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REVIEW ARTICLE

Molecular communication in the rhizosphere

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Abstract This paper will exemplify molecular communications in the rhizosphere, especially between plants and bacteria, and between bacteria and bacteria. More specifically, we describe signalling pathways that allow bacteria to sense a wide diversity of plant signals, plants to respond to bacterial infection, and bacteria to coordinate gene expression at population and community level. Thereafter, we focus on mechanisms evolved by bacteria and plants to disturb bacterial signalling, and by bacteria to modulate hormonal signalling in plants. Finally, the dynamics of signal exchange and its biological significance we elaborate on the cases of *Rhizobium* symbiosis and *Agrobacterium* pathogenesis.

Keywords Rhizosphere · Signal · Rhizobium · Agrobacterium · Quorum-sensing · Plant hormones · Plantbacteria interactions

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Introduction

This paper will exemplify molecular communications in the rhizosphere, especially between plants and bacteria, and between bacteria and bacteria. More specifically, we describe signalling pathways that allow bacteria to sense a wide diversity of plant signals, plants to respond to bacterial infection, and bacteria to coordinate gene expression at population and community level. Thereafter, we focus on mechanisms evolved by bacteria and plants to disturb bacterial signalling, and by bacteria to modulate hormonal signalling in plants. Finally, the dynamics of signal exchange and its biological significance we elaborate on the cases of *Rhizobium* symbiosis and *Agrobacterium* pathogenesis. For a complete overview of communication in the rhizosphere, we recommend other papers that illustrate plant-plant interactions, and that give additional insights about nitrogen-fixing microorganisms, plant-driven selection of microbes, plant growth promoting microorganisms, and plant pathogens.

Communication in the rhizosphere: mechanisms and functions

How bacteria sense plant signals

The bulk soil is generally a very poor, nutrient-diluted and therefore hostile environment in which nutrient bioavailability is often hampered by the soil biochemistry. Within this nutritional desert, the presence of plant roots provides the means for the formation of true oases with flourishing microbial populations because all roots have the ability to actively secrete low- and high-molecular-weight molecules into the rhizosphere. Root exudation is largely mediated by the root hairs, but also the root cap and apical epidermal cells make a significant contribution. These actively secreted compounds are composed of excretions—waste products from the plants' internal metabolic processes without any identified function—and secretions—a mixture of compounds that facilitate external processes like lubrication or nutrient acquisition. Moreover, root growth is accompanied by sloughing-off of living cells, senescence, cell wounding and leakage from plant cells which represent more passive release mechanisms of diverse components that nonetheless are very important for the provision of carbon in the soil. The compounds released by these processes are termed mucilages and exudates, respectively. Finally, the microbial community actively participates in defining the composition of the rhizosphere by degrading and secreting complex organics compounds, and by lysing plant cells. These types of molecules are part of mucilages and lysates, respectively (Bertin et al. 2003; Somers et al. 2004). The whole of these root-associated components accumulating in the rhizosphere is termed rhizodeposit and it has a large impact on plant growth and soil ecology. Rhizodeposition is a dynamic process that is developmentally regulated and varies with the plant species and cultivar; it is also altered upon biotic and abiotic stress. Moreover, the microbial community influences the composition of the exudates to its advantage (Yang and Crowley 2000; Paterson et al. 2006; Shaw et al. 2006; Yoneyama et al. 2007).

From the above it is clear that root exudates are complex molecular mixtures and in Table 1 the diversity of molecules identified in rhizodeposits is illustrated. Generally, rhizodeposition is involved in primary and secondary plant metabolic processes, nutrient and water acquisition, plant defence and stimulatory or inhibitory interactions with other soil organisms (Bertin et al. 2003). However, depending on their relative abundance, the different components of rhizodeposits also affect the soil microorganisms. It is not difficult to envision that many of these compounds are chemoattractants and welcome nutrients for the microbes living in or nearby the rhizosphere (Somers et al. 2004; Brencic and Winans 2005). Whereas many micro-organisms can only utilise rather general plant metabolites, some bacteria have the capacity to catabolize certain plant secondary metabolites providing a selective advantage to colonize the rhizosphere of specific plants (Savka et al. 2002). Examples of such nutritional mediators are glycosides and aryl-glycosides (Faure et al. 1999, 2001), calystegin (Tepfer et al. 1988; Guntli et al. 1999), certain flavonoids (Hartig et al. 1991), proline (Jiménez-Zurdo et al. 1997), 1-aminocyclopropane-1-carboxylic acid (Penrose and Glick 2001), and homoserine and betaines (Boivin et al. 1990; Goldmann et al. 1991). Another well described effect of often unidentified components of rhizodeposits is the activation of bacterial gene expression culminating in more or less intimate interactions with the producing plant host (Stachel et al. 1985; Koch et al. 2002; Brencic et al. 2005; Brencic and Winans 2005; Cooper 2007; Reddy et al. 2007; Franks et al. 2008; Johnston et al. 2008). Recent genome-wide studies have shown that root exudates modulate the expression of a significant number of bacterial genes of which the function in rhizosphere colonisation and competitiveness had not been anticipated (Mark et al. 2005; Matilla et al. 2007; Yuan et al. 2008b). Moreover, plants have been shown to secrete components that interfere with quorum sensing (Teplitski et al. 2000; Dunn and Handelsman 2002; Gao et al. 2003), a cell-cell signalling mechanism in bacteria that is very important in group-coordinated processes that impact interactions with Eukaryotes (von Bodman et al. 2003; Waters and Bassler 2005). In order to trigger these diverse molecular, physiological and behaviour responses, soil bacteria first have to sense the presence of the root exudates via one- and two-component signal perception systems.

A widespread mechanism by which bacteria sense their environment and respond accordingly is the two-component system which is typically comprised of a usually membrane-bound sensor histidine protein

Table 1 Organic compounds and enzymes released by plants in root exudates and their function in the rhizosphere

Class of compounds	Components	Functions
Sugars	arabinose, desoxyribose, fructose, galactose, glucose, maltose, oligosaccharides, raffinose, rhamnose, ribose, sucrose, xylose, mannitol, complex polysaccharides	lubrication; protection of plants against toxins; chemoattractants; microbial growth stimulation
Amino acids and amides	all 20 proteinogenic amino acids, γ-aminobutyric acid, cystathionine, cystine, homoserine, mugenic acid, ornithine, phytosiderophores, betaine, stachydrine,	inhibit nematodes and root growth; microbial growth stimulation; chemoattractants, osmoprotectants; iron scavengers
Aliphatic acids	acetic, acetonic, aconitic, aldonic, butyric, citric, erythronic, formic, fumaric, gluconic, glutaric, glycolic, isocitric, lactic, maleic, malic, malonic, oxalic, oxaloacetic, oxaloglutaric, piscidic, propionic, pyruvic, shikimic, succinic, tartaric, tetronic, valeric acid	plant growth regulation; chemoattractants; microbial growth stimulation
Aromatic acids	*p*-hydroxybenzoic, caffeic, *p*-coumeric, ferulic, gallic, gentisic, protocatechuic, sinapic, syringic acid	plant growth regulation; chemoattractants
Phenolics	flavanol, flavones, flavanones, anthocyanins, isoflavonoids, acetosyringone	plant growth regulation; allelopathic interactions; plant defence; phytoalexins; chemoattractants; initiate legume-rhizobia, arbuscular mycorrhizal and actinorhizal interactions; microbial growth stimulation; stimulate bacterial xenobiotic degradation
Fatty acids	linoleic, linolenic, oleic, palmitic, stearic acid	plant growth regulation
Vitamins	p-aminobenzoic acid, biotin, choline, *n*-methionylnicotinic acid, niacin, panthothenate, pyridoxine, riboflavin, thiamine	microbial growth stimulation
Sterols	campestrol, cholesterol, sitosterol, stigmasterol	plant growth regulation
Enzymes and proteins	amylase, invertase, phosphatase, polygalacturonase, protease, hydrolase, lectin	plant defence; Nod factor degradation
Hormones	auxin, ethylene and its precursor 1-aminocyclopropaan-1-carboxylic acid (ACC), putrescine, jasmonate, salicylic acid	plant growth regulation
Miscellaneous	unidentified acyl homoserine lactone mimics, saponin, scopoletin, reactive oxygen species, nucleotides, calystegine, trigonelline, xanthone, strigolactones	quorum quenching; plant growth regulation; plant defence; microbial attachment; microbial growth stimulation; initiate arbuscular mycorrhizal interactions

Adapted from Bertin et al. (2003) and Somers et al. (2004)

kinase and a response regulator most often mediating differential gene expression. The structural genes are frequently organised as an operon, although many orphan kinases have been detected in the available bacterial genomes, and both encoded proteins consist of at least two domains. Via an N-terminal input domain the sensor perceives a specific stimulus, which upon interaction results in a conformational change of the cytoplasmic transmitter domain resulting in autophosphorylation at a conserved histidine residue. The activated transmitter domain will then in turn activate the N-terminal receiver domain of the cognate response regulator by phosphotransfer to a conserved aspartate residue. Next, the activated response regulator will mediate a cellular response via its C-terminal effector or output domain mainly by protein-protein interactions or protein-DNA interactions (see Fig. 1). Finally, dephosphorylation of the response regulator brings the system back to the pre-stimulus state (Laub and Goulian 2007). A common variation on this prototypical two-component system is the phosphorelay in which the histidine kinase has an additional receiver-like domain. Such hybrid histidine kinases will, upon signal perception and subsequent autophosphorylation, transfer their phosphoryl group intramolecularly to an aspartate residue in their receiver domain. This phosphoryl group is then transferred to a histidine residue of a cytoplasmic

histidine phosphotransferase which finally shuttles it to the aspartate residue of the terminal response regulator (see Fig. 1a; Hoch and Varughese 2001). Whereas the histidine kinase domains of the sensors and the receiver domains of the response regulators comprise paralogous gene families that share considerable sequence and structural similarity, their input and output domains vary extensively although many conserved modules have been identified (Galperin 2006; Mascher et al. 2006; Szurmant et al. 2007). Classification of the sensor histidine protein kinases based on their domain architecture, reflecting the mechanism of sensing and signal transduction, revealed three major groups: the periplasmic- or

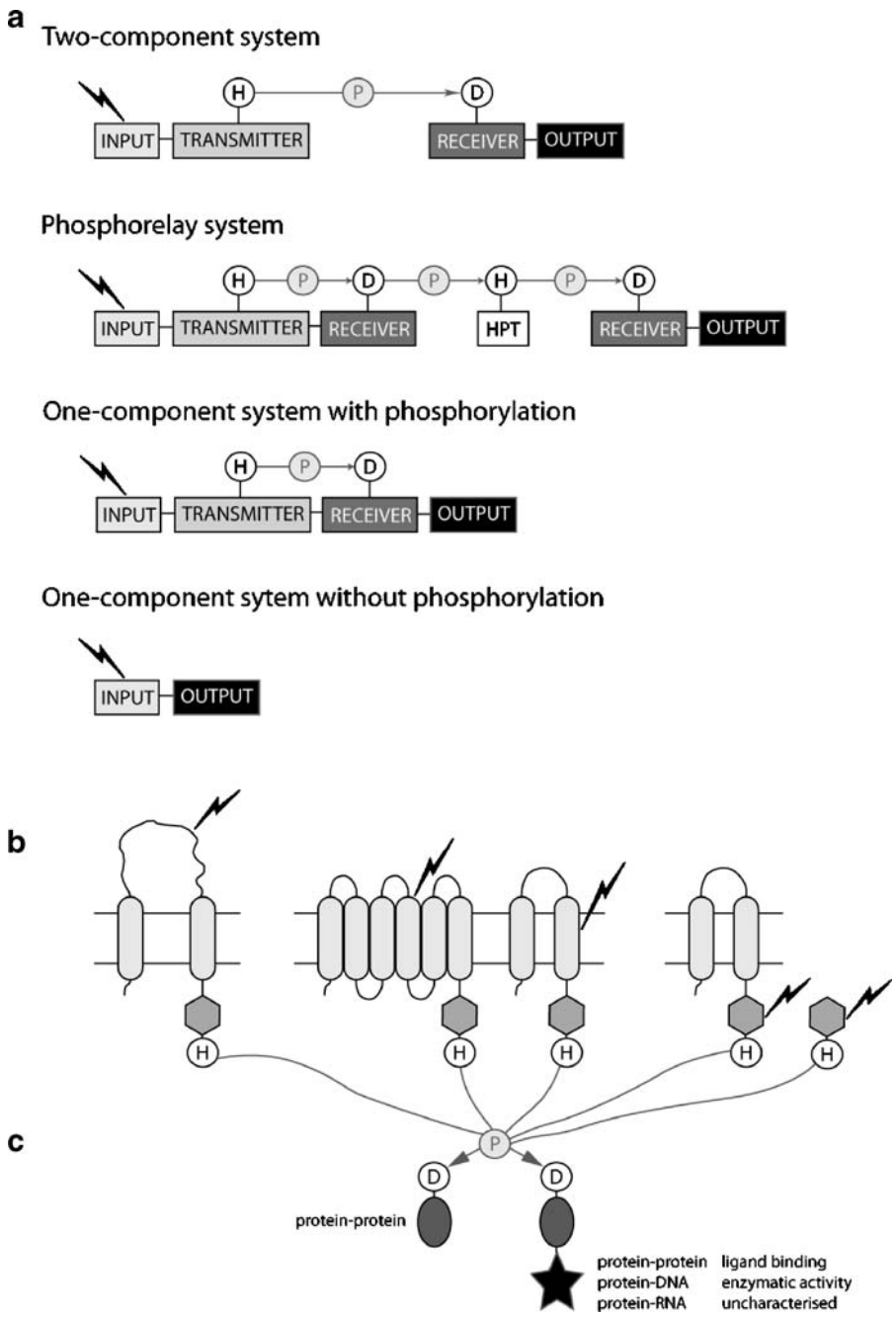

Fig. 1 Different signal perception and transduction mechanisms in bacteria. **a** Overview of the signal transduction systems; **b** Classification of the sensor histidine protein kinases: the periplasmic- or extracellular-sensing histidine kinases (*left*), histidine kinases with sensing mechanisms linked to transmembrane regions (*middle*), and cytoplasmic-sensing histidine kinases (*right*); **c** Classification of the response regulators: stand-alone receiver domains (*left*), and receiver domains combined with an output domain (*right*). H, histidine residue; D, aspartate residue; P, phosphotransfer; HPT, histidine phosphotransferase; lightening flash, incoming signal

extracellular-sensing histidine kinases, histidine kinases with sensing mechanisms linked to transmembrane regions, and cytoplasmic-sensing histidine kinases (see Fig. 1b; Mascher et al. 2006). The first class is the largest and signal detection occurs directly via binding of a small molecule to the sensor domain, indirectly through interaction with a periplasmic solute-binding protein, or via a conformational change of the input domain after a mechanical or electrochemical stimulus. The hybrid histidine kinases of phosphorelay systems belong to this class. Typically, the periplamic sensor kinases recognise solutes and nutrients, and so are part of many two-component systems involved in rhizosphere sensing. The second and smallest class of sensor kinases lack elaborate extracellular input domains and rely mainly on their transmembrane helices for perception of stimuli that are either associated with the membrane or occur within the membrane interphase. The third class groups the cytoplasmic-sensing histidine kinases which can be membrane-anchored or soluble and detect diffusible or internal stimuli (Mascher et al. 2006). A structural classification of the response regulators based on their domain architectures resulted in six major types that reflect their functionality: stand-alone receiver domains, and receiver domains combined with DNA- or RNA-binding, enzymatic, protein- or ligand-binding and uncharacterized output domains (see Fig. 1c; Galperin 2006). The transcriptional regulators with a DNA-binding output domain encompass 75% of all response regulators and typically have a important role in rhizosphere signal transduction.

Although two-component systems have been considered as the paradigm signal perception and transduction systems in prokaryotes, large scale genome analyses have recently shown that a bacterial cell contains a plethora of the much simpler one-component systems (Ulrich et al. 2005). Typically, these systems are single proteins that contain input and output domains, but lack the phosphotransfer histidine kinase and receiver domains (see Fig. 1a). Another type of one-component systems resembles fusions of classical histidine kinases with full-length response regulators and consists of single proteins with input, transmitter, receiver and output domains (see Fig. 1a; Galperin 2006). The repertoire of input and output domains in one-component systems is much more diverse than in two-component systems, with many domains unique for the one-component systems. This finding suggests that one-component systems likely perceive similar stimuli and elicit similar responses as two-component systems; their greater variability however is related to their extensive involvement in cytoplasmic sensing (Ulrich et al. 2005).

The list of one- and mainly two-component systems involved in plant recognition by rhizospheric bacteria is obviously extensive and several of them will be described in detail throughout this chapter. The following examples illustrate that almost every class of sensors and response regulators are involved in rhizosphere sensing. The periplasmic-sensing histidine kinase VirA of *Agrobacterium tumefaciens* recognises acidic pH, phenolic compounds, and monosaccharides (the latter via the periplasmic sugar-binding protein ChvE) released by wounded plant cells and its cognate DNA-binding response regulator VirG activates *vir* gene expression initiating T-DNA transfer (Mukhopadhyay et al. 2004). The GacS hybrid histidine kinase of many proteobacteria recognises environmental signals and activates the transcription factor GacA that controls for instance the biosynthesis of extracellular enzymes and secondary metabolites involved in virulence (Heeb and Haas 2001). The CbrAB system of *Pseudomonas aeruginosa* senses the intracellular carbon/nitrogen ratio via the transmembrane sensor CbrA and CbrB adjusts its catabolism by modulating expression of catabolic operons (Nishijyo et al. 2002); in *Pseudomonas putida*, a CbrAB system is involved in the degradation of IAA (Leveau and Gerards 2008). The membrane-associated cytoplasmic sensor kinase FixL and its cognate response regulator FixJ mediate O_2-controlled gene expression in root-nodulating bacteria (Gilles-Gonzalez and Gonzalez 2004). The soluble sensor CheA with its response regulator CheY controls chemotaxis in many bacteria via protein-protein interactions (Szurmant and Ordal 2004). The best described one-component system implicated in perception of the plant is likely the cytoplasmic possibly membrane-associated NodD protein of rhizobia (Brencic and Winans 2005). It is a LysR type transcription factor that perceives flavonoids and then activates transcription of the *nod* genes that encode the biosynthesis of the lipochito-oligosaccharide Nod factor (Peck et al. 2006).

Although many signal transduction systems have been described and keep on being identified via

genome-wide approaches (Mascher et al. 2006; Qian et al. 2008), a lot of the mechanistic details and the identity of many of the primary stimuli remain to be uncovered. Nevertheless, from the above it is clear that the simple and exchangeable modular design of one- and two-component systems combined with extensive cross-regulation permits bacteria to perform sophisticated information processing allowing them to survive in the dynamic rhizosphere environment.

How plants sense bacteria

Plants evolved complex and diverse mechanisms to sense and respond to bacterial presence. Morphogens such as cytokinines, auxins and Nod factors, can profoundly affect plants. Plants sense Nod factors via receptor kinases of the LysM family (primary Nod factor receptor MtLYK4/NFP, and secondary Nod factor receptor or entry receptor MtLYK3/HCL), upon which a complex signal transduction cascade is triggered involving other extracellular-domain-containing receptors (Jones et al. 2007 and references therein). Plants also respond to presence of bacterial quorum-sensing signals, but the mechanism involved is still unknown (Mathesius et al. 2003; Schuhegger et al. 2006; von Rad et al. 2008). However pathogen-associated molecular patterns (PAMPs) such as lipopolysaccharides (LPS), peptidoglycan, and abundant proteins like the translational factor EF-tu and flagellin, are perceived via specific receptors, the pattern recognition receptors (PRRs). Perception of PAMPS constitutes the primary immune response of plants and is referred as PAMP-triggered immunity (PTI) (Zipfel 2008). Regulatory cascades implicating several classes of kinases activate the PTI. Until today, FLS2 and EFR are the only known PRRs in Arabidopsis; other examples of plant PRRs are very scarce (Zipfel 2008). However, the genome of *Arabidopsis* possesses numerous (hundreds) potential PRRs (Schwessinger and Zipfel 2008). The availability of new genomic resources and novel tools should enable the discovery of additional PRRs from crop species.

In the co-evolution of host-microbe interactions (Chisholm et al. 2008), pathogens acquired the capacity to suppress PTI by interfering with recognition at the plasma membrane or by secreting effector proteins into the plant cell cytosol that alter resistance signalling and PTI. Remarkably, the ability to deliver proteins directly into plant host cells is a common feature among phytopathogens. Bacterial effectors that are released into plant cells can possess enzyme activities, such as proteases and phosphatases, which are responsible for modifying host protein to enhance pathogen virulence and evade detection. Some other effectors are protein chaperones protecting the pathogen itself from these potentially detrimental enzymatic activities or keeping the effector protein unfolded prior to secretion.

In response to the delivery of pathogen effector proteins, plants acquired surveillance proteins (R proteins) to recognize and either directly or indirectly block or modify the properties of bacterial effectors. This response constitutes the secondary immune response of plants and is referred to as effector-triggered immunity (ETI). The connection between PTI and ETI is an emerging field of research. Furthermore, the role of small RNAs in immunity and that of PTI in symbiosis are valuable areas to investigate.

How bacteria sense bacteria

Bacteria have evolved sophisticated mechanisms to coordinate gene expression at population and community levels via the synthesis and perception of diffusible molecules. Because the concentration of the emitted signal in a confined environment reflects the bacterial cell number per volume unit (commonly cell density), such a regulatory pathway was termed quorum sensing (QS) (Fuqua et al. 1994). In an open environment, however, the concentration of the signal reflects both the bacterial cell number and the signal diffusion coefficient. In such open environments, the term diffusion sensing was proposed (Redfield 2002). A recent tentative to unify quorum and diffusion sensing states that the perception of a signal by a cell (efficiency sensing) is modulated by three essential factors: cell density (quorum sensing), mass-transfer properties (diffusion sensing), and spatial distribution of the cells (Hense et al. 2007). However, additional environmental factors may directly modify the synthesis rate and stability of the signals in the rhizosphere, which will be discussed in a latter paragraph.

The nature of QS signals is highly diverse (Schaefer et al. 2008; Whitehead 2001). Oligopeptides and substituted gamma-butyrolactones have been described in Gram-positive bacteria, while other substituted

gamma-butyrolactones, the N-acyl-homoserine lactones (AHLs), are synthesized by a large number of Gram-negative bacteria. In this latter bacterial group, 3-hydroxypalmitic acid methyl ester (Flavier et al. 1997), 3,4-dihydroxy-2-heptylquinoline (Holden et al. 1999), and a furanosyl borate diester (Chen et al. 2002) can also act as QS signals. The most studied QS signals among rhizobacteria are AHLs (Whitehead et al. 2001). The synthesis of AHL depends upon synthases generally belonging to two classes: the LuxI and the AinS homologs. The perception of the signal relies on a sensor protein, a LuxR homolog, which is also the transcriptional regulator controlling the expression of QS-regulated genes.

The rhizosphere is potentially favorable for QS signalling, because it is a spatially structured habitat that is colonized, at a high cell density, by diverse bacterial populations. Experimental evidence supports this assertion. Ten to twenty percent of the cultivable bacteria in soil and rhizospheric environments are AHL-producing (D'Angelo-Picard et al. 2004). They are able to communicate both at the intra- and inter-species level (Steidle et al. 2001, 2002). Moreover, AHL signalling is implicated in the manifestation of plant-associated phenotypes in pathogenic, symbiotic, and biocontrol bacterial strains. The functions controlled by QS are highly diverse, including the horizontal transfer of plasmids, and the regulation of rhizospheric competence factors such as antibiotics, as well as functions that are directly implicated in plant-bacteria associations, such as virulence factors (Whitehead et al. 2001).

The AHL QS-signals show variations in the length and side chains of a core structure, and each AHL receptor can recognize a specific AHL structure. Even though some correlation exists between the genetic position of a strain or a group of strains and their AHL production patterns (D'Angelo et al. 2005), most AHL profiles are not strictly conserved at the genus or species level. Indeed, some phylogenetically distant species exhibit similar AHL profiles, supporting inter-species communication. Several explanations may account for this phenomenon. At the molecular level, the amino acid sequences of the AHL synthases are sometimes more distant within one species than between distinct species (Gray and Garey 2001). At the ecological and evolutionary levels, the presence of multiple AHL synthase homologues in species such as in Rhizobium legumi-nosarum (González and Marketon 2003) and the fact that multiple *luxI-luxR* determinants in a bacterium may be acquired independently (Gray and Garey 2001), can explain the occurrence of these complex patterns of AHLs. As an example, in the genus *Rhizobium*, some strains produce a single AHL, while others synthesize several AHLs (González and Marketon 2003). Such heterogeneity within AHL profiles may result from a selective pressure that tends to stimulate the emergence of distinct molecular languages at sub-species level, especially when related organisms share common ecological niches. An alternative explanation calls for another selective pressure that would authorize inter-species cooperation. One can not exclude the possibility that bacterial populations use distinct communication pathways to discriminate different levels of genetic proximity (clone, population and community). One of the QS signals facilitating communication at community level would be a furanosyl borate diester (AI-2) that is synthesized and recognized by a large range of Gram-positive and Gram-negative bacteria (Chen et al. 2002). The multiplicity of QS-signals, their interconnection and their modulation by environmental factors, especially the plant host, as well as spatial and temporal constraints remain to be elaborated.

How bacteria and plants interfere with bacterial signals

Bacteria and plants, as well as their genetically modified derivatives generated for research and biotechnological purposes, can produce QS-signal biomimics or QS-interfering molecules, including QS-signal modifying enzymes (Dong et al. 2007). The term quorum quenching (QQ) encompasses various natural phenomena or engineered procedures that lead to the perturbation of the expression of QS-regulated functions.

QS-biomimics were discovered in plants and in bacteria; their function is still speculative (McDouglas et al. 2007). In contrast, numerous reports evaluated QQ mechanisms, their function *in vivo*, and their potential agricultural applications (Dong et al. 2007). The three main steps of QS regulation that seem to be targeted are signal synthesis, and the much better described signal stability and sensing. For instance, the red algae *Delisea pulchra* limits bacterial colonization (fouling) of its lamina by interfering with the

QS-controlled motility and biofilm-formation ability. This process is mediated by halogenated furanones produced by the algae that bind the bacterial LuxR receptor, prevent the binding of or displace the AHL signal, and thereby accelerate the degradation of the LuxR protein (Rasmussen and Givskov 2006). Other inhibitors have been found in plants such as pea and soybean, Medicago, fruit extracts such as those from grape and strawberry, garlic, vanilla, lily and pepper, *Clematis vitalba*, *Geranium molle*, and *Tropaeolum majusi* (Rasmussen and Givskov 2006). Fungi such as *Penicillum* species also produce inhibitors of QS, identified as the lactones patulin and penicillic acid (Rasmussen et al. 2005). Interestingly, patulin naturally occurs in fruits such as apple, pear, peach, apricot, banana, pineapple, and grape, where the compound may also contribute to the inhibition of QS. The impact of these molecules on the behavior of rhizobacteria remains to be clarified. Aside from the investigations on natural inhibitors, efforts have been made to identify or design chemical compounds that may target the LuxR-like receptor(s). Most of the designs are based on actual AHL structures and analogues with either activating or inhibitory activity have been identified (Reverchon et al. 2002).

QS-signals are subject to enzymatic degradation. The AHL- lactonases catalyze a reaction that is identical to pH-mediated lactonolysis (opening the gamma-butyrolactone ring), while acylases/amidohydrolases convert AHL to homoserine lactone and a fatty acid. These enzymatic activities were observed in bacteria such as *Variovorax* (Leadbetter and Greenberg 2000) and *Bacillus* (Dong et al. 2000). Since these pioneer reports, numerous bacteria inactivating AHLs have been identified (Faure and Dessaux 2007). Some dissimilate AHL, i.e. use these substrates as growth substrates, and some do not (Leadbetter and Greenberg 2000; Uroz et al. 2003). To date, AHL inactivation has been described in α-proteobacteria (e.g. *Agrobacterium*, *Bosea*, *Sphingopyxis* and *Ochrobactrum*), β-proteobacteria (e.g. *Variovorax*, *Ralstonia*, *Comamonas*, and *Delftia*), and γ-proteobacteria (e.g. *Pseudomonas* and *Acinetobacter*). AHL inactivation also occurs in Gram-positive strains, both amongst low-G+C% strains or firmicutes such as *Bacillus* and high-G+C% strains or actinobacteria, e.g. *Rhodococcus*, *Arthrobacter*, and *Streptomyces*. *Rhodococcus erythropolis* has lactonase and acylase activies, as well as an oxidoreductase that converts 3-oxo-AHL to 3-hydroxy-AHL, which represents a different AHL-modifying activity that is not sensu stricto degrading (Uroz et al. 2005, 2008). Since the substitution at C3 is crucial for signal specificity, the oxidoreductase leads to a change in or loss of the signaling capability of the QS molecules. Aside from bacteria, AHL-degradation abilities have also been observed in animals (Chun et al. 2004) and plants (Delalande et al. 2005).

Several authors have proposed to take advantage of quenching to develop novel medical and animal therapies or novel biocontrol strategies for plant pathogens (Dong et al. 2007; Rasmussen and Givskov 2006). QQ applications therefore fall into the family of anti-virulence/anti-disease strategies. QQ-enzymes may be also used to identify the QS-regulated functions in bacteria (Smadja et al. 2004). For agricultural developments, the frequently proposed strategies imply the degradation of QS signal by plants and bacteria. They are illustrated by the following examples: (i) plants, which are genetically modified to gain the capacity to inactivate AHL because they express the AHL-lactonase AiiA of *Bacillus*, were more resistant to *Pectobacterium carotovorum* infection than the parental, wild-type plants (Dong et al. 2001); (ii) QQ bacteria were proposed as biocontrol agents to interfere with the virulence of plant pathogens (Uroz et al. 2003); (iii) chemicals that either directly interfere with QS-signalling or stimulate the growth of QQ-bacteria in the treated rhizosphere (Cirou et al. 2007). All QQ strategies were developed in vitro or under greenhouse conditions, so their efficiency in the field remains to be evaluated. However, QQ strategies may also prevent QS-regulated functions in plant benefic bacteria, such as antifungal synthesis by biocontrol strains (Molina et al. 2003).

How bacteria can interfere with plant hormones

Plant hormones control plant growth and development by acting as signal molecules. They affect the spatial and temporal expression of various phenotypes such as plant cell elongation, division, and differentiation. In addition, they play an important role in a plant's response to biotic and abiotic stresses. Several plant-associated bacteria have evolved ways to tap into these hormone signalling pathways and to manipulate plant physiology accordingly and to their own advantage.

One such way is stimulation of hormone synthesis by the plant itself. For example, the pathogenic bacterium *Pseudomonas syringae* pv *tomato* DC3000 is able to induce the biosynthesis of the hormones auxin (Schmelz et al. 2003) and abscisic acid (de Torres-Zabala et al. 2007) in *Arabidopsis thaliana*. Another intriguing example is the ability of bacterial quorum sensing molecules such as AHLs to downregulate auxin-induced genes (Mathesius et al. 2003). A different and well-known type of bacterial manipulation of plant hormone levels is the transfer, integration and expression of bacterial DNA coding for the biosynthesis of auxin and cytokinin in plant tissues, as described for *Agrobacterium tumefaciens* and *A. rhizogenes* (Francis and Spiker 2005).

Another route for exploitation of the plant hormone system is through bacterial synthesis or degradation of plant hormones (Costacurta and Vanderleyden 1995; Patten and Glick 1996; Tsavkelova et al. 2006; Spaepen et al. 2007; Glick et al. 2007). Table 2 shows examples for the five classical plant hormones (Kende and Zeevaart 1997), i.e. auxin (indole 3-acetic acid or IAA), ethylene, abscisic acid (ABA), cytokinin (zeatin) and gibberellin (gibberellic acid or GA). As is clear from the table, every one of these hormones can be synthesized and/or degraded by bacteria. Obviously, our understanding of the pathways, genes, and enzymes underlying bacterial synthesis and/or degradation is biased towards what is known about a small number of intensively studied cases. These include the synthesis of IAA (Patten and Glick 1996; Spaepen et al. 2007) and the activity of 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which lowers ethylene concentrations through degradation of the ethylene precursor ACC (Glick 2005; Glick et al. 2007). Much less is known about other activities, such as the phenomenon of bacterial IAA degradation which has long been recognized but until recently (Leveau and Lindow 2005) did not receive serious attention as a means by which bacteria might affect plant physiology. Only very recently the first bacterial genes for IAA degradation were discovered in a *Pseudomonas putida* species (Leveau and Gerards 2008).

Many bacteria are capable of producing more than one type of plant hormone (Boiero et al. 2007; Karadeniz et al. 2006). Moreover, some bacteria can produce and degrade the same hormone (Leveau and Lindow 2005), produce one and degrade the precursor of another (Patten and Glick 2002), or harbor the genes for more than one biosynthetic pathway, e.g. *Pantoea agglomerans* pv *gypsophilae*, which features an IAM as well as an IPyA biosynthetic pathway for IAA (Manulis et al. 1998). This potential of even single bacterial strains to interfere differently with plant hormone levels remains one of the challenges towards better understanding, predicting, and possibly controlling plant hormone manipulation in complex plant-associated bacterial communities.

Plant signalling and physiology are affected by bacterial hormone synthesis and/or degradation in different ways, depending on the physiological role of the hormone, on the recalcitrance of plant tissue to changes in the hormone pool, and on the magnitude of the hormonal sink or source that these bacteria represent. Bacterially produced IAA may be beneficial or detrimental to plants. In *Azospirillum brasilense* (Dobbelaere et al. 1999) and *P. putida* GR12-2 (Patten and Glick 2002) it enhances root proliferation which results in greater root surface area through which more nutrients and water can be absorbed from the soil. In *P. syringae* pv *savastanoi* (Robinette and Matthysse 1990), *Erwinia chrysanthemi* (Yang et al. 2007) and *Rhodococcus fascians* (Vandeputte et al. 2005), IAA synthesis has been shown to be necessary for pathogenesis. Bacteria with ACC deaminase activity are generally considered beneficial to plants, as they promote root elongation and increase root density (Glick 2005). For cytokinins, it was suggested that bacteria are indispensable to plant growth because they would represent the only source of this type of hormone in plants (Holland 1997). This hypothesis was later rejected however with the discovery of plant genes encoding cytokinin synthesis (Sakakibara and Takei 2002).

From the bacterial perspective, there are several advantages to invest in plant hormone production or degradation. It has been suggested (Robert-Seilaniantz et al. 2007) that plant pathogens benefit from the production of phytohormones as this suppresses plant defense responses. In galls and tumours, production of IAA and cytokinin stimulates cell division, which acts as a sink for exploitable nutrients from other parts of the plant. IAA production may also locally stimulate ethylene biosynthesis, which indirectly prevents water and nutrient losses to the shoot organs above the tumor (Aloni et al. 1995). IAA production or ACC deaminase activity by plant-growth promoting rhizobacteria results in increased root density and therefore more

Table 2 Bacterial synthesis and degradation of plant hormones

Hormone	Pathway	Key enzyme(s)	Gene(s)	Representative species	Reference
IAA	Trp→IAM→IAA	Trp 2-monooxygenase, IAM hydrolase	*iaaM*, *iaaH*	*Agrobacterium tumefaciens*	(Inze et al. 1984)
				Pseudomonas syringae pv. *savastanoi*	(Yamada et al. 1985)
				Bradyrhizobium japonicum (IAM→IAA)	(Sekine et al. 1989)
				Pantoea agglomerans pv. *gypsophilae*	(Clark et al. 1993)
				Pseudomonas syringae pv. *syringae*	(Mazzola and White 1994)
	Trp→IPyA→IAAld→IAA	IPyA decarboxylase	*ipdC*	*Enterobacter cloacae*	(Koga et al. 1991)
				Azospirillum brasilense	(Costacurta et al. 1994)
				Pantoea agglomerans	(Brandl and Lindow 1996)
				Pseudomonas putida	(Patten and Glick 2002)
	Trp→TAM→IAAld→IAA	Trp decarboxylase, TAM oxidase	–	*Bacillus cereus* (Trp → TAM)	(Perley and Stowe 1966)
				Azospirillum brasilense (TAM → IAA)	(Hartmann et al. 1983)
	Trp→IAAld→IAA	Trp side-chain oxidase	–	*Pseudomonas fluorescens*	(Oberhansli et al. 1991)
	Trp→IAN→IAA	IAN nitrilase	*nitA*	*Alcaligenes faecalis*	(Kobayashi et al. 1993)
				Pseudomonas fluorescens	(Kiziak et al. 2005)
	IAA→IAA-Lys	IAA-lysine synthase	*iaaL*	*Pseudomonas savastanoi*	(Glass and Kosuge 1986)
	IAA→Cat→	catechol ortho cleavage into β-ketoadipate pathway	*iac* locus, *catABC-pcaD*	*Pseudomonas putida*	(Leveau and Gerards 2008)
	IAA→Ska→Ind→Sal→Cat	–	–	*Pseudomonas* sp.	(Proctor 1958)
	IAA→Dio→Isa→IsA→Ant	isatin amidohydrolase	–	*Bradyrhizobium japonicum*	(Olesen and Jochimsen 1996)
	IAA→2-FABA→Ant	–	–	unidentified	(Tsubokura et al. 1961)
C_2H_4	Met→KMBA→C_2H_4	methionine transaminase	–	*Escherichia coli*	(Ince and Knowles 1985)
				Agrobacterium rhizogenes	(Kepczynska et al. 2003)
	Glu→2-OG→C_2H_4	ethylene-forming enzyme	*efe*	*Pseudomonas syringae*	(Nagahama et al. 1994)
	ACC→C_2H_4	–	–	*Bacillus* sp.	(Bae and Kim 1997)
	ACC→2-OBA	ACC deaminase	*acdS*	*Agrobacterium rhizogenes*	(Kepczynska et al. 2003)
				Enterobacter cloacae	(Shah et al. 1998)
				Achromobacter, Azospirillum, Burkholderia, Pseudomonas, Ralstonia. Rhizobium, Kluyvera species	(Blaha et al. 2005)
	C_2H_4→CO_2	–	–	*Pseudomonas* sp.	(Kim 2006)
ABA	–	–	–	*Bradyrhizobium japonicum*	(Boiero et al. 2007)
				Azospirillum brasilense	(Perrig et al. 2007)
Z/ZR	AMP→iAMP→Z/ZR	isopentenyl transferase (cytokinin synthase)	*ipt*	*Agrobacterium tumefaciens*	(Akiyoshi et al. 1984)
			ptz	*Pseudomonas savastanoi*	(Powell and Morris 1986)
			etz	*Rhodococcus fascians*	(Crespi et al. 1992)
			fas1	*Erwinia herbicola*	(Lichter et al. 1995)

	tRNA→isopentenyl-tRNA→iAMP→Z/ZR	tRNA:isopentenyl transferase	*miaA*	*Agrobacterium tumefaciens* *Methylobacterium* sp.	(Gray et al. 1996) (Koenig et al. 2002)
	Z/ZR→	cytokinin oxidase/dehydrogenase	*fas5*	*Rhodococcus fascians*	(Galis et al. 2005)
GA	→GA	–	–	*Rhizobium phaseoli*, *Azospirillum* sp. *A. diazotrophicus, H. seropedicae* *Bacillus* sp.	(Rademacher 1994) (Bastian et al. 1998) (Gutierrez-Manero et al. 2001)
	GA→	–	–	Unspecified	(Riviere et al. 1966)

Abbreviations: -, not known, *2-FABA* 2-formaminobenzoylacetic acid, *2-OBA* 2-oxobutyric acid, *2-OG* 2-oxoglutarate, *ABA* abscisic acid, *ACC* 1-aminocyclopropane-1-carboxylic acid, *Ant* anthranilic acid, C_{24} ethylene, *Cat* catechol, *Dio* dioxindole, *GA* gibberellic acid, *Glu* glutamate, *IAA* indole 3-acetic acid, *IAA-Lys* IAA-lysine, *IAAld* indole 3-acetaldehyde, *IAM* indole 3-acetamide, *iAMP* isopentenyl-AMP, *IAN* indole 3-acetonitrile, *Ind* indoxyl, *IPyA* indole 3-pyruvate, *Isa* isatin, *IsA* isatinic acid, *KMBA* 2-keto-4-methylthiobutyric acid, *Sal* salicylic acid, *Ska* skatole, *TAM* tryptamine, *Trp* Tryptophan, *Z* zeatin, *ZR* zeatin riboside

surface to colonize and greater return in root exudation. Several studies have shown that the ability to grow on or in plants is reduced in bacterial mutants unable to produce IAA (Brandl et al. 2001; Suzuki et al. 2003) or ethylene (Weingart et al. 2001), although the basis of this remains unclear.

There might also be other reasons for bacteria to produce or degrade plant hormones. Ethylene, for example, is a fungistatic (Smith 1973), the production of which might help bacteria to compete with fungi for plant-derived nutrients. Similarly, IAA has been shown to be inhibitory at high concentrations to plant-associated bacteria (Liu and Nester 2006). A less obvious reason to degrade plant hormones is that they represent sources of nutrition. For example, *P. putida* 1290 can use IAA as sole source of carbon and energy (Leveau and Lindow 2005). Given the relatively low concentrations of IAA and other hormones in the plant environment, it is doubtful that these compounds contribute greatly to bacterial biomass. However, it is noteworthy that three of the five classic hormones represent sources of nitrogen which might be of importance under conditions of nitrogen limitation. In fact, several of the degrading enzymes listed in Table 2 release readily available nitrogen from plant hormones or their precursors. For example, ACC deaminase produces ammonia, a property that has greatly facilitated the search for bacteria with ACC deaminase activity by selection for growth on ACC as sole source of nitrogen (Penrose and Glick 2003). Similarly, the transaminase enzyme involved in bacterial ethylene production from methionine releases the amino group from methionine as a source of nitrogen for growth (Ince and Knowles 1985). Several bacteria can use IAA as sole source of nitrogen (Leveau and Lindow 2005), but more than one enzymatic step is required for the release of nitrogen from the indole ring.

Degradation and utilization of plant hormones represent an extreme form of hormone inactivation, analogous to IaaL activity which conjugates and biologically inactivates IAA (Glass and Kosuge 1986). However, it is worth noting that the bacterial degradation products of some plant hormones are in turn signal molecules. For example, a *Pseudomonas* sp. from soil (Proctor 1958) was shown to convert IAA to catechol via salicylate, which is a plant hormone (Raskin 1992) involved in the plant response to pathogens. Thus, bacteria may have the

potential to re-circuit certain plant signalling pathways by conversion of one hormone to another. Such bacterially induced re-circuiting may not be limited to plant signalling pathways. For example, the IAA degradation pathway described for *Bradyrhizobium japonicum* (Jensen et al. 1995) and an Alcaligenes sp. (Claus and Kutzner 1983) features isatin, which has a demonstrated signalling function in bacteria, e.g. in biofilm formation by strains of *E. coli* (Lee et al. 2007). Furthermore, there is a growing body of evidence to suggest that IAA can actually act as a signal molecule in bacteria and fungi (Spaepen et al. 2007). For example, IAA induces the expression of genes in *E. coli* related to survival under stress conditions (Bianco et al. 2006), stimulates by a positive feedback mechanism its own synthesis in *Azospirillum* species (Vande Broek et al. 1999), and provokes invasive growth in *Saccharomyces cerevisiae* (Prusty et al. 2004). Thus, the use of hormones as signalling molecules does not appear to be exclusive to plants, but may also underlie part of the communication between bacteria and other microorganism.

Integrative examples

In the rhizobia-plant interaction

The legume rhizosphere has a strong attractive power on rhizobia since abundantly secreted polycyclic aromatic compounds called flavonoids trigger chemotactic responses directing the bacteria to their compatible host (Reddy et al. 2007). Subsequently, specific flavonoids are perceived by the NodD protein, a LysR-type transcription factor, which initiates the transcription of *nod*ulation genes that encode the biosynthetic machinery for the primary bacterial signal, the Nod factor. This lipochitooligosaccharide consists of a β-1,4-linked *N*-acetylglucosamine backbone with four or five residues, carries an acyl chain at the C-2 position at the non-reducing end, and can be decorated at defined positions with acetyl, sulfonyl, carbamoyl, fucosyl or arabinosyl moieties depending on the rhizobial strain (reviewed by D'Haeze and Holsters 2002, 2005). Upon perception of the Nod factors by the plant multiple signal transduction pathways are redirected culminating in the initiation of nodule formation. However, the paramount role of legume flavonoids and rhizobial Nod factors in the initiation of the rhizobium-plant interaction has masked the appreciation of other signals derived from both partners in mediating the onset of a successful interaction. Moreover, it has become increasingly clear that flavonoids play several roles (in addition to *nod* gene induction), and likewise that Nod factors are not only essential for inducing plant responses like root hair curling and cortical cell division (Cooper 2007). The complexity of the molecular dialogue between both partners of the rhizobial symbiosis will be illustrated by two examples: the interaction between Sinorhizobium meliloti and Medicago, and between Rhizobium sp. NGR234 and one of its many hosts.

Typically, the rhizodeposits of alfalfa (*Medicago sativa*) and one of the model legumes, barrel medic (*M. truncatula*), are complex and consist of flavonoids, sugars, amino acids, dicarboxylic acids, hydroxy-aromatic acids, biotin and other vitamins that trigger chemotactic responses in and support growth of their microsymbiotic partner *Sinorhizobium meliloti* (Cooper and Rao 1995; Streit et al. 1996; Heinz et al. 1999). These plant metabolites are sensed and appropriate responses generated via one- and two-component systems, but recently a downstream role for trans-acting riboregulators has been revealed (del Val et al. 2007). The nutritional advantage for the bacteria inhabiting the rhizosphere is reinforced by the secretion of a riboflavin degradation product, lumichrome, by *S. meliloti*. It is suggested that lumichrome enhances root respiration and that the root-evolved CO_2 increases net carbon accumulation improving both plant and bacterial growth, but alternative mechanisms explaining the plant growth stimulatory effect have not been ruled out (Phillips et al. 1999; Matiru and Dakora 2005). Moreover, once a functional nodule is established, bacteroids synthesize rhizopines that are secreted into the rhizosphere and can be utilised by some *S. meliloti* strains, further strengthening the nutritional relation between both partners (Galbraith et al. 1998). At high cell densities long chain acyl homoserine lactones (AHLs), quorum sensing signals secreted by *S. meliloti*, accumulate beyond a threshold level and trigger responses in the population that positively affect the efficiency of root colonisation and nodule invasion, such as the down-regulation of bacterial motility (Hoang et al. 2008) and the production of symbiotically active galactoglucan (Marketon et al. 2003). Unexpectedly it was

shown that the AHLs produced by *S. meliloti* had a strong impact on the proteome of *M. truncatula*, modulating 7% of the total resolved proteins affecting diverse functions such as primary metabolism, protein processing, transcriptional regulation, host defence, hormone responses and cytoskeletal activity (Gao et al. 2003; Mathesius et al. 2003). *M. truncatula* itself produces quorum sensing mimics that can potentially modulate the bacterial behaviour in the rhizosphere (Teplitski et al. 2000), and interestingly, exposure of the roots to AHLs of *S. meliloti* altered the amounts and types of AHL mimics secreted by *M. truncatula* (Mathesius et al. 2003), illustrating a strong interplay between both partners. At this point of the interaction the bacterial population is located close to the root, sufficiently dense and not motile which allows it to colonize the root hairs. Biofilm formation represents the "natural way of life" for bacterial populations because it offers a protective environment and the possibility for co-operative behaviour (Morris and Monier 2003; Lasa 2006). Typically surface polysaccharides play an important role in biofilm maturation (Branda et al. 2005), and in *S. meliloti* cyclic β-glucans are mediating efficient root hair attachment (Dickstein et al. 1988), a first and essential step in biofilm formation. The *nod*D-like gene *syr*M is involved in controlling biosynthesis of succinoglycan, which contributes to the capacity to form highly structured biofilms (Fujishige et al. 2006). Interestingly, it was discovered that core Nod factors synthesized by the common *nod* genes *nod*ABC, and regulated by NodD1 but independent of *nod* gene-inducing plant flavonoids, are also required for biofilm formation and efficient attachment to roots. The core Nod factors apparently facilitate cell-to-cell adhesion which is thought to allow the bacteria to remain closely attached to the roots until, in response to plant inducers, a sufficient localized concentration of the host-specific signalling Nod factor is produced, required for triggering plant developmental processes that mark the onset of the symbiotic interaction (Fujishige et al. 2008). Indeed, upon perception of luteolin by NodD1 (Peck et al. 2006), or non-flavonoid inducers by NodD2 (Phillips et al. 1992; Gagnon and Ibrahim 1998), expression of both the common and the host-specific *nod* genes is activated and fully decorated Nod factors are synthesized (Lerouge et al. 1990). However, the rhizobial response to plant flavonoids goes far beyond the synthesis of host-specific Nod factors. Several genome-wide studies have identified multiple luteolin- or apigenin-induced genes that have no *nod*-box in their promotors and hence do not belong to the *nod* gene family (Barnett et al. 2004; Zhang and Cheng 2006). The function of most these genes awaits elucidation, but these results strongly suggest that the early stages of symbiosis are likely to be more complex than originally anticipated. In a last step of the rhizospheric signalling between *S. meliloti* and its legume host, the localized production of host-specific Nod factors is perceived by the plant via the LysM-type receptor kinases and the subsequent complex signal transduction cascade that culminates in early plant responses such as initiation of cortical cell division, calcium spiking and formation of colonized curled root hairs (Jones et al. 2007 and references therein). From the latter, the bacteria induce inward tip growth of the root hair and via these infection threads gain access to plant tissues, start their endophytic life phase and initiate their journey to the nodule primordium. Although beyond the scope of this chapter, clearly, during this endophytic part of the infection process many signals are exchanged, some of which are identified and known to be involved for instance in formation and progression of the infection threads (Nod factors, EPS and LPS; Jones et al. 2007, 2008), suppression of and protection against plant defence (SPS; Campbell et al. 2002; Ferguson et al. 2005; Jones et al. 2008) and activation of cortical cell division (flavonoids and cytokinins; Gonzalez-Rizzo et al. 2006; Wasson et al. 2006); many signals however remain to be discovered.

As for other legume-rhizobium examples, the signal exchange occurring at the onset of the symbiotic interaction between the promiscuous nodulator *Rhizobium* sp. NGR234 (hereafter NRG234) and one of its over 112 hosts (Pueppke and Broughton 1999) overlaps with the one described above for the *S. meliloti-Medicago* interaction. Indeed, flavonoid and non-flavonoid *nod* gene inducers (Le Strange et al. 1990), rhizopines, bacterial surface polysaccharides (Broughton et al. 2006; Staehelin et al. 2006) and Nod factors are important players in the communication between this bacterium and its host, but other signals play a role also. The Nod factors secreted by NGR234 activate flavonoid release in soybean (Schmidt et al. 1994), and the flavonoids activate transcription of 19 *nod*-box-containing pro-

motors and 147 other genes in a *nod*-box-independent way. Whereas the functions of the latter largely remain to be discovered, the *nod*-box controlled genes encode typical pathways involved in Nod factor biosynthesis, rhizopine catabolism, SPS synthesis and modification, and nitrogen fixation, but also in transcriptional control, hopanoid synthesis, auxin (IAA) production, and type III secretion (Kobayashi et al. 2004). The presence of *nod*-boxes in the promotors of transcriptional regulators creates a complex regulatory network that allows sequential activation of gene expression. In this network, NodD1 is the key regulator of all 19 flavonoid-inducible loci including *syr*M2. SyrM2 in its turn controls the delayed flavonoid-induction of a number of loci that have SyrM binding sites in their promotors. One of these is *nod*D2 of which the gene product is required for the optimal activation of specific-*nod* boxes that control the expression of genes involved in the later stages of the symbiotic interaction. NodD2 also represses *nod*D1 expression, which results in a self-attenuation of the flavonoid-induced regulatory cascade (Kobayashi et al. 2004). Expression of hopanoid biosynthetic genes is NodD1 dependent and thus flavonoid inducible (Kobayashi et al. 2004). These lipids function as membrane reinforcers and could mediate resistance to environmental stress in the soil. However, hopanoids have been discovered in a number of nitrogen-fixing soil bacteria (Kannenberg et al. 1996), and in the actinomycete Frankia they are located in the envelope of specialised nitrogenase-containing vesicles possibly reducing oxygen diffusion and thereby protecting the nitrogenase (Rosa-Putra et al. 2001; Alloisio et al. 2007). Hence, hopanoids might function either during the rhizospheric or the endophytic phase of the symbiotic interaction. NodD1-controlled expression of the response regulator TtsI results in the activation of genes that carry a *tts*-box in their promotors and, amongst others, code for part of a type III secretion system, nodulation outer proteins (Nops) and homologs of effectors of pathogens, and the rhamnan component of LPS (Marie et al. 2004). The proteins secreted via the type III secretion system are rhizobial keys that are needed when the bacteria have entered the root hairs and, upon injection into the plant cells, they are thought to interfere with the eukaryotic cellular metabolism, altering plant defence or signalling networks permitting the continuation of nodule development (Marie et al. 2004; Skorpil et al. 2005). The rhamnose-rich LPS is likely also only implicated in the later stages of the interaction, and could be required for protection against plant defence molecules and for bacterial release from infection threads (Marie et al. 2004; Broughton et al. 2006). Auxin production is widespread amongst plant-associated bacteria including rhizobia, and it is often related to epiphytic fitness and suppression of defence (Prinsen et al. 1991; Robert-Seilaniantz et al. 2007; Spaepen et al. 2007). NGR234 synthesizes IAA via three independent pathways: the indole-3-acetamide, the tryptamine and the indole-3-pyruvic acid pathway. The latter is predominant and expression of the genes encoding this pathway is controlled by the NodD1-SyrM2-NodD2 regulatory circuit implying a function during the later stages of the interaction when a more intimate contact between both partners has been established (Theunis et al. 2004). Although no obvious nodulation phenotype was obtained upon mutation of the indole-3-pyruvic acid pathway, a putative role has been postulated in vascularisation of the nodule tissue, facilitating carbon and nitrogen exchange, or acting as a synergistic factor for other signals (Theunis et al. 2004).

From the above it is clear that the action radius of flavonoids and Nod factors has been underestimated. Moreover, the molecular dialogue between legumes and rhizobia has proven to go far beyond these two established signals. Instead a true communication network is established between both partners reflecting the complexity of setting up a successful interaction in the rhizosphere.

In the agrobacteria-plant interaction

Agrobacterium tumefaciens is a soil α-proteobacterium that can infect a broad range of dicotyledonous plants and transfers an oncogenic DNA fragment, the T-DNA, from its tumour-inducing (Ti) plasmid to the nuclear genome of plants (Gelvin 2000). This natural engineer largely contributed to the enormous advances in plant sciences. In the transformed plant tissues, the expression of T-DNA genes leads to the uncontrolled synthesis of growth regulators, auxin and cytokinins, resulting in the formation of tumours, a phenomenon known as crown gall disease. Three main steps could be proposed to describe the dynamics of the *A. tumefaciens*-plant interaction: (1) the colonization of rhizosphere and plant tissues by virulent and avirulent

(free of Ti plasmid) agrobacteria; (2) the transfer of T-DNA from virulent agrobacteria to plants; (3) the emergence and development of a tumour in which avirulent bacteria may be converted into virulent ones by horizontal transfer of the Ti plasmid. In the course of their interaction, plants and agrobacteria exchange a wide variety of signals including, sugars, amino acids, phenolics, and lactones.

The number of agrobacteria increases (from 100 to 1,000 fold), as the structure of these populations varies, when the plant environment was compared to bulk soil (Sanguin et al. 2006). Agrobacteria can survive inside roots and root nodules (Wang et al. 2006), and invade the plants via vessels and apoplasm (Cubero et al. 2006). Microarray analysis of bacterial diversity revealed the predominance of agrobacteria in rhizosphere of maize (Sanguin et al. 2006). A high diversity of agrobacteria can coexist in one cubic centimetre of soil (Vogel et al. 2003). Commonly, most of the agrobacteria recovered from soil and rhizospheric samples are avirulent, lacking the Ti plasmid (Mougel et al. 2001). However, in conductive soils, virulent strains may dominate (Krimi et al. 2002). Several functions contribute to the capacity of agrobacteria to colonize the root, including motility, chemotaxis, surface characteristics and assimilation of a large spectrum of plant compounds. The genome of *A. tumefaciens* C58 is rich in ABC-genes that would participate in the sensing and transport of a large range of organic and inorganic compounds (Wood et al. 2001).

A complex machinery is required for the transfer of T-DNA to a plant cell. The *A. tumefaciens* VirB/D4 system is an archetypal Type IV secretion system composed of 11 VirB mating pair formation subunits and a VirD4 substrate receptor that form a trans-envelope secretion channel (Christie et al. 2005). The substrate of translocation is a single-stranded copy of the T-DNA that becomes integrated into the plant nuclear genome. Transfer of T-DNA operates in a few of hours (Sykes and Matthysse 1986). The transcription of the *vir* regulon is induced by specific plant-released phenolic compounds in combination with several other stimuli, such as monosaccharides, acidic pH and temperature below 30°C (Brencic and Winans 2005). The VirA-VirG two-component system and ChvE sugar binding protein are involved in the perception of these stimuli. Activation of *vir* genes and T-DNA transfer were observed in wounded and unwounded plant tissues. In unwounded transformed plant tissues, the synthesis of opines from T-DNA genes is observed even in the absence of tumour (Brencic et al. 2005), suggesting that cell division during wound healing may play a role in tumour formation.

T-DNA encodes the synthesis of the plant growth factors, cytokinines and auxin, as well as opines, which are specific growth substrates and signals for the bacteria colonizing the plant host. The cytokinine biosynthesis enzyme, which is encoded by the T-DNA, is targeted to and functions in plastids to shunt the original cytokinine pathway (Sakakibara et al. 2005). This feature illustrates that agrobacteria manipulate several compartments of the plant cells. The emergence and development of a tumour is a complex process in which overproduction of auxin and its gradual, flavonoid-dependent retention in the tissue, play an essential role (Schwalm et al. 2003). Furthermore, high vascularisation and epidermal disruption are associated with the establishment of tumours. These phenomena are linked to the redirection of the nutrient-bearing water flow and carbohydrate delivery for growth of the tumour tissues and the inhabiting bacteria (Wächter et al. 2003).

The synthesis of opines defines a specific microhabitat in the plant host. The assimilation of opines as carbon and nitrogen sources confer a selective advantage to the Ti plasmid harbouring bacteria in plant tumours, the so called opine niche. Some opines, termed conjugative opines, are required for high-rate of synthesis of 3-oxo-octanoyl-homoserine lactone (OC8HSL), a cell-to-cell signal implicated in the QS regulation of the conjugative transfer of the Ti plasmid (Piper et al. 1993). The recipient bacteria for the Ti plasmid may be Ti plasmid free agrobacteria, which represent up to 1% of the total cultivable bacteria in the rhizosphere, as well as other rhizobacteria belonging to different genera, such as *Sinorhizobium*, *Rhizobium*, and *Phyllobacterium* (Teyssier-Cuvelle et al. 1999, 2004). The Ti plasmid confers to these non-*Agrobacterium* hosts the capacity to assimilate opine and, in some instances, to induce tumours on the plant hosts; it also remains transferable to other bacteria (Teyssier-Cuvelle et al. 2004). These data strongly suggest that the Agrobacterium populations may not be unique reservoirs for the maintenance and propagation of the Ti plasmid in the rhizosphere. In addition to conjugation, Ti plasmid copy-number (Li and Farrand 2000) and severity of

tumour symptoms are also subjected to QS regulation (Pappas and Winans 2003; Chevrot et al. 2006). Even though the mechanism that places emergence of tumours under QS regulation remains unknown, anti-virulence strategies targeting QS, termed quorum-quenching, have been proposed to decrease the *Agrobacterium*-induced symptoms on plants (Molina et al. 2003; Chevrot et al. 2006).

In *A. tumefaciens* C58-induced tumours, the conjugative opines, agrocinopines A and B, tightly control the synthesis of the OC8HSL signal at the transcriptional level. The AccR-mediated transcriptional repression of the *arc* (agrocinopine catabolism) operon (*orfA-orfB-splA-traR-mcpA*) of the Ti plasmid is released in the presence of agrocinopines A and B (Beck von Bodman et al. 1992; Piper et al. 1999). The *traR* gene of the *arc* operon encodes the transcriptional regulator TraR that binds OC8HSL and permits the expression of the OC8HSL synthase encoded by the *traI* gene. This latter gene belongs to the *trb* operon, located on the Ti plasmid. The TraR/OC8HSL complex also activates the expression of the *tra* and *rep* operons that are required for conjugative transfer and copy-number amplification, respectively, of the Ti plasmid. However, TraR activity is modulated at the post-translational level by TraM, which directly interacts with TraR (Luo et al. 2000) and thereby prevents the interaction between the TraR/OC8HSL complex and target DNA-sequences of QS-regulated promoters. In the presence of conjugative opines, the antagonistic effect of TraM would be compensated by the high synthesis rate of TraR.

The enzymatic inactivation of OC8HSL by lactonases AttM (Zhang et al. 2002) and AiiB (Carlier et al. 2003) also participates in the fine tuning of QS-controlled functions in *A. tumefaciens* C58. The expression of the lactonase AttM is regulated at the transcriptional level by plant signals, such as gamma-aminobutyrate (GABA) and its by-products such as gamma-hydroxybutyrate (GHB) and succinic semialdehyde (SSA) (Carlier et al. 2004; Chevrot et al. 2006). In wounded tissues and in *A. tumefaciens*-induced plant tumours GABA accumulates to high levels (Deeken et al. 2006). Noticeably, increasing evidences would suggest that GABA plays a key-role in interactions between plants and other organisms, including bacteria, fungi and insects (Shelp et al. 2006). In *A. tumefaciens*, the lactonase-encoding gene *attM* is part of the *attKLM* operon, the expression of which is controlled by the transcription factor AttJ (Zhang et al. 2002). In the presence of SSA and GHB, the repressing activity of AttJ is altered and the *attKLM* operon is expressed (Chai et al. 2007). Although GABA and gamma-butyrolactone (GBL) do not directly alter the repressing activity of AttJ, the expression of *attKLM* is also observed in the presence of these compounds. It is assumed that GABA and GBL are converted to SSA and GHB by *A. tumefaciens* and/or the plant host. In addition to the implication of AttM in the GBL-ring cleavage of OC8HSL, the *attKLM* operon encodes a complete degradation pathway of GBL into succinate, with GHB and SSA as intermediates (Carlier et al. 2004; Chai et al. 2007).

Plants recognize agrobacteria as invaders, and induce plant defense genes; in parallel agrobacteria have developed strategies to avoid plant defenses, including phenolics and reactive oxygen species (Kalogeraki et al. 1999; Citovsky et al. 2007; Saenkham et al. 2007). Noticeabely, benefic bacteria are also able to induce and avoid some chemical plant-defenses (examples in Faure et al. 1995, 1996; Dombrecht et al. 2005; Madhaiyan et al. 2006). *A. thaliana* detects different *A. tumefaciens* effectors, such as a conserved domain of flagellin and the transcriptional factor EF-Tu of A. tumefaciens. Specific receptors belonging to the Leu-rich repeat transmembrane receptor (LRR) family are implicated in perception of these effectors, such as EFR for EF-Tu and FLS2 for flagellin in *A. thaliana* (Chinchilla et al. 2006; Zipfel et al. 2006). Remarkably, Nicotiana benthamiana, a plant unable to perceive EF-Tu, acquires EF-Tu binding sites and responsiveness upon transient expression of the EFR receptor of A. thaliana. The LRR receptor kinase activates the mitogen-activated protein kinases (MAPK) to activate the immune response. One of the phosphorylated targets of MAPK3 is the transcription factor VIP1 that relocalizes from the cytoplasm to the nucleus and regulates the expression of the *PR1* pathogenesis-related gene. *A. tumefaciens* uses a Trojan horse strategy by hijacking VIP1 to import the VirE2 protein (associated with the T-DNA) into the nucleus (Djamei et al. 2007). Finally, two recent studies described the essential role of salicylic acid (SA) and auxin (IAA) in the control of virulence. IAA inhibits the expression of *vir* genes and the growth of *A. tumefaciens* (Liu and Nester 2006). This feature suggests a retro-control of T-DNA transfer by a

product encoded by the T-DNA; therefore IAA avoids the cost—for plant and bacteria— of an additional transformation. However, SA, which accumulates upon bacterial infection, also shuts down the expression of the *vir* regulon (Yuan et al. 2007). Recently, multidisciplinary approaches are taken to give an integrative view of the fascinating A. tumefaciens-plant host interaction (Deeken et al. 2006; Yuan et al. 2008a).

Conclusions and perspectives

A multiplicity of signals controls the responses of plants and their associated organisms in the rhizosphere. The deciphering of the interconnections between all these signals is a future challenge that will be supported by global and fine analytic tools including transcriptomics, proteomics and metabolomics. Moreover, the analysis of temporal and spatial factors in these processes will give more precise insights into the dynamics of the interactions in the rhizosphere. Finally, in addition to model organisms, approaches such as metagenomics (Leveau 2007; Riaz et al. 2008), will take into account the diversity of organisms that communicate in the rhizosphere and the mechanisms implicated in this communication.

References

Akiyoshi DE, Klee H, Amasino RM, Nester EW, Gordon MP (1984) T-DNA of *Agrobacterium tumefaciens* encodes an enzyme of cytokinin biosynthesis. Proc Natl Acad Sci USA 81:5994–5998 doi:10.1073/pnas.81.19.5994

Alloisio N, Felix S, Marechal J et al (2007) *Frankia alni* proteome under nitrogen-fixing and nitrogen-depleted conditions. Physiol Plant 130:440–453 doi:10.1111/j.1399-3054.2007.00859.x

Aloni R, Pradel KS, Ullrich CI (1995) The 3-dimensional structure of vascular tissues in *Agrobacterium tumefaciens*-induced crown galls and in the host stems of *Ricinus communis* L. Planta 196:597–605 doi:10.1007/BF00203661

Bae M, Kim MY (1997) A new alkalophilic bacterium producing ethylene. J Microbiol Biotechnol 7:212–214

Barnett MJ, Tolman CJ, Fisher RF et al (2004) A dual-genome symbiosis chip for coordinate study of signal exchange and development in a prokaryote-host interaction. Proc Natl Acad Sci USA 101:16636–16641 doi:10.1073/pnas.0407269101

Bastian F, Cohen A, Piccoli P, Luna V, Baraldi R, Bottini R (1998) Production of indole-3-acetic acid and gibberellins A(1) and A(3) by *Acetobacter diazotrophicus* and *Herbaspirillum seropedicae* in chemically-defined culture media. Plant Growth Regul 24:7–11 doi:10.1023/A:1005964031159

Beck von Bodman S, Hayman GT, Farrand SK (1992) Opine catabolism and conjugal transfer of the nopaline Ti plasmid pTiC58 are coordinately regulated by a single repressor. Proc Natl Acad Sci USA 89:643–647 doi:10.1073/pnas.89.2.643

Bertin C, Yang X, Weston L (2003) The role of root exudates and allelochemicals in the rhizosphere. Plant Soil 256:67–83 doi:10.1023/A:1026290508166

Bianco C, Imperlini E, Calogero R, Senatore B, Amoresano A, Carpentieri A et al (2006) Indole-3-acetic acid improves *Escherichia coli*'s defences to stress. Arch Microbiol 185:373–382 doi:10.1007/s00203-006-0103-y

Blaha D, Prigent-Combaret C, Mirza MS, Moënne-Loccoz Y (2005) Phylogeny of the 1-aminocyclopropane-1-carboxylic acid deaminase-encoding gene *acdS* in phytobeneficial and pathogenic Proteobacteria and relation with strain biogeography. FEMS Microbiol Ecol 56:455–470 doi:10.1111/j.1574-6941.2006.00082.x

Boiero L, Perrig D, Masciarelli O, Penna C, Cassan F, Luna V (2007) Phytohormone production by three strains of *Bradyrhizobium japonicum* and possible physiological and technological implications. Appl Microbiol Biotechnol 74:874–880 doi:10.1007/s00253-006-0731-9

Boivin C, Camut S, Malpica CA et al (1990) *Rhizobium meliloti* genes encoding catabolism of trigonelline are induced under symbiotic conditions. Plant Cell 2:1157–1170

Branda SS, Vik Å, Friedman L et al (2005) Biofilms: the matrix revisited. Trends Microbiol 13:20–26 doi:10.1016/j.tim.2004.11.006

Brandl MT, Lindow SE (1996) Cloning and characterization of a locus encoding an indolepyruvate decarboxylase involved in indole-3-acetic acid synthesis in *Erwinia herbicola*. Appl Environ Microbiol 62:4121–4128

Brandl MT, Quinones B, Lindow SE (2001) Heterogeneous transcription of an indoleacetic acid biosynthetic gene in *Erwinia herbicola* on plant surfaces. Proc Natl Acad Sci USA 98:3454–3459 doi:10.1073/pnas.061014498

Brencic A, Winans SC (2005) Detection of and response to signals involved in host-microbe interactions by plant-associated bacteria. Microbiol Mol Biol Rev 69:155–194 doi:10.1128/MMBR.69.1.155-194.2005

Brencic A, Angert ER, Winans SC (2005) Unwounded plants elicit *Agrobacterium* vir gene induction and T-DNA transfer: transformed plant cells produce opines yet are tumour free. Mol Microbiol 57:1522–1531 doi:10.1111/j.1365-2958.2005.04763.x

Broughton WJ, Hanin M, Relić B et al (2006) Flavonoid-inducible modifications of rhamnan O antigens are necessary for *Rhizobium* sp. strain NGR234-legume symbiosis. J Bacteriol 188:3654–3663 doi:10.1128/JB.188.10.3654-3663.2006

Campbell GRO, Reuhs BL, Walker GC (2002) Chronic intracellular infection of alfalfa nodules by *Sinorhizobium meliloti* requires correct lipopolysaccharide core. Proc Natl Acad Sci USA 99:3938–3943 doi:10.1073/pnas.062425699

Carlier A, Uroz S, Smadja B, Fray R, Latour X, Dessaux Y, Faure D (2003) The Ti plasmid of *Agrobacterium tumefaciens* harbors an *attM*-paralogous gene, *aiiB*, also encoding N-Acyl homoserine lactonase activity. Appl

Environ Microbiol 69:4989–4993 doi:10.1128/AEM.69.8.4989-4993.2003

Carlier A, Chevrot R, Dessaux Y, Faure D (2004) The assimilation of gamma-butyrolactone in *Agrobacterium tumefaciens* C58 interferes with the accumulation of the N-acyl-homoserine lactone signal. Mol Plant Microbe Interact 17:951–957 doi:10.1094/MPMI.2004.17.9.951

Chai Y, Tsai CS, Cho H, Winans SC (2007) Reconstitution of the biochemical activities of the AttJ repressor and the AttK, AttL, and AttM catabolic enzymes of *Agrobacterium tumefaciens*. J Bacteriol 189:3674–3679 doi:10.1128/JB.01274-06

Chen X, Schauder S, Potier N, Van Dorsselaer A, Pelczer I, Bassler BL, Hughson FM (2002) Structural identification of a bacterial quorum-sensing signal containing boron. Nature 415:545–549 doi:10.1038/415545a

Chevrot R, Rosen R, Haudecoeur E, Cirou A, Shelp BJ, Ron E, Faure D (2006) GABA controls the level of quorum-sensing signal in *Agrobacterium tumefaciens*. Proc Natl Acad Sci USA 103:7460–7464 doi:10.1073/pnas.0600313103

Chinchilla D, Bauer Z, Regenass M, Boller T, Felix G (2006) The Arabidopsis receptor kinase FLS2 binds flg22 and determines the specificity of flagellin perception. Plant Cell 18:465–476 doi:10.1105/tpc.105.036574

Chisholm ST, Coaker G, Day B, Staskawisz BJ (2008) Host-microbe interactions: shaping the evolution of the plant immune response. Cell 124:803–814 doi:10.1016/j.cell.2006.02.008

Christie PJ, Atmakuri K, Krishnamoorthy V, Jakubowski S, Cascales E (2005) Biogenesis, architecture, and function of bacterial type IV secretion systems. Annu Rev Microbiol 59:451–485 doi:10.1146/annurev.micro.58.030603.123630

Chun CK, Ozer EA, Welsh MJ, Zabner J, Greenberg EP (2004) Inactivation of a *Pseudomonas aeruginosa* quorum-sensing signal by human airway epithelia. Proc Natl Acad Sci USA 101:3587–3590 doi:10.1073/pnas.0308750101

Cirou A, Diallo S, Kurt C, Latour X, Faure D (2007) Growth promotion of quorum-quenching bacteria in the rhizosphere of *Solanum tuberosum*. Environ Microbiol 9:1511–1522 doi:10.1111/j.1462-2920.2007.01270.x

Citovsky V, Kozlovsky SV, Lacroix B, Zaltsman A, Dafny-Yelin M, Vyas S, Tovkach A, Tzfira T (2007) Biological systems of the host cell involved in *Agrobacterium* infection. Cell Microbiol 9:9–20 doi:10.1111/j.1462-5822.2006.00830.x

Clark E, Manulis S, Ophir Y, Barash I, Gafni Y (1993) Cloning and characterization of *iaaM* and *iaaH* from *Erwinia herbicola* pathovar *gypsophilae*. Phytopathol 83:234–240 doi:10.1094/Phyto-83-234

Claus G, Kutzner HJ (1983) Degradation of indole by *Alcaligenes* spec. Syst Appl Microbiol 4:169–180

Cooper JE (2007) Early interactions between legumes and rhizobia: disclosing complexity in a molecular dialogue. J Appl Microbiol 103:1355–1365 doi:10.1111/j.1365-2672.2007.03366.x

Cooper JE, Rao JR (1995) Flavonoid metabolism by rhizobia—Mechanisms and products. Symbiosis 19:91–98

Costacurta A, Vanderleyden J (1995) Synthesis of phytohormones by plant-associated bacteria. Crit Rev Microbiol 21:1–18 doi:10.3109/10408419509113531

Costacurta A, Keijers V, Vanderleyden J (1994) Molecular cloning and sequence analysis of an *Azospirillum brasilense* indole-3-pyruvate decarboxylase gene. Mol Gen Genet 243:463–472

Crespi M, Messens E, Caplan AB, Vanmontagu M, Desomer J (1992) Fasciation induction by the phytopathogen *Rhodococcus fascians* depends upon a linear plasmid encoding a cytokinin synthase gene. EMBO J 11:795–804

Cubero J, Lastra B, Salcedo CI, Piquer J, López MM (2006) Systemic movement of *Agrobacterium tumefaciens* in several plant species. J Appl Microbiol 101:412–421 doi:10.1111/j.1365-2672.2006.02938.x

D'Angelo-Picard C, Faure D, Carlier A, Uroz S, Raffoux A, Fray R, Dessaux Y (2004) Bacterial populations in the rhizosphere of tobacco plants producing the quorum-sensing signals hexanoyl-homoserine lactone and 3-oxo-hexanoyl-homoserine lactone. FEMS Microbiol Ecol 51:19–29 doi:10.1016/j.femsec.2004.07.008

D'Angelo-Picard C, Faure D, Penot I, Dessaux Y (2005) Diversity of N-acyl homoserine lactone-producing and -degrading bacteria in soil and tobacco rhizosphere. Environ Microbiol 7:1796–1808 doi:10.1111/j.1462-2920.2005.00886.x

Deeken R, Engelmann JC, Efetova M, Czirjak T, Müller T, Kaiser WM, Tietz O, Krischke M, Mueller MJ, Palme K, Dandekar T, Hedrich R (2006) An integrated view of gene expression and solute profiles of *Arabidopsis* tumors: a genome-wide approach. Plant Cell 18:3617–3634 doi:10.1105/tpc.106.044743

Delalande L, Faure D, Raffoux A, Uroz S, D'Angelo C, Elasri M, Carlier A, Berruyer R, Petit A, Williams P, Dessaux Y (2005) N-Hexanoyl-L-homoserine lactone, a mediator of bacterial quorum-sensing regulation, exhibits a plant-dependent stability in the rhizosphere and may be inactivated by germinating *Lotus corniculatus* seedlings. FEMS Microbiol Ecol 52:13–20 doi:10.1016/j.femsec.2004.10.005

del Val C, Rivas E, Torres-Quesada O et al (2007) Identification of differentially expressed small non-coding RNAs in the legume endosymbiont *Sinorhizobium meliloti* by comparative genomics. Mol Microbiol 66:1080–1091 doi:10.1111/j.1365-2958.2007.05978.x

de Torres-Zabala M, Truman W, Bennett MH, Lafforgue G, Mansfield JW, Egea PR et al (2007) *Pseudomonas syringae* pv. *tomato* hijacks the *Arabidopsis* abscisic acid signalling pathway to cause disease. EMBO J 26:1434–1443 doi:10.1038/sj.emboj.7601575

D'Haeze W, Holsters M (2002) Nod factor structures, responses, and perception during initiation of nodule development. Glycobiology 12:79R–105R doi:10.1093/glycob/12.6.79R

D'Haeze W, Holsters M (2005) Surface polysaccharides enable bacteria to evade plant immunity. Trends Microbiol 12:555–561 doi:10.1016/j.tim.2004.10.009

Dickstein R, Bisseling T, Reinhold V et al (1988) Expression of nodule-specific genes in alfalfa root-nodules blocked blocked at an early stage of development. Genes Dev 2:677–687 doi:10.1101/gad.2.6.677

Djamei A, Pitzschke A, Nakagami H, Rajh I, Hirt H (2007) Trojan horse strategy in *Agrobacterium* transformation: abusing MAPK defense signaling. Science 318:453–456 doi:10.1126/science.1148110

Dobbelaere S, Croonenborghs A, Thys A, Vande Broek A, Vanderleyden J (1999) Phytostimulatory effect of *Azospirillum brasilense* wild type and mutant strains altered in IAA production on wheat. Plant Soil 212:155–164 doi:10.1023/A:1004658000815

Dombrecht B, Heusdens C, Beullens S, Verreth C, Mulkers E, Proost P, Vanderleyden J, Michiels J (2005) Defence of *Rhizobium etli* bacteroids against oxidative stress involves a complexly regulated atypical 2-Cys peroxiredoxin. Mol Microbiol 55:1207–1221 doi:10.1111/j.1365-2958.2005.04457.x

Dong YH, Xu JL, Li XZ, Zhang LH (2000) AiiA, an enzyme that inactivates the acylhomoserine lactone quorum-sensing signal and attenuates the virulence of *Erwinia carotovora*. Proc Natl Acad Sci USA 97:3526–3531 doi:10.1073/pnas.060023897

Dong YH, Wang LH, Xu JL, Zhang HB, Zhang XF, Zhang LH (2001) Quenching quorum-sensing-dependent bacterial infection by an N-acyl homoserine lactonase. Nature 411:813–817 doi:10.1038/35081101

Dong YH, Wang LY, Zhang LH (2007) Quorum-quenching microbial infections: mechanisms and implications. Philos Trans R Soc Lond B Biol Sci 362:1201–1211 doi:10.1098/rstb.2007.2045

Dunn AK, Handelsman J (2002) Towards understanding of microbial communities through analysis of communication networks. Antonie Van Leeuwenhoek 81:565–574 doi:10.1023/A:1020565807627

Faure D, Dessaux Y (2007) Quorum sensing as a target for developing biocontrol strategies towards the plant pathogen *Pectobacterium*. Eur J Plant Pathol 119:353–365 doi:10.1007/s10658-007-9149-1

Faure D, Bouillant M, Bally R (1995) Comparative Study of Substrates and Inhibitors of *Azospirillum lipoferum* and *Pyricularia oryzae* Laccases. Appl Environ Microbiol 61:1144–1146

Faure D, Bouillant ML, Jacoud C, Bally R (1996) Phenolic derivatives related to lignin metabolism as substrates for *Azospirillum* laccase activity. Phytochem 42:357–359 doi:10.1016/0031-9422(95)00869-1

Faure D, Desair J, Keijers V, Bekri MA, Proost P, Henrissat B, Vanderleyden J (1999) Growth of *Azospirillum irakense* KBC1 on the aryl beta-glucoside salicin requires either salA or salB. J Bacteriol 181(10):3003–3009

Faure D, Henrissat B, Ptacek D, Bekri MA, Vanderleyden J (2001) The celA gene, encoding a glycosyl hydrolase family 3 beta-glucosidase in *Azospirillum irakense*, is required for optimal growth on cellobiosides. Appl Environ Microbiol 67:2380–2383 doi:10.1128/AEM.67.5.2380-2383.2001

Ferguson GP, Datta A, Carlson RW et al (2005) Importance of unusually modified lipid A in *Sinorhizobium* stress resistance and legume symbiosis. Mol Microbiol 56:68–80 doi:10.1111/j.1365-2958.2005.04536.x

Flavier AB, Clough SJ, Schell MA, Denny TP (1997) Identification of 3-hydroxypalmitic acid methyl ester as a novel autoregulator controlling virulence in *Ralstonia solanacearum*. Mol Microbiol 26:251–259 doi:10.1046/j.1365-2958.1997.5661945.x

Francis KE, Spiker S (2005) Identification of *Arabidopsis thaliana* transformants without selection reveals a high occurrence of silenced T-DNA integrations. Plant J 41:464–477

Franks A, Mark-Byrne GL, Dow JM et al (2008) A putative RNA-binding protein has a role in virulence in *Ralstonia solanacearum*. Mol Plant Pathol 9:67–72

Fujishige NA, Kapadia NN, De Hoff PL et al (2006) Investigations of *Rhizobium* biofilm formation. FEMS Microbiol Ecol 56:195–205 doi:10.1111/j.1574-6941.2005.00044.x

Fujishige NA, Lum MR, De Hoff PL et al (2008) *Rhizobium* common *nod* genes are required for biofilm formation. Mol Microbiol 67:504–515

Fuqua WC, Winans SC, Greenberg EP (1994) Quorum sensing in bacteria: the LuxR/LuxI family of cell density-responsive transcriptional regulators. J Bacteriol 176:269–275

Gagnon H, Ibrahim RK (1998) Aldonic acids: a novel family of nod gene inducers of *Mesorhizobium loti, Rhizobium lupini* and *Sinorhizobium meliloti*. Mol Plant Microbe Interact 11:988–998 doi:10.1094/MPMI.1998.11.10.988

Galbraith MP, Feng SF, Borneman J et al (1998) A functional myo-inositol catabolism pathway is essential for rhizopine utilization by *Sinorhizobium meliloti*. Microbiology 144:2915–2924

Galis I, Bilyeu K, Wood G, Jameson PE (2005) *Rhodococcus fascians*: shoot proliferation without elevated cytokinins? Plant Growth Regul 46:109–115 doi:10.1007/s10725-005-7752-8

Galperin M (2006) Structural classification of bacterial response regulators: diversity of output domains and domain combinations. J Bacteriol 188:4169–4182 doi:10.1128/JB.01887-05

Gao MS, Teplitski M, Robinson JB et al (2003) Production of substances by *Medicago truncatula* that affect bacterial quorum sensing. Mol Plant Microbe Interact 16:827–834 doi:10.1094/MPMI.2003.16.9.827

Gelvin SB (2000) *Agrobacterium* and plant genes involved in T-DNA transfer and integration. Annu Rev Plant Physiol Plant Mol Biol 51:223–256 doi:10.1146/annurev.arplant.51.1.223

Gilles-Gonzalez MA, Gonzalez G (2004) Signal transduction by heme-containing PAS-domain proteins. J Appl Physiol 96:774–783 doi:10.1152/japplphysiol.00941.2003

Glass NL, Kosuge T (1986) Cloning of the gene for indoleacetic acid-lysine synthetase from *Pseudomonas syringae* subsp *savastanoi*. J Bacteriol 166:598–603

Glick BR (2005) Modulation of plant ethylene levels by the bacterial enzyme ACC deaminase. FEMS Microbiol Lett 251:1–7 doi:10.1016/j.femsle.2005.07.030

Glick BR, Cheng Z, Czarny J, Duan J (2007) Promotion of plant growth by ACC deaminase-containing soil bacteria. Eur J Plant Pathol 119:329–339 doi:10.1007/s10658-007-9162-4

Goldmann A, Boivin C, Fleury V et al (1991) Betaine use by rhizospere bacteria: genes essential for trigonelline, stachydrine, and carnitine catabolism in *Rhizobium meliloti* are located on pSym in the symbiotic region. Mol Plant Microbe Interact 4:571–578

González JE, Marketon MM (2003) Quorum sensing in nitrogen-fixing rhizobia. Microbiol Mol Biol Rev 67:574–592 doi:10.1128/MMBR.67.4.574-592.2003

Gonzalez-Rizzo S, Crespi M, Frugier F (2006) The *Medicago truncatula* CRE1 cytokinin receptor regulates lateral root development and early symbiotic interaction with *Sino-*

rhizobium meliloti. Plant Cell 18:2680–2693 doi:10.1105/tpc.106.043778

Gray KM, Garey JR (2001) The evolution of bacterial LuxI and LuxR quorum sensing regulators. Microbiology 147:2379–2387

Gray J, Gelvin SB, Meilan R, Morris RO (1996) Transfer RNA is the source of extracellular isopentenyladenine in a Ti-plasmidless strain of *Agrobacterium tumefaciens*. Plant Physiol 110:431–438

Guntli D, Heeb M, Moenne-Loccoz Y et al (1999) Contribution of calystegine catabolic plasmid to competitive colonization of the rhizosphere of calystegine-producing plants by *Sinorhizobium meliloti* Rm41. Mol Ecol 8:855–863 doi:10.1046/j.1365-294X.1999.00640.x

Gutierrez-Manero FJ, Ramos-Solano B, Probanza A, Mehouachi J, Tadeo FR, Talon M (2001) The plant-growth-promoting rhizobacteria *Bacillus pumilus* and *Bacillus licheniformis* produce high amounts of physiologically active gibberellins. Physiol Plant 111:206–211 doi:10.1034/j.1399-3054.2001.1110211.x

Hartmann A, Singh M, Klingmuller W (1983) Isolation and characterization of *Azospirillum* mutants excreting high amounts of indoleacetic acid. Can J Microbiol 29:916–923

Hartwig UA, Joseph CM, Phillips DA (1991) Flavonoids released naturally from alfalfa seeds enhance growth rate of *Rhizobium meliloti*. Plant Physiol 95:797–803

Heeb S, Haas D (2001) Regulatory roles of the GacS/GacA two-component system in plant-associated and other Gram-negative bacteria. Mol Plant Microbe Interact 14:1351–1363 doi:10.1094/MPMI.2001.14.12.1351

Heinz EB, Phillips DA, Streit WR (1999) BioS, a biotin-induced, stationary-phase, and possible LysR-type regulator in *Sinorhizobium meliloti*. Mol Plant Microbe Interact 12:803–812 doi:10.1094/MPMI.1999.12.9.803

Hense BA, Kuttler C, Müller J, Rothballer M, Hartmann A, Kreft JU (2007) Does efficiency sensing unify diffusion and quorum sensing? Nat Rev Microbiol 5:230–239 doi:10.1038/nrmicro1600

Hoang HH, Gurich N, González JE (2008) Regulation of motility by the ExpR/Sin quorum-sensing system in *Sinorhizobium meliloti*. J Bacteriol 190:861–971 doi:10.1128/JB.01310-07

Hoch JA, Varughese KI (2001) Keeping signals straight in phosphorelay signal transduction. J Bacteriol 183:4941–4949 doi:10.1128/JB.183.17.4941-4949.2001

Holden MT, Ram Chhabra S, de Nys R, Stead P, Bainton NJ et al (1999) Quorum-sensing cross talk: isolation and chemical characterization of cyclic dipeptides from *Pseudomonas aeruginosa* and other gram-negative bacteria. Mol Microbiol 33:1254–1266 doi:10.1046/j.1365-2958.1999.01577.x

Holland MA (1997) Occam's razor applied to hormonology—are cytokinins produced by plants? Plant Physiol 115:865–868

Ince JE, Knowles CJ (1985) Ethylene formation by cultures of *Escherichia coli*. Arch Microbiol 141:209–213 doi:10.1007/BF00408060

Inze D, Follin A, Vanlijsebettens M, Simoens C, Genetello C, Vanmontagu M et al (1984) Genetic analysis of the individual T-DNA genes of *Agrobacterium tumefaciens*—further evidence that 2 genes are involved in indole-3-acetic-acid synthesis. Mol Gen Genet 194:265–274 doi:10.1007/BF00383526

Jensen JB, Egsgaard H, Vanonckelen H, Jochimsen BU (1995) Catabolism of indole-3-acetic acid and 4-chloroindole-3-acetic and 5-chloroindole-3-acetic acid in *Bradyrhizobium japonicum*. J Bacteriol 177:5762–5766

Jiménez-Zurdo JI, García-Rodríguez FM, Toro N (1997) The *Rhizobium meliloti putA* gene: its role in the establishment of the symbiotic interaction with alfalfa. Mol Microbiol 23:85–93 doi:10.1046/j.1365-2958.1997.1861555.x

Johnson EG, Joshi MV, Gibson DM et al (2007) Cello-oligosaccharides released from host plants induce pathogenicity in scab-causing *Streptomyces* species. Physiol Mol Plant Pathol 7:18–25 doi:10.1016/j.pmpp.2007.09.003

Jones K, Kobayashi H, Davies BW et al (2007) How rhizobial symbionts invade plants: the *Sinorhizobium-Medicago* model. Nat Rev Microbiol 5:619–633 doi:10.1038/nrmicro1705

Jones K, Sharopova N, Lohar DP et al (2008) Differential response of the plant *Medicago truncatula* to its symbiont *Sinorhizobium meliloti* or an exopolysaccharide-deficient mutant. Proc Natl Acad Sci USA 105:704–709 doi:10.1073/pnas.0709338105

Kalogeraki VS, Zhu J, Eberhard A, Madsen EL, Winans SC (1999) The phenolic vir gene inducer ferulic acid is O-demethylated by the VirH2 protein of an *Agrobacterium tumefaciens* Ti plasmid. Mol Microbiol 34:512–522 doi:10.1046/j.1365-2958.1999.01617.x

Kannenberg EL, Perzl M, Muller P et al (1996) Hopanoid lipids in *Bradyrhizobium* and other plant-associated bacteria and cloning of the *Bradyrhizobium japonicum* squalene-hopene cyclase gene. Plant Soil 186:107–112 doi:10.1007/BF00035063

Karadeniz A, Topcuoglu SF, Inan S (2006) Auxin, gibberellin, cytokinin and abscisic acid production in some bacteria. World J Microbiol Biotechnol 22:1061–1064 doi:10.1007/s11274-005-4561-1

Kende H, Zeevaart JAD (1997) The five "classical" plant hormones. Plant Cell 9:1197–1210 doi:10.1105/tpc.9.7.1197

Kepczynska E, Zielinska S, Kepczynski J (2003) Ethylene production by *Agrobacterium rhizogenes* strains in vitro and in vivo. Plant Growth Regul 39:13–17 doi:10.1023/A:1021897203840

Kim JG (2006) Assessment of ethylene removal with *Pseudomonas* strains. J Hazard Mater 131:131–136 doi:10.1016/j.jhazmat.2005.09.019

Kiziak C, Conradt D, Stolz A, Mattes R, Klein J (2005) Nitrilase from *Pseudomonas fluorescens* EBC191: cloning and heterologous expression of the gene and biochemical characterization of the recombinant enzyme. Microbiol 151:3639–3648 doi:10.1099/mic.0.28246-0

Kobayashi M, Izui H, Nagasawa T, Yamada H (1993) Nitrilase in biosynthesis of the plant hormone indole-3-acetic-acid from indole-3-acetonitrile—cloning of the *Alcaligenes* gene and site-directed mutagenesis of cysteine residues. Proc Natl Acad Sci USA 90:247–251 doi:10.1073/pnas.90.1.247

Kobayashi H, Naciri-Graven Y, Broughton WJ et al (2004) Flavonoids induce temporal shifts in gene-expression of *nod-*

box controlled loci in *Rhizobium* sp. NGR234. Mol Microbiol 51:335–347 doi:10.1046/j.1365-2958.2003.03841.x

Koch B, Nielsen TH, Sorensen D et al (2002) Lipopeptide production in *Pseudomonas* sp strain DSS73 is regulated by components of sugar beet seed exudate via the Gac two-component regulatory system. Appl Environ Microbiol 68:4509–4516 doi:10.1128/AEM.68.9.4509-4516.2002

Koenig RL, Morris RO, Polacco JC (2002) tRNA is the source of low-level trans-zeatin production in *Methylobacterium* spp. J Bacteriol 184:1832–1842 doi:10.1128/JB.184.7.1832-1842.2002

Koga J, Adachi T, Hidaka H (1991) Molecular cloning of the gene for indolepyruvate decarboxylase from *Enterobacter cloacae*. Mol Gen Genet 226:10–16 doi:10.1007/BF00273581

Krimi Z, Petit A, Mougel C, Dessaux Y, Nesme X (2002) Seasonal fluctuations and long-term persistence of pathogenic populations of *Agrobacterium* spp. in soils. Appl Environ Microbiol 68:3358–3365 doi:10.1128/AEM.68.7.3358-3365.2002

Lasa I (2006) Towards the identification of the common features of bacterial biofilm development. Int Microbiol 9:21–28

Laub MT, Goulian M (2007) Specificity in two-component signal transduction pathways. Annu Rev Genet 41:121–145 doi:10.1146/annurev.genet.41.042007.170548

Leadbetter JR, Greenberg EP (2000) Metabolism of acyl-homoserine lactone quorum-sensing signals by *Variovorax paradoxus*. J Bacteriol 182:6921–6926 doi:10.1128/JB.182.24.6921-6926.2000

Lee J, Bansal T, Jayaraman A, Bentley WE, Wood TK (2007) Enterohemorrhagic *Escherichia coli* biofilms are inhibited by 7-hydroxyindole and stimulated by isatin. Appl Environ Microbiol 73:4100–4109 doi:10.1128/AEM.00360-07

Lerouge P, Roche P, Faucher C et al (1990) Symbiotic host-specificity of *Rhizobium meliloti* is determined by a sulphated and acylated glucosamine oligosaccharide signal. Nature 344:781–784 doi:10.1038/344781a0

Le Strange KK, Bender GL, Djordjevic MA et al (1990) The *Rhizobium* strain NGR234 *nod*D1 gene product responds to activation by the simple phenolic compounds vanillin and isovanillin present in wheat seedling extracts. Mol Plant Microbe Interact 3:214–220

Leveau JHJ (2007) The magic and menace of metagenomics: prospects for the study of plant growth-promoting rhizobacteria. Eur J Plant Pathol 119:279–300 doi:10.1007/s10658-007-9186-9

Leveau JHJ, Gerards S (2008) Discovery of a bacterial gene cluster for catabolism of the plant hormone indole 3-acetic acid. FEMS Microbiol Ecol 65:238–250 doi:10.1111/j.1574-6941.2008.00436.x

Leveau JHJ, Lindow SE (2005) Utilization of the plant hormone indole-3-acetic acid for growth by *Pseudomonas putida* strain 1290. Appl Environ Microbiol 71:2365–2371 doi:10.1128/AEM.71.5.2365-2371.2005

Li PL, Farrand SK (2000) The replicator of the nopaline-type Ti plasmid pTiC58 is a member of the *repABC* family and is influenced by the TraR-dependent quorum-sensing regulatory system. J Bacteriol 182:179–188

Lichter A, Manulis S, Sagee O, Gafni Y, Gray J, Meilan R et al (1995) Production of cytokinins by *Erwinia herbicola* pv *gypsophilae* and isolation of a locus conferring cytokinin biosynthesis. Mol Plant Microbe Interact 8:114–121

Liu P, Nester EW (2006) Indoleacetic acid, a product of transferred DNA, inhibits vir gene expression and growth of *Agrobacterium tumefaciens* C58. Proc Natl Acad Sci USA 103:4658–4662 doi:10.1073/pnas.0600366103

Luo ZQ, Qin Y, Farrand SK (2000) The antiactivator TraM interferes with the autoinducer-dependent binding of TraR to DNA by interacting with the C-terminal region of the quorum-sensing activator. J Biol Chem 275:7713–7722 doi:10.1074/jbc.275.11.7713

Madhaiyan M, Suresh Reddy BV, Anandham R, Senthilkumar M, Poonguzhali S, Sundaram SP (2006) Plant growth-promoting *Methylobacterium* induces defense responses in groundnut (*Arachis hypogaea* L.) compared with rot pathogens. Curr Microbiol 53:270–276

Manulis S, Haviv-Chesner A, Brandl MT, Lindow SE, Barash I (1998) Differential involvement of indole-3-acetic acid biosynthetic pathways in pathogenicity and epiphytic fitness of *Erwinia herbicola* pv *gypsophilae*. Mol Plant Microbe Interact 11:634–642 doi:10.1094/MPMI.1998.11.7.634

Marie C, Deakin WJ, Ojanen-Reuhs T et al (2004) TtsI, a key regulator of *Rhizobium* species NGR234 is required for type III-dependent protein secretion and synthesis of rhamnose-rich polysaccharides. Mol Plant Microbe Interact 17:958–966 doi:10.1094/MPMI.2004.17.9.958

Mark GL, Dow M, Kiely PD et al (2005) Transcriptome profiling of bacterial responses to root exudates identifies genes involved in microbe-plant interactions. Proc Natl Acad Sci USA 102:17454–17459 doi:10.1073/pnas.0506407102

Marketon MM, Glenn SA, Eberhard A et al (2003) Quorum sensing controls exoplysaccharide production in *Sinorhizobium meliloti*. J Bacteriol 185:325–331 doi:10.1128/JB.185.1.325-331.2003

Mascher T, Helmann JD, Unden G (2006) Stimulus perception in bacterial signal-transducing histidine kinases. Microbiol Mol Biol Rev 70:910–938 doi:10.1128/MMBR.00020-06

Mathesius U, Mulders S, Gao M et al (2003) Extensive and specific responses of a eukaryote to bacterial quorum-sensing signals. Proc Natl Acad Sci USA 100:1444–1449 doi:10.1073/pnas.262672599

Matilla MA, Espinosa-Urgel M, Rodríguez-Herva JJ et al (2007) Genomic analysis reveals the major driving forces of bacterial life in the rhizosphere. Genome Biol 8:R179 doi:10.1186/gb-2007-8-9-r179

Matiru VN, Dakora FD (2005) The rhizosphere signal molecule lumichrome alters seedling development in both legumes and cereals. New Phytol 166:439–444 doi:10.1111/j.1469-8137.2005.01344.x

Mazzola M, White FF (1994) A mutation in the indole-3-acetic-acid biosynthesis pathway of *Pseudomonas syringae* pv *syringae* affects growth in *Phaseolus vulgaris* and syringomycin production. J Bacteriol 176:1374–1382

McDougald D, Rice SA, Kjelleberg S (2007) Bacterial quorum sensing and interference by naturally occurring biomimics. Anal Bioanