# Acyl Homoserine Lactone-Producing Rhizobacteria Elicit Systemic Resistance in Plants

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**Abstract**

*N*-acyl homoserine lactone (AHLs) produced by bacteria play a unique role in altering the expression of plant defence genes. AHL signals are constitutively produced by the vast majority of the rhizosphere and other groups of bacteria; and also varied levels of plant response are elicited through different types of AHL signals. Moreover, the defence mechanism of AHL-induced ISR is distinct from other bacterial compound-mediated plant response. It was also evident that the response of plants to bacterial AHLs may depend on plant species and chemical structure of AHLs. However, the question of how plants perceive the AHLs and distinguish between those molecules remains open. To date, no information is available either about plant AHL receptors or how plant cells can incorporate AHL signal molecules. Even though plants produce compounds similar to AHL signals, the precise source, structure and biological significance of these AHL mimics from plants are currently unknown. The specificity of plant mimics to stimulate or inhibit different types of AHL signals needs to be addressed. A thorough understanding of how plants perceive and respond to AHLs needs to be investigated. Copious questions remain to be addressed for the better understanding of quorum sensing of bacteria and trans-kingdom interactions of AHLs with plant cells.

## 9.1 Introduction

Rhizosphere microbiome influence plant growth and development; therefore, a collaborative action is essential for establishment of an efficient plant-bacteria interaction. Bacteria employ a variety of chemical molecules as their signals for communication across interspecies, intraspecies

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and intra-kingdom (Atkinson and Williams 2009). The bacterial communication is mediated by the exchange of small extracellular chemical signals which influence bacterial gene expression and physiological behaviour in a density-dependent signalling mechanism termed quorum sensing (QS). Among them, the best-studied QS mechanisms are from Gram-negative Proteobacteria, which use distinct group of biologically active metabolites, namely, *N*-acyl homoserine lactone (AHL) autoinducers as signal molecules (Swift et al. 1999; Whitehead et al. 2001). The QS-controlled phenotypes play a vital role for successful bacteria-host interactions, whether symbiotic or pathogenic (Boyer and Wisniewski-Dye 2009). The ecological distribution of AHL producers in natural environments and their potential roles have attracted much attention, and hence the diversity and distribution of AHL producers have been explored in different eco-niches (Cha et al. 1998; Huang et al. 2013; Lv et al. 2013; Viswanath et al. 2015), especially the rhizosphere regions which were reported to harbour high AHL population (DeAngelis et al. 2008; Elasri et al. 2001; Viswanath et al. 2015). The rhizosphere-associated AHL producers play a crucial role in plant health and growth and influence phenotypes such as root colonization and induction of systemic resistance in plants (Hartmann et al. 2004, 2014; Pang et al. 2009). Despite the intense study of AHL signalling in biocontrol bacteria, namely, *Pseudomonas* spp. (Wood et al. 1997; Chin-A-Woeng et al. 2001; De Maeyer et al. 2011), *Rhizobium* spp. (Wisniewski-Dye and Downie 2002) and *Serratia* spp. (Van Houdt et al. 2007), there is only limited information on AHL-dependent regulation in other beneficial plant-associated rhizobacteria. The ability of plant growth-promoting rhizobacteria (PGPRs) such as *Pseudomonas*, *Serratia*, *Bacillus* and non-pathogenic *Fusarium oxysporum* has been reported to promote plant health mediated through induced systemic resistance (ISR) (Kloepper et al. 2004; De Vleesschauwer and Hofte 2009). Similarly AHL-producing PGPRs triggered induced systemic resistance which had profound effect on the modulation of plant development and defence activity (Hartmann et al. 2014; Schenk and Schikora 2015). The AHL signalling molecules elicit plant response by systemic induction of defence gene expression especially against biotic stress (Schuhegger et al. 2006). To date, reports on diversity of AHL producers among PGPR and AHL-elicited ISR response in multiple plant species are limited. This chapter discusses the current status on the diversity of AHL bacterial communities associated with plant rhizosphere and the mechanism of AHL-elicited ISR-mediated defence response during plant-microbe interaction.

