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Article Addendum

Homoserine lactones

Do plants really listen to bacterial talk?

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The bacterial quorum sensing signals N-acyl-L-homoserine lactones (AHL) enable bacterial cells to regulate gene expression depending on population density, which eventually leads to invasion of hosts. Only little is known about the molecular ways of plants reacting to these bacterial signals. Recently, we showed that the contact of *Arabidopsis thaliana* roots with N-hexanoyl-DL-homoserine-lactone (HHL) resulted in distinct transcriptional changes in roots and shoots, respectively. In addition, we provided evidence that Arabidopsis takes up bacterial AHLs, which are obviously transported throughout the plant. In sum, the bacterial quorum sensing signal AHL seems to influence plant growth, and may contribute to reprogram plants encountering bacterial pathogens or rhizosphere bacteria. However, as pointed out here, the response of plants to bacterial AHLs may depend on plant species and chemical structure of AHLs.

The interaction between plants and bacteria is mediated by a plethora of signals. The bacterial quorum sensing signals N-acyl-L-homoserine lactones (AHLs) enable bacterial cells to regulate growth and behaviour of their community. Strikingly, they seem to be also involved in processes associated with infection of plants and animals. AHLs are produced by plant growth promoting rhizobacteria (PGPRs) but also by pathogenic bacteria as e.g., *Pseudomonas syringae*. However, nothing is known about perception of AHL and bacterial patterns, and subsequent signal transduction cascades and their role in the complex network of other effectors. Currently, transcriptomic, proteomic and metabolomic approaches are being undertaken in order to characterize the pathogenic systems as well as symbiotic relationships. We have analyzed the physiological and molecular response of *Arabidopsis thaliana* to various AHLs.[1]

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Bacterial quorum sensing signals enable bacterial cells to regulate gene expression depending on population density.[2] This enables single bacterial individuals in a local population to coordinate the expression of certain genes and such act similar to a multicellular organism. AHLs are the most common quorum sensing signals in Gram-negative bacterial quorum sensing.[3] They are known to orchestrate important temporal events during the infection process, including the production of virulence factors and the formation of biofilms in nature and in man.[4] Bacterial mutants that are defective in quorum sensing are usually avirulent or significantly reduced in virulence. AHL signaling in the opportunistic animal and plant pathogen *Pseudomonas aeruginosa* is a model for the relationships among quorum sensing, pathogenesis, and community behavior. In the *P. aeruginosa* model, quorum sensing is required for normal biofilm maturation and for virulence.

However, AHLs are not only produced by pathogenic bacteria but also orchestrate important processes (e.g., swarming, production of proteolytic enzymes or biofilm formation) of many beneficial rhizosphere colonizing PGPRs. For example: deletion of the gene pcoI, responsible for the production of the AHLs 3-oxo-C6-HSL and 3-oxo-C8-HSL in *Pseudomonas fluorescen*s 2P24, left the mutant significantly defective in biofilm formation, colonization on wheat rhizosphere and biocontrol ability against wheat take-all, while complementation of pcoI restored the biocontrol activity to the wild-type level.[5]

Many plant-associated bacteria living in the rhizosphere promote plant growth by suppressing pathogenic micro-organisms, synthesizing growth-stimulating plant hormones and promoting increased plant disease resistance. Previously, we could show that two important soil bacteria, *Seratia liquefaciens* MG1 and *Pseudomonas putida* IsoF, colonize tomato roots and produce AHL in the rhizosphere. Tomato plants inoculated with these bacteria had an increased systemic resistance against the fungal leaf pathogen *Alternaria alternate*.[6] In our current paper on Arabidopsis we found no significant difference in induction of resistance between AHL-producing and AHL non-producing strains. Thus, in contrast to tomato the positive influence of root colonization of *Serratia liquefaciens* on pathogen resistance of *A. thaliana* is not dependent on AHL-production, but on colonization by Serratia spp. per se.[1] But bacterial-plant communication is complex and other factors can influence the response of a plant to AHLs. In a natural system AHLs are not perceived alone but always in combination with PAMPs or bacterial effectors.[7,8]

Figure 1. Plant growth promoting effects by AHLs in barley. Plants are shown after 14 days AHL treatment (10 μM C6-HSL). The experiment has been carried out as described.[1]

Another important point is that plant recognition of PGPRs should not induce a direct defense response as interaction with these bacteria is beneficial for the plant.[9,10] It is important for the PGPRs to overcome the plants' direct defense responses to form a successful mutualistic interaction.

Important questions to be answered address the fate of AHLs in plants and the existence of an AHL receptor in plants. Currently, nothing is known about AHL binding sites at plant cells or whether plant cells can internalize AHL. We need to know if all AHLs move throughout the plant and whether AHLs represent a systemic signal activating plant immunity. Furthermore, do AHLs have different effects in different plant tissues? In Arabidopsis, AHLs induce root growth.[1] Figure 1 shows growth promotion of shoot/leaf in barley treated with AHL. Unlike for Arabidopsis, root architecture and length are not influenced by AHLs. This result adds another aspect to the growth promoting features of AHLs; and, together with the difference in induction of systemic resistance, it tells us that the response of plants to AHLs might depend on the specific plant-AHL combination.

Regarding the existence of a putative AHL receptor it is certainly too early to speculate upon a putative binding protein in plants. Considering the ultrahigh affinity of bacterial receptors[2,3] in conjunction with the comparable low responsiveness of plants to AHLs, it is very unlikely that we will discover a similar system in plants. However, the identification of genes strongly responsive to AHL may enable us to set up a screen of Arabidopsis mutant collections. These will provide us with valuable tools to further characterize the response of plants to AHLs.

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