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**Beneficial effects of bacteria-plant communication based on quorum sensing molecules of the** *N***-acyl homoserine lactone group**

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# Abstract:

Bacterial quorum sensing (QS) mechanisms play a crucial role in the proper performance and ecological fitness of bacterial populations. Many key physiological processes are regulated in a QS-dependent manner by auto-inducer molecules, like *N*-acyl homoserine lactones (AHLs) in numerous Gram-negative bacteria. In addition, the interaction between bacteria and eukaryotic hosts are also regulated by AHLs. Those mechanisms gained much attention, because of the positive effects of different AHL molecules on plants. The positive impact ranges from growth promotion to induced resistance and is quite contrasting to the rather negative effects observed in the interactions between bacterial AHL molecules and animals. Only very recently, we began to understand the molecular mechanisms underpinning plant responses to AHL molecules. In this review, we gathered the latest information in this research field. The first part of this review gives an overview on the bacterial aspects of quorum sensing. Then, we focus on the impact of AHLs on plant growth and AHL-priming, as one of the most understood phenomenon in respect to the inter-kingdom interactions based on AHL-quorum sensing molecules. Finally we discuss the potential benefits for our understanding of bacteria-plant interaction as well as for the future agricultural applications, which may result from a profound understanding of AHL-plant interactions.

# Bacterial communication systems

Bacteria living in communities, like biofilms on abiotic or biotic surfaces, and also free-living, planktonic bacteria produce small molecules (chemical signals) in order to organize concerted activities in a process called autoinduction (AI). The signal molecules are generated constitutively at a very low rate and released from the cell into the medium. A receptor protein / transcription factor (R-protein) senses the concentration. When the concentration of these signal molecules reaches, due to an increased cell density or habitat conditions, a threshold level (quorum) the R-protein AI complex induces the transcription of key AI biosynthesis genes (I-gene), thus accelerating the response intensity (Fuqua and Winans 1994). This autoinduction process is able to integrate additional environmental and physiological signals and optimize the expression of a series of target genes. In this manner the expression of the genetic diversity and capacity of bacteria can be organized very efficiently. Autoinducers are the basis of “quorum sensing” (signaling a critical cell density). Sometimes, because of the more general aspect integrating the optimized gene expression, the term “efficiency sensing” was used (Hense et al. 2007). Since this behavior has exceptional evolutionary importance, autoinducing systems are found ample in nature. AI-systems guarantee homeostatic control of costly cooperative behavior, like the secretion of public goods or switch to pathogenic or mutualistic life styles. The production of AI-signals constitutes a pre-assessment strategy with core principles described by the hybrid “push-pull” model (Hense and Schuster 2015).

In many Gram-negative bacteria, *N*-acyl homoserine lactones (AHLs) are frequently used as autoinducers (Figure 1). These molecules consist of a hydrophilic lactone ring and a carbon chain with quite different length (C4 to C18), which changes the molecule from hydrophilic to strongly hydrophobic. The C3-atom can be unsubstituted, substituted with a carbonyl group or hydroxylated. In some cases even double bonds are formed in the lipid chain. While the product of a *luxI*-type gene performs the biosynthesis, hydrolytic enzymes with lactonase activity can degrade these signal molecules. This seems to guarantee, that the important AI-signal truly functions as a signal for specific physiological or environmental circumstances, examples for this can be found in *Agrobacterium tumefaciens* or *Pseudomonas putida* (Buddrus-Schiemann et al. 2014). There are also bacteria with just the lactonase activity, apparently using the released AHLs as carbon sources, such actives are called quorum quenching. Some other variations of the autoduction system in bacteria are bacteria having just the LuxR-gene, so-called “LuxR-solos” (Patel et al. 2013). These bacteria are able to sense AI, but are unable to produce their own AI. Interestingly, some of the LuxR solos have evolved from the ability to bind AHLs and respond to other molecules/signals.

The relevance of the signaling systems based on AHLs is reflected in the abundance of quorum quenching activities in plants and animals, which obviously have the function to destroy the signaling activity of bacterial pathogens. Many plant extracts, e.g. from garlic (Bjarnsholt et al. 2005) or horseradish (Jakobsen et al. 2012), inhibit quorum sensing. Those extracts may have distinctive inhibitory activities against many bacteria, including pathogens like *Pseudomonas aeruginosa* (Jakobsen et al. 2012). In the *Brassicaceae* family, Iberin and related isothiocyanate compounds, are shown to specifically block the expression of QS-regulated genes in *P. aeruginosa*. These are just some examples of how plants regulate the AHL-signaling of associated Gram-negative bacteria. In addition to these defense-oriented responses to pathogenic bacteria, below we discuss the beneficial responses to AHLs observed in different plants.

