonas*, future experiments could reveal whether *myo*-inositol can promote surface exploration by *Streptomyces* that has been previously reported to be driven by non-branching vegetative hyphal conformation in

response to inter-kingdom volatile compounds⁶.

The generality of inositol catabolism in plant colonizing microbes is further supported by the conserved occurrence of the *iol* gene cluster in the *Pseudomonas* genus, except for in the human pathogen *Pseudomonas aeruginosa*³. Indeed, 67% of the 6962 *Pseudomonas* genomes (without *P. aeruginosa*) examined carry six or more *iol* genes within 20 kbp of each other or distributed over a limited number of loci. Analogous to *P. protegens* CHA0, disruption of *P. simiae* WCS417 genes related to inositol transport and transcriptional regulation of inositol catabolism appears to lessen root colonization by the bacterium, as identified in publicly available transposon-insertion sequencing data^{3,7}. Finally, *iol* genes were found to be expressed in *P. protegens* CHA0 when colonizing an insect gut and the wheat root^{3,8}, hinting toward a broader context of inositol catabolism during microbe–host interaction.

Moreover, the broad correlation of inositol catabolism and plant root colonization has also been reinforced by comparison of plant colonization

properties of 12 isolates representing 10 families commonly found in plant microbiomes, where the 8 highest root colonizing isolates encode the putative genetic pathways for inositol catabolism, independent of their phylogenetic distribution or their bulk soil establishment attributes². Such inositol-driven plant microbiome competence could potentially guide the assembly of synthetic communities (SynComs) for plant root colonization experiments and offers a tractable genetic trait that can be tested in the SynComs developed for *Arabidopsis*⁹.

The prevalence of *myo*-inositol in root exudates offers a trait that should be considered in plant breeding strategies for belowground characters to positively shape the root microbiome¹⁰. Indeed, recruitment of plant-beneficial bacterial species by the exuded inositol could potentially increase the microbiome's ability to prevent the establishment of plant pathogens using antimicrobial natural products^{11–13} or to promote plant root development during adverse conditions, like mitigation of abiotic stress by *Streptomyces*¹⁴. However, plant-pathogenic microbes seem to have also learned to respond to these beckoning plant signals. Pathogenesis of *Pseudomonas syringae* pv. *syringae* requires the bacterial *iol* gene cluster^{15,16}.

In summary, the studies by O'Banion *et al.* and Sánchez-Gil *et al.* demonstrate that different plant species employ *myo*-inositol-mediated recruitment of bacterial species. Moreover, their work highlights the significance of bacterial lifestyles, including motility and biofilm development, in the bacterial response to root exuded *myo*-inositol. In the future, testing phylogenetically diverse bacterial collections will potentially establish whether *myo*-inositol shifts the balance of the plant microbiome towards

plant-beneficial species and therefore benefits plant fitness.

DECLARATION OF INTERESTS

The author declares no competing interests.

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