## 9.2 Induced Systemic Resistance in Plants

Plants develop local defence response due to colonization of beneficial bacteria or infection by pathogenic bacteria, which triggers immunity by the recognition of microbe-associated molecular patterns (MAMP) or effector proteins, resulting in systemic resistance. The two best understood mechanisms of systemic resistance are systemic acquired resistance (SAR) and induced systemic resistance (ISR). The SAR-mediated induced resistance is acquired upon local induction by a pathogen, whereas ISR is triggered by plant-associated beneficial microbes (Berendsen et al. 2012; Pieterse et al. 2014; Schenk et al. 2014). In both the systems, plants activate an elaborate matrix of signal transduction pathways via phytohormones such as salicylic acid (SA), jasmonic acid (JA), ethylene (ET) and abscisic acid (ABA) which act as key signalling molecules.

Induced systemic resistance (ISR) of plants against pathogens has been intensively investigated with respect to the underlying signalling pathways involved in defence response as well as its potential use in plant protection (Choudhary et al. 2007; Heil and Bostock 2002). In plants, ISR defence response is elicited by diverse bacterial determinants including bacterial surface components (flagellin, lipopolysaccharides and exopolysaccharides), volatile organic compounds (acetoin and 2,3-butanediol) and bacterial secondary metabolites (2,4-diacetylphloroglucinol

(DAPG) and pyocyanin) (De Vleesschauwer and Hofte 2009; Kloepper et al. 2004; Ryu et al. 2004). The triggered ISR activates defence response through various mechanisms, viz. induction of pathogenesis-related proteins (PRP), phytoalexins, cell wall reinforcement and priming defence responses (Beckers et al. 2009; Ryu et al. 2003; Slaughter et al. 2012; Van Wees et al. 2008).

## 9.3 *N*-Acyl Homoserine Lactone (AHL)

Bacteria use small chemical molecules to synchronize gene regulation within a population in a process called quorum sensing (Bassler 1999). The AHLs are the most common signal molecules used exclusively by Gram-negative bacteria. These molecules are composed of a fatty acyl chain ligated to a lactonized homoserine through an amide band. The length of the acyl side chain ranges from 4 to 18 carbon atoms, and based on the length of the acyl groups, AHLs can be broadly classified as short- or long-chain molecules. Short-chain AHLs have 4–8 carbon atoms in the acyl moiety, while long-chain AHLs have 10–18 carbons. The acyl side group can be substituted with an oxo or hydroxyl group at position C3 which confers signal specificity (Fuqua and Greenberg 2002; Thiel et al. 2009; Waters et al. 2008; Waters and Bassler 2005). Short-chain AHLs are believed to freely diffuse across the cell membrane, whereas AHLs with longer acyl side chains require multidrug efflux pump for transportation (Kaplan and Greenberg 1985; Pearson et al. 1999; Whitehead et al. 2001).

The canonical AHL QS involves two regulatory genes, a *luxI* family of AHL synthase genes and a *luxR* family of AHL-responsive transcriptional regulatory genes. Homologous to *luxI/luxR* QS system have been described in several Gram-negative bacteria, although the AHLs produced by the LuxI homologues as well as the genes regulated by them vary at the species or strain level (Whitehead et al. 2001).