# AHL-molecules modulate plant performance in different ways

The first study reporting an impact of bacterial AHLs on plant physiology was published more than a decade ago (Mathesius et al. 2003). The authors performed a differential proteome analysis and revealed that amongst defense- and stress-related proteins, also proteins associated with flavonoid metabolism, hormones and several regulatory proteins (including protein degradation and synthesis) were differentially accumulated in AHL-treated plants. The authors also provided the first report on an activation of the auxin-responsible *GH3* promoter after application of AHLs (Mathesius et al. 2003). During the following years several detailed studies on the relation between the changed auxin level and the modification of plant growth upon AHL perception were published. Very remarkable was the fact that in addition to an up-regulation of auxin-related genes, genes related to cytokinin were down-regulated (von Rad et al. 2008). The resulting change in the ratio between auxin and cytokinin could explain the root growth-promoting effect observed after the application of C4- and C6- short side chain AHLs. Using another system, the AHL-induced basipetal auxin transport was postulated to play a crucial role in the formation of adventitious roots, as observed in mung bean plants (Bai et al. 2012). Importantly, this effect seems to depend on cyclic GMP signaling and H2O2 and NO production (see also the chapter Perception of AHLs).

Based on the observations from recent studies and our own experiments, we proposed a dual function of the AHL molecules in *Arabidopsis* *thaliana* (Hartmann and Schikora 2012; Schenk et al. 2012). AHLs with a short acyl chain, like C4 or C6, where shown to increase the growth rate and primary root elongation (Bai et al. 2012; Liu et al. 2012; Schenk et al. 2012; von Rad et al. 2008). In contrast, molecules with longer acyl chains (e.g. C12 and C14) induced resistance in a phenomenon named AHL-priming (Schenk et al. 2014; Schenk and Schikora 2015; Schikora et al. 2011). The impact of AHLs on plant growth in other plant species seems more complex, nonetheless very specific, as demonstrated in mung bean and *Medicago* *truncatula* plants. 3-oxo-C14-HSL produced by *Sinorhizobium meliloti* enhanced the nodulation in roots of *Medicago truncatula* (Veliz-Vallejos et al. 2014). Very striking was the fact that the increased number of nodules was observed only after a treatment with 3-oxo-C14-HSL, the predominant AHL of *S. meliloti*, treatment with other AHLs showed no effect. In mung bean plants only the 3-oxo-C10-HSL, and not the unsubstituted C10-HSL or C12-HSL, was able to induce adventitious roots (Bai et al. 2012). Although several reports linked the growth-modulating effect of AHLs to auxin, some postulated that the impact of 3-oxo-C10-HSL on *Arabidopsis* (an increased formation of lateral roots) is independent on auxin concentration (Ortiz-Castro et al. 2008). Yet another mechanism, based on changes in transpiration rate, was proposed recently by Palmer and coworkers (Palmer et al. 2014). The authors postulate that AHLs could be metabolized to *L*-homoserine, which increase stomata opening and consequently foster the water and mineral flow through the plant.

# Uptake and physiological influence of AHL

The strong impact of AHLs on plants raised the question whether those molecules act via a systemic signal (or signals), which would be initiated after the perception of AHLs on the root surface, or whether they are taken up into the plant’s tissues and act locally. Only few reports addressed this question in a systemic manner. Using radioactively labeled C8- and C10-HSL, Sieper and colleagues reported an ATP-dependent transport of AHLs within barley roots. The majority of the molecules were transported within the central cylinder. The transport rate of the AHL-molecules within the root and shoot tissues correlated negatively with the length of the acyl chain (Sieper et al. 2013). Similarly, in *Arabidopsis* the short-chain AHL, C6-HSL, was relocated into leaves after application to roots. However, the long carbon carbon chain AHL, oxo-C14-HSL, was not transported (Schikora et al. 2011). Both studies confirm earlier report on barley (*Hordeum vulgare*) and yam beans (*Pachyrhizus erosus*) (Götz et al. 2007). More recent study on the same plants revealed that C6-, C8- and C10-HSLs influence the activity of specific detoxification enzymes, namely glutathione S-transferase and dehydro-ascorbate reductase in barley with the largest influence on the leaf-located enzyme even when C6-HSL was applied to the roots; in yam bean no influence was measured (Götz-Rösch et al. 2015). This difference might be due to lack of AHL-transport to the shoot in yam bean probably caused by a lactonase-driven degradation. Yet another interesting example is the modification of plant cells in AHL-primed plants (see below). In this primed stage, plants upregulate the transcription of several genes related to secondary metabolism (e.g. phenols) as well as to cell wall. In consequence upon a challenge with pathogens, those plants accumulate callose and phenolic compounds (Schenk and Schikora 2015). The first report on interaction between the perception of AHLs and plant reproduction was a study on the green macroalgae *Ulva* and the red macroalgae *Gracilaria*. Here, the short-chained C4- and C6-HSLs produced by bacteria in biofilms stimulated the release of carpospores (Singh et al. 2015). Interestingly, algae’s cystocarps and the cystocarp-bearing plantlets treated with AHLs had a protein pattern different from the pattern in control algae.

# AHLs prime for induced resistance

In preparation for an upcoming biotic or abiotic stress, plants can strengthen their defense mechanisms with a sensibilisation mechanism, called priming. Diverse low-molecular weight metabolites and natural compounds can induce this state. In the last decades several priming phenomena were described which generally result in a stronger and faster response to a stress agent. Priming has been shown e.g. for β-aminobutyric acid (BABA), which improves plants ability to resist biotic and abiotic stresses (Ton et al. 2005). The mobile metabolite azelaic acid primes the plant for higher salicylic acid-related defense response (Jung et al. 2009). Also pipecolic acid can sensitize plants for systemic aquired resistance (Navarova et al. 2012). Other priming inducers comprise biocontrol bacteria, which can prepare the plant for an upcoming pathogen attack (Ryu et al. 2003). In the last years, many molecular aspects of priming were discovered, including an involvement of MAP-kinases, modifications of histones in promoter regions of defense-associated transcription factors, and other epigenetic mechanisms conveying a trans-generational memory effect (Beckers et al. 2009; Jaskiewicz et al. 2011; Luna et al. 2012).

Several reports documented that also AHLs are able to function as priming agents. AHLs induce resistance against a broad spectrum of plant pathogens in different plant species. Short and medium length carbon chain AHLs produced by *Serratia liquefaciens* strain MG1 and *Pseudomonas putida* strain IsoF were responsible for an induced systemic resistance against the fungal leaf pathogen *Alternaria alternata* in tomato plants (Hartmann et al. 2004; Schuhegger et al. 2006). The AHL-induced resistance was proposed to depend on salicylic acid (SA)- and ethylene-related defense reactions. Pang et al., (2009) demonstrated resistance induction by AHLs produced by the strain *Serratia plymuthica* HRO-C48, which protected cucumber plants against the damping-off disease-causing *Pythium apahnidermatum* (Pang et al. 2009). Furthermore, the authors described an AHL-dependent stimulation of systemic resistance to *Botrytis cinerea* in beans and tomatoes (Pang et al. 2009). In addition to AHL-producing bacteria, pure AHL-molecules also have resistance priming properties. The long chain AHL, oxo-C14-HSL, activates resistance towards different obligate biotrophic pathogens such as *Golovinomyces orontii* and *Blumeria graminis* in *Arabidopsis* and barley, respectively, as well as against the hemibiotrophic pathogen *Pseudomonas syringae* pathovar *tomato* (*Pst*) in *Arabidopsis* (Schenk et al. 2014; Schikora et al. 2011). Similarly to previous observations, the resistance against *Pst* was enhanced also by the oxo-C14-HSL-producing *Sinorhizobium meliloti* strain *expR*+ in *Arabidopsis* (Zarkani et al. 2013). The potential significance of AHL-priming for agriculture became more obvious with a study on the resistance against *Blumeria graminis*, *Puccinia graminis* and *Phytophtora infestans,* induced by the same AHL-producing *S. meliloti* strain *expR*+, which induced resistance in barley, wheat and tomato (Hernández-Reyes et al. 2014). The AHL-effects triggered by *S. meliloti expR+* seems to be based on an enhanced production of reactive oxygen species (ROS). The induced accumulation of ROS in AHL-primed plants was observed in barley plants, which showed an elevated level of hypersensitive response (HR) after infection with *Blumeria graminis*. This high level of HR correlated with increased number of vesicle formation at the site of infection and increased transcription of the *Peroxidase7* (*HvPRX7*) gene (Hernández-Reyes et al. 2014). Very recently, the molecular mechanism of the AHL-induced priming was deciphered in *Arabidopsis* (Schenk and Schikora 2015), we postulated a SA and oxylipin-dependent pathway, which could activate cell wall and stomata-based defense responses (Schenk et al. 2014). Schuhegger and colleagues also suggested also the involvement of SA in AHL-systemic effects on plants in tomato plants (Schuhegger et al. 2006). Those first findings were later corroborated by mutant analysis in *Arabidopsis*: mutants impaired in SA-signaling, such as *npr1-1* or *tga2/5/6,* as well as the mutant in oxylipin synthesis, *lox2*, failed to induce AHL-priming. In addition, an enhanced accumulation of SA and the defense-related hormone OPDA was detected in AHL-primed plants (Schenk et al. 2014). The strong upregulation of oxylipin-dependent *GST6, GSTU19, HSP70, HSP17* and of *cytochrome P450* (*CYP81D11*), all of them are usually regulated by OPDA treatment (Mueller et al. 2008), after oxo-C14-HSL pretreatment and following inoculation with *Pst* was in line with this observation (Schenk et al. 2014). Altogether, several evidences indicate the importance of oxylipins (and SA) in AHL-priming.

In addition to the changed transcriptome and hormonal balance, modification of the cell wall could account for the defense mechanisms induced upon AHL-priming. Higher number of papilla formed at the site of fungal infection (Schikora et al. 2011) enhanced accumulation of callose and cell wall-bound phenolic compounds as well as accumulation of lignins (Schenk et al. 2014), suggest that cell wall undergoes substantial changes during AHL-priming. Another AHL-resistance phenotype could be the increased amount of closed stomata in response to *Pst* challenge in oxo-C14-HSL-pretreated plants (Schenk et al. 2014). This AHL-induced stomata defense response seems similar to the flg22-induced stomata closure described as RES-oxylipin and SA-dependent by (Montillet et al. 2013).

# Comparison of perception of AHLs in plant and animal cells

In mammalian cells, AHLs can trigger multiple signaling pathways including calcium mobilization, activation of Rho GTPases, MAPK, and NFκB. Those pathways control diverse functions and behaviors modified upon AHL perception, such as cytoskeleton remodeling, chemotaxis, migration, phagocytosis, epithelial barrier function, differentiation, proliferation, apoptosis, and production of immune mediators. However, in contrast to plant cells, the biological activity requires more than 10 C-atoms in the acyl chain. Recently, these findings were reviewed by (Holm and Vikström 2014). Similar to animal cells, where the MAP kinases p38 and p44/42 are involved in the response to AHLs, the AHL-priming was abolished in plants lacking MPK6 (Schikora et al. 2011). Similarly, the Ca-signaling plays an important role during perception of AHL in animals and plants. For example in animals, the 3O-C12-HSL can increase the intracellular calcium concentrations through influx from surrounding and release from thapsigargin-sensitive stores (Vikström et al. 2010). In plants, treatment with C4-HSL induced a transient and immediate increase in cytosolic Ca2+ levels. Since pretreatments with La3+, verapamil or ethylene glycol tetraacetic acid (EGTA) inhibited this increase, but a pretreatment with Li+ failed to do so, the contributing Ca2+ was, similarly to animals, mobilized from the extracellular medium *via* the plasma membrane Ca2+ channels (Song et al. 2011). Moreover, a recent study on 3-oxo-C6-HSL revealed that in *Arabidopsis* mutants in calmodulin (CaM) genes do not show the growth-promoting effect of C6-HSL, otherwise observed after treatment with C6-HSL in wild type plants (von Rad et al. 2008; Zhao et al. 2015). A very interesting but still rather elusive, is the role of G-proteins in the perception of short side chain AHLs in *Arabidopsis*. Whereas in animal cells, the IQ-motif-containing GTPase-activating protein IQGAP1 interacts directly with 3-oxo-C12-HSL (Karlsson et al. 2012), such interaction for plant proteins remains uncharacterized. Analysis of mutants in the G-protein coupled receptors GCR1 and two others (named: cand2 and cand7) as well as the canonical subunit G-alpha GPA1 revealed that those proteins are required for the stimulatory effect of C6- and C8-HSLs in *Arabidopsis* (Jin et al. 2012; von Rad et al. 2008; Zhao et al. 2015). Nevertheless, besides those very promising results, *bona fide* AHL-interactor proteins in plants remain still undiscovered.

# Potential use of quorum sensing mechanisms

The increasing demand for food as well as the concerns about food quality are today the driving forces leading to new strategies in agriculture. Efficient (crop) plant protection methods hold a great potential to ensure sufficient and high-quality food supply. Amongst them, the use of *biologicals* or *biocontrol agents*, even though widely spread, still didn't reveal its full abilities. Today several products based on bacterial inoculum, mainly consisting of *Bacillus*, *Psudomonas* or *Seratia* spp., reached the market. Our research however, show that the use of N2-fixiting *Rhizobia* (e.g. *S. meliloti*) with enhanced production of specific AHLs, could enhance the beneficial effects of bacteria and enlarge the impact to plant species usually not associated with the particular strain (Hernández-Reyes et al. 2014; Zarkani et al. 2013). Such strategy could be a great addition, or alternative to those which are currently used. On a different scale, a profound understanding of the interaction between bacterial quorum sensing molecules and eukaryotic cells could open new possibilities also in medicine. During the infection process AI molecules not only govern the bacterial ability to form biofilms, expression of virulence factors and other density-regulated features, they also play crucial role in the interaction with animal and human cells by regulating their vital functions. Therefore, the possibility to interfere with bacterial QS or with the impact of AL-molecules on eukaryotic targets could be the center of new strategies to overcome infectious diseases and biofilm formation (Jakobsen et al. 2013; LaSarre and Federle 2013).

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# Figures and Tables

## Table 1

Different effects were observed on plants after application of pure AHL molecules or inoculation with AHL-producing bacteria. The findings are arranged accordingly to the increasing length of the AHL acyl chain.

|  |  |  |  |
| --- | --- | --- | --- |
| **AHL** | **Effect** | **Plant** | **Reference** |
| C4-HSL | Intracellular Ca2+ elevation | *Arabidopsis* | (Song et al. 2011) |
| C4-HSL, C6-HSL, C8-HSL | Primary root growth | *Arabidopsis* | (Liu et al. 2012; von Rad et al. 2008) |
| Serratia liquefaciens (C4-HSL, C6-HSL) | Resistance against necrotrophic pathogens, SA-levels, defense-gene regulation | Tomato | (Schuhegger et al. 2006) |
| Serratia phymuthica (AHL+) | Resistance against necrotophic pathogens | Tomato, Beans, Cucumber | (Pang et al. 2009) |
| C6-HSL | Transcriptom data, auxin/cytokini level | *Arabidopsis* | (von Rad et al. 2008) |
| oxo-C6-HSL | Primary root growth, calmodulin signaling | *Arabidopsis* | (Zhao et al. 2015) |
| C6-HSL | Herbivore susceptibility | *N. attenuata* | (Heidel et al. 2010) |
| C6-HSL, C8-HSL | Root growth, plant biomass increase | *Arabidopsis* | (Schenk et al. 2012) |
| oxo-C8-HSL | Proteomic analyses | Arabidopsis | (Miao et al. 2012) |
| oxo-C8-HSL | Primary root growth promotion, ethylene-level | *Arabidopsis* | (Palmer et al. 2014) |
| C6-HSL, oxo-C10-HSL,  oxo-C14-HSL, | Transcriptome data | *Arabidopsis* | (Schenk et al. 2014) |
| oxo-C10-HSL | Axin-induced adventitious root formation | Mung beans | (Bai et al. 2012) |
| oxo-C10-HSL | Root development, root hair formation | *Arabidopsis* | (Ortiz-Castro et al. 2008) |
| C10-HSL, C12-HSL | Inhibition of primary root growth | *Arabidopsis* | (Zhao et al. 2015) |
| oxo-C12-HSL, oxo-C16-HSL | Proteomic data, auxin-response | *M. truncatula,* White Clover | (Mathesius et al. 2003) |
| *Sinorihzobium meliloti*  (oxo-C14-HSL) | Enhanced nodulation in roots | *M. truncatula* | (Vikström et al. 2010) |
| oxo-C14-HSL | Resistance to biotrophic pathogenes, activation of MAP-Kinases, defense- gene regulation | *Arabidopsis*, Barley | (Schikora et al. 2011) |
| oxo-C14-HSL | SA/oxylipine- related defense against biotrophic pathogenes | *Arabidopsis* | (Schenk et al. 2014) |
| *Sinorhizobium meliloti*  (oxo-C14-HSL) | Resistance against biotrophic pathogens | Tomato, Barley, Wheat, *Arabidopsis* | (Hernández-Reyes et al. 2014) |

# Figure 1

Shown is the general structure of *N*-acyl homoserine lactones (AHLs), the AI-molecules in many Gramm-negative bacteria. R - acyl chain can range from 4 to 18 carbon atoms.