The genes encoding these two proteins are often located adjacent to one another on the chromosome in almost all the AHL-producing proteobacteria (Fuqua et al. 1996; Churchill and Chen 2011; Gelencser et al. 2012). The LuxI proteins synthesize AHL signal molecules using the substrate *S*-adenosyl methionine for the backbone lactone ring, and acylated carbon chain from fatty acid biosynthesis pathway (Schaefer et al. 1996). LuxR-like proteins are transcriptional regulators which recognize the cognate AHL signals and mediate either activation or repression of QS-dependent gene expression (Fuqua and Winans 1994; Fuqua et al.1996). Also, the activated LuxR proteins up regulate *luxI* transcription and enhance the rate of AHL synthesis (Fuqua et al. 1996, 2001; Case et al. 2008). The recognition of bacterial AHL receptors to their corresponding AHL signals is highly specific, and hence the AHLs are classified as intraspecies signals among the proteobacteria (Huse and Whiteley 2011; Taga and Bassler 2003). A generalized scheme for an AHL quorum-sensing circuit in a bacterial cell is shown in Fig. 9.1.

## 9.4 Diversity of AHL-Producing Rhizosphere Bacterial Communities

The rhizosphere habitat provides a favourable environment for QS signalling since it contains significantly higher densities of microorganisms. A wide range of plant-associated PGPR, symbiotic, endophytic, epiphytic and pathogenic bacteria regulate their physiological functions through AHL signals (Ortiz-Castro et al. 2009; Venturi and Fuqua 2013). Recent studies indicate that AHL-based QS is highly prevalent in rhizosphere and endophytic communities of plants (Schaefer et al. 2013). The diversity of AHL-producing bacteria in the rhizosphere-associated bacterial communities of different plant species has been extensively studied and was represented only by the proteobacteria. In general, the proteobacteria group constitutes an estimated two thirds of

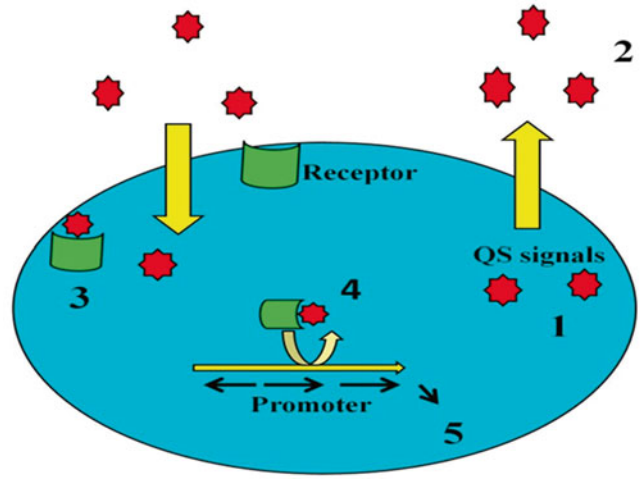


**Fig. 9.1** Schematic representation of quorum-sensing mechanism. QS process: *1* synthesis of signal molecules, *2* diffusion of signal molecules, *3* signal recognition by receptor, *4* binding of signal receptor complex to promoter and *5* expression or repression of target genes (Source: Viswanath 2015)

many temperate plant rhizospheres (Hawkes et al. 2007). AHL-producing proteobacteria have been found to be more common in the rhizosphere than bulk soil (Cha et al. 1998; Elasri et al. 2001; d'Angelo-Picard et al. 2005).

In addition, several endophytic and epiphytic bacteria are also known to produce AHLs; however QS-dependent behaviours are poorly understood in these bacterial groups (Lv et al. 2013; Schaefer et al. 2013). The AHL-producing rhizobacteria were represented by α-, β- and γ-proteobacteria, isolated from the rhizospheres of tobacco (d'Angelo-Picard et al. 2005), potato, strawberry, oilseed rape (Berg et al. 2002), tomato (Steidle et al. 2001), wild oats (De Angelis et al. 2008), wheat (Pierson et al. 1998), cottonwoods (Schaefer et al. 2013), citrus (Trivedi et al. 2011), paddy (Steindler et al. 2008; Vial et al. 2006), cocoyam (De Maeyer et al. 2011), finger millet (Sekar and Prabavathy 2014), mangrove (Viswanath et al. 2015) and wetland plants (Zeng et al. 2014). The majority of the AHL-producing isolates from the plant rhizospheres belonged to the genera *Pseudomonas*, *Rhizobium*, *Serratia*, *Burkholderia*, *Erwinia* and *Pantoea* (Cha et al. 1998; d'Angelo-Picard 2005; Viswanath et al. 2015). The diversity of AHL-producing rhizobacteria was found to be ecological niche specific, e.g. majority of the AHL producers isolated from the mangrove rhizosphere were represented by the genera *Vibrio*, *Halomonas* and *Photobacterium* which were absent in the agriculture plant crops. Similarly, the genera *Rahnella*, *Pantoea*, *Enterobacter*, *Erwinia* and *Burkholderia* isolated from agriculture crops were not represented in the mangrove and other wetland rhizospheres (Viswanath 2015; Viswanath et al. 2015; Zeng et al. 2014).

The AHL signalling molecules produced by the rhizosphere bacteria varied from short to long chains and are reported to produce more than one type of AHL molecules, and its AHL profile was not strictly conserved at the genus or species levels. Even though rhizobacterial isolates produced similar group of AHL molecules, the role of AHLs involved in the regulation of phenotypes differed from strain to strain (Fuqua and Greenberg 2002; Gonzalez and Keshavan 2006; Venturi and Subramoni 2009). For example, in *Serratia marcescens* MG1, C6-HSL regulated swarming motility and biofilm formation, whereas in *S. marcescens* SS1, the same AHL regulated sliding motility and prodigiosin production (Eberl et al. 1996; Horng et al. 2002). The distribution of AHL molecules among the rhizobacteria was species or strain dependent. This could be due to the acquisition of AHL homologue genes through horizontal gene transfer (Gray and Garey 2001; Lerat and Moran 2004). The production of a similar type of AHL molecules in different genera might help interspecies communication in the natural environment where mixed communities are often represented (Atkinson and Williams 2009). Although the

diversity of AHL-producing rhizobacteria has been explored in recent times, still identifying a myriad of AHL signals from bacteria inhabiting diverse plant species is less studied. The predominant occurrence of AHL producers in rhizosphere suggests that AHL QS might be a trait of significant importance in bacterial growth and colonization in the rhizosphere. Therefore, research focus to understand the ecological roles of AHLs in plant-bacteria interaction is needed.

## 9.5 Interactions of AHL with Plants

In recent years, numerous studies have shown that plants also have evolved means to perceive and respond to AHL signal molecules produced by bacteria. Many of the AHL-regulated phenotypes in bacteria such as biofilm formation, motility and antibiotic and biosurfactant production have profound impact on plant health. Recent reports have revealed that plants have marked response to the AHL signals produced by its associated microbiome. The first indication of plant responses to bacterial AHLs was studied in the legume *Phaseolus vulgaris* (Joseph and Phillip 2003) and in *Medicago truncatula* (Mathesius et al. 2003). The exposure of AHLs from symbiotic *Sinorhizobium meliloti* or pathogenic *Pseudomonas aeruginosa* at nano to micromolar concentrations induced significant changes in defence and stress management genes and accumulation of over 150 proteins (Mathesius et al. 2003). The influence of AHL molecules in plant defence response was established during interaction of *Serratia liquefaciens* MG1 and tomato plants (Hartmann et al. 2004; Schuhegger et al. 2006). The rhizobacteria *S. liquefaciens* MG1 produced short-chain AHLs C4- and C6-HSL when colonizing the tomato root surface, which induced systemic resistance against the leaf-pathogenic fungus *Alternaria alternata*. The AHLs increased salicylic acid concentration and also induced the ethylene and salicylic acid-dependent defence genes. Similarly, 3-oxo-C6-HSL producing *Serratia plymuthica* HRO-C48 elicited defence response against damping-off disease caused by *Pythium aphanidermatum* in cucumber plants and grey mould-causing fungus *Botrytis cinerea* in tomato and bean plants (Liu et al. 2007; Pang et al. 2009). The production of 3-oxo-C14-HSL by *Ensifer meliloti* (*Sinorhizobium meliloti*) associated with *Arabidopsis* plant roots showed resistance against *Pseudomonas syringae* (Zarkani et al. 2013). Likewise, Hernandez-Reyes et al. (2014) described the induction of systemic resistance by 3-oxo-C14-HSL-producing *S. meliloti* in tomato, barley and wheat plants against diverse pathogens. In addition, constitutive expression of AHL genes in transgenic tobacco plants applied with rhizobacterium *S. marcescens* 90–166 showed increased induced systemic resistance against bacterial pathogens *Pectobacterium carotovorum* subsp. *carotovorum* and *P. syringae* pv. *tabaci* (Ryu et al. 2013).

Also, the application of synthetic AHLs at a concentration range of 1–10 μM to roots in an axenic system was shown to induce resistance in diverse plants. Tomato plants treated with C4 or C6-HSL directed a systemic induction of genes involved in defence (Schuhegger et al. 2006). Schikora et al. (2011) demonstrated increased systemic resistance against obligate biotrophic fungi *Golovinomyces orontii* in *Arabidopsis thaliana* and against *Blumeria graminis* f. sp. *hordei* in *H. vulgare* (barley) plants when treated with synthetic 3-oxo-C14-HSL and 3-oxo-C12-HSL. In addition, the molecule 3-oxo-C14-HSL treated *A. thaliana* plants showed more resistance towards the hemibiotrophic bacterial pathogen *P. syringae* pv. *tomato* DC3000 (Schikora et al. 2011). Likewise, 3-OH-C14-HSL and 3-oxo-C12-HSL showed similar level of defence response against biotic stress in *A. thaliana* but comparatively weaker than 3-oxo-C14-HSL (Schikora et al. 2011). The degraded product of AHL, namely, homoserine lactone, when added to legume *P. vulgaris* roots at a concentration of 10 nM increases stomatal conductance and transpiration (Joseph and Phillips 2003). In *Trifolium repens* (white clover), transcriptional analysis indicated that treatment with 3-oxo-C12-HSL increased transcription of elements associated with auxin-responsive promoters (Mathesius et al. 2003). In *Arabidopsis*, short-chain (C4- and C6-) AHLs increased the plant's hormone

auxin/cytokinin ratio, which resulted in root elongation (von Rad et al. 2008). Ortiz-Castro et al. (2008) demonstrated that C10-HSL elicited developmental changes in the root system in *Arabidopsis* plants by altering the expression of cell division and differentiation-related genes, and C12-HSL strongly induced root hair formation. Furthermore, treatment with 3-oxo-C6-HSL and 3-oxo-C8-HSL promoted root elongation in *Arabidopsis* at concentration range of 1–10 μM (Jin et al. 2012; Liu et al. 2012). In *Vigna radiata*, 3-oxo-C10-HSL induced the formation of adventitious roots (Bai et al. 2012). *H. vulgare* (L.) and *Pachyrhizus erosus* L. (yam bean) plants treated with C6-, C8- and C10-HSL triggered tissue- and compound-specific changes in the activity of important detoxification enzymes (Gotz-Rosch et al. 2015).

The plant response to bacterial AHL signals is dependent on the type of AHL molecules. The length of the AHL side chain is essential for its effect on plants; for example, C4-HSL, C6-HSL, 3-oxo-C6-HSL and 3-oxo-C8-HSL promoted growth in *Arabidopsis* and barley (Gotz et al. 2007; Liu et al. 2012; Schenk et al. 2012; von Rad et al. 2008), whereas 3-oxo-C10-HSL induced the formation of adventitious roots in mung beans (Bai et al. 2012). On the other hand, C6- and 3-oxo-C6-HSL induced systemic resistance in tomato, cucumber and barley (Pang et al. 2009; Schikora et al. 2011; Schuhegger et al. 2006), while 3-oxo-C12- and 3-oxo-C14-HSL were reported to have resistance-inducing attributes in *A. thaliana* and *M. truncatula* (Mathesius et al. 2003; Schikora et al. 2011). The apparent different reactions to long and short chain HSLs may suggest that different receptors or at least different signalling pathways are involved in these responses. Moreover, the reaction of plants to AHLs might also depend on the specific plant-AHL combination. Different acyl length chains of AHL that induce systemic resistance and growth promotion in plants are shown in Fig. 9.2.

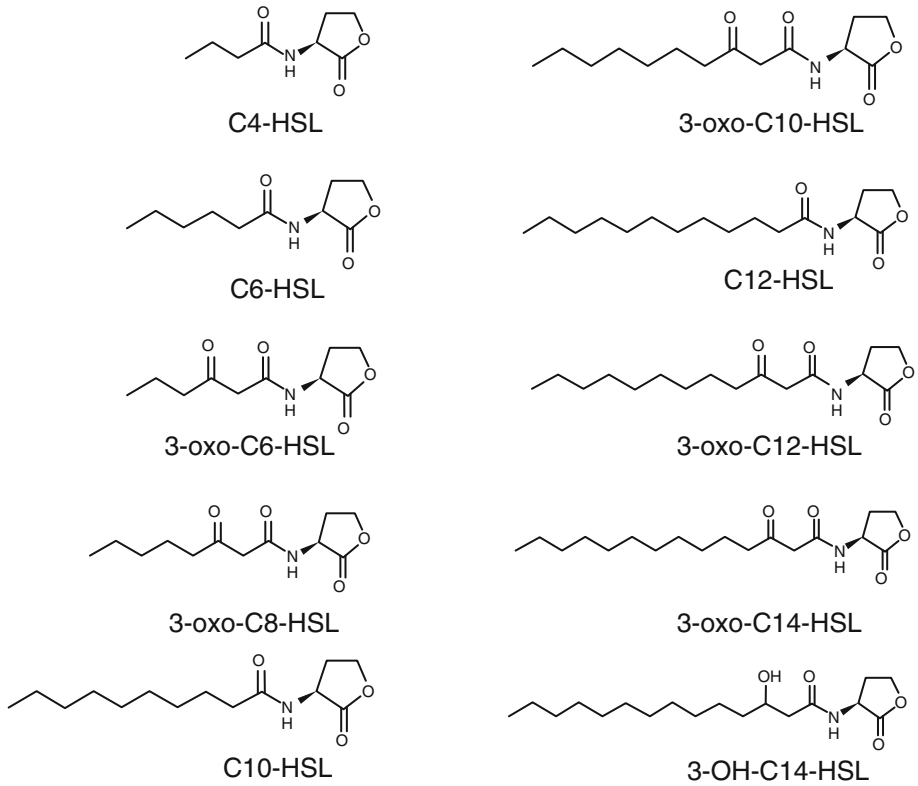


**Fig. 9.2** Structures of AHL elicitors which induce ISR in plants (Source: Gera and Srivastava 2006; Ortiz-Castro et al. 2008)

Furthermore, plants also control the bacterial QS system by producing compounds that mimic AHL signals. Higher plants including *Pisum sativum* (pea), *Solanum lycopersicum* (tomato), *Oryza sativa* (rice) and *M. truncatula* secrete compounds that either stimulate or inhibit AHL responses (Bauer and Mathesius 2004; Degrassi et al. 2007; Gao et al. 2003; Perez-Montano et al. 2013; Teplitski et al. 2000).

## 9.6 Mechanisms of AHL Interaction in Plants

Although the response of plants to AHLs has been more extensively studied, understanding the molecular mechanisms of how plants perceive and respond to AHLs is still unclear. Very recently, possible mechanisms have been proposed to show how AHL signals influence plant defence and reinforce resistance in different plants against bacterial and fungal pathogens.

### 9.6.1 AHL in Plant Defence

The AHL signals use "priming" mechanisms for the induction of defence response in plants. The following possible mechanisms of plant defence response triggered by AHL molecules have been postulated:

1. Induction of SA-dependent pathway – The AHLs that triggered immune response in plants are activated through SA-mediated systemic resistance. The induction of systemic resistance in tomato against fungal leaf pathogen *A. alternata* is enhanced due to the increased levels of SA when treated with AHL-producing rhizobacterium *S. liquefaciens* MG1. Also, enhanced expression of pathogenesis-related 1a (*PR1a*) and two chitinase genes involved in SA-/ET-dependent pathways were identified in tomato leaves when C6-HSL or C4-HSL was applied to the roots of tomato plants. This strongly emphasizes that the systemic response mediated by short-chain AHL signals in tomato plant functions via an SA-dependent pathway (Schuhegger et al. 2006).
2. Induction via oxylipin-/salicylic acid (SA)-dependent pathway – The oxylipin *cis*-OPDA, a precursor of JA, and SA involved in plant defence response are elicited by AHL signal molecules (Schenk et al. 2014). The 3-oxo-C14-HSL-treated *Arabidopsis* plant showed increased accumulation of SA and *cis*-OPDA on leaves, which resulted in enhanced expression of heat shock proteins, GST6, GSTU19 encoding *HSP70* and *HSP17* genes and the cytochrome P450-encoding *CYP81D11* gene. The lack of enhanced expression of JA-dependent genes such as *MYC2* and *VSP2* and the ET-dependent genes *PR3*, *ERF5* and *ETR1* showed that AHL-treated *Arabidopsis* plants are independent of JA/ET pathway (Schenk et al. 2014).
3. Induction of stomatal defence response – The induction of SA/*cis*-OPDA pathway enhanced the stomatal defence response in 3-oxo-C14-HSL-treated *Arabidopsis* plants when encountered with the bacterial pathogen *P. syringae* DC3000 pathovar *tomato* (*Pst*). Stomatal responses such as an increased rate of stomatal closure and reduced open stomata were observed in AHL-pretreated plants (Schenk et al. 2014). The stomatal defence response in AHL-treated plants was independent of ABA pathway, which was revealed by the lack of *RD22*, *RD29* and *RAB18 gene* (Montillet et al. 2013; Schenk et al. 2014).
4. Induction via mitogen-activated protein kinase (MAPK) – The 3-oxo-C14-HSL-treated *Arabidopsis* plant roots induced systemic resistance through altered activation of MAPKs. AHL-treated plants inducted with pathogen-associated molecular pattern (PAMP) flg22 showed altered activation of MAPKs, AtMPK3 and AtMPK6. Further, the altered MAPKs induced high expression of the defence-related WRKY22 and WRKR29 transcription factors, as well as the pathogenesis-related 1 (PR1) gene (Schikora et al. 2011).
5. Induction via cell wall reinforcement – In 3-oxo-C14-HSL-treated *Arabidopsis* plants,

increased level of cell wall components such as callose, phenolic compounds and lignin was observed, which induced resistance through cell wall reinforcement (Schenk et al. 2014). When encountered with fungal plant pathogen *B. graminis* f. sp. *hordei*, 3-oxo-C14-HSL-treated barley plants showed induced resistance by the formation of papilla (cell wall apposition) structures, as a result of reactive oxygen species (ROS) accumulation (Schikora et al. 2011). Likewise, inoculation with 3-oxo-C14-HSL-producing *S. meliloti*, as well as pretreatment with the pure 3-oxo-C14-HSL molecule, primed barley and wheat plants for enhanced reactive oxygen species (ROS) production, which resulted in papilla formation and hence induced the defence response (Hernandez-Reyes et al. 2014).

### 9.6.2 Role of AHL in Plant Development

The growth promotion activity mediated by AHL signal molecules majorly depended on the induction of phytohormone auxin (von Rad et al. 2008; Bai et al. 2012; Liu et al. 2012). The proteome analysis in AHL-treated *M. truncatula* plants showed the accumulation of several auxin-induced proteins and enzymes involved in auxin metabolism (Mathesius et al. 2003). Furthermore, the exposure of 3-oxo-C12-HSL to the roots of transgenic *T. repens* plants with a β-*glucuronidase* (GUS) reporter gene under the promoters auxin-responsive *GH3* promoter and three chalcone synthases substantially increased the expression of auxin-responsive and flavonoid synthesis proteins (Mathesius et al. 2003).

The 3-oxo-C6- and 3-oxo-C8-HSL induced root elongation in *Arabidopsis*, eventually by the elevated expression of two G-protein receptors, namely, Cand2 and Cand7, which are involved in the activation of signal transduction pathways (Jin et al. 2012; Liu et al. 2012). The addition of 3-oxo-C10-HSL to the roots of mung bean actively accelerated the adventitious root formation by the induction of auxin metabolism via increased accumulation of $H_2O_2$, NO and cGMP (Bai et al. 2012).

The response to bacterial AHL QS molecules was very well understood in three different plant species, namely, *Arabidopsis*, barley and tomato. Two different response patterns, i.e. defence and growth stimulation, are induced by long-side-chain or short-side-chain HSLs, respectively. In accordance with plant response and interruption of AHL signals, it becomes clear that AHL signalling is an important factor in determining the outcome of plant-bacteria interaction. Moreover, production of AHL signal molecule is apparent in total microbiome of plants, including rhizobacteria, epiphytic and endophytic bacteria (Hosni et al. 2011; Kimura 2014; Lv et al. 2013). The AHL signals found in many species of legume-nodulating rhizobia are known to regulate phenotypes, including nodulation, nitrogen fixation, growth rate and polysaccharide production, which are all important for the establishment of a successful bacteria-plant symbiosis (Gonzalez and Marketon 2003). The current understanding of plant interaction with bacterial AHLs was limited to only AHL-producing PGPR strains; it is necessary to explore the role of other AHL-producing bacteria associated with plants. The plant growth is also influenced by AHL derivatives, which are obtained by the hydrolysis of AHL molecules through plant enzyme fatty acid amide hydrolase (FAAH). AHLs presented to the roots are taken up by the plants and hydrolyzed to L-homoserine by the enzyme FAAH. The accumulation of AHL derivative, L-homoserine, positively influenced the plant growth through increased level of nutrient uptake via transpiration and enhanced photosynthetic activity (Palmer et al. 2014). Also, bioengineered tobacco and tomato plants with AHL synthases promoted beneficial plant-bacteria interactions, thereby altering the plant growth and tolerance to biotic and abiotic stress (Barriuso et al. 2008; Mae et al. 2001; Scott et al. 2006).

So, future studies in plant-associated AHL-producing pathogenic, endophytic and epiphytic bacteria will reveal whether these groups have

similar effects of modulation in plant development as the rhizobacteria.

## 9.7 Conclusion

AHL defence response in plants may also have an impact on development of biocontrol or biological agents, which are useful in both integrated agriculture management and organic farming. To ensure food security, agriculture industry has to develop modern plant protection strategies, which provide sufficient yield and quality food and reduce impact of chemical pesticides on the environment. The development of biocontrol agents or biological products from beneficial, soil-borne microorganisms could be a competent approach to support agriculture. Moreover, the knowledge of microbe-plant interactions could contribute the success rate of products in natural environment. The bacterial QS molecules could be of use, since both purified AHL molecules and bacteria with increased production of AHLs have an impact on plant defence mechanisms and portrait the agricultural potential of homoserine lactones. Further, studies are needed to refine our understanding of AHL function in plant interactions under field conditions, where the AHL-producing bacteria or AHLs per se could be in a position to compete with other environmental factors.

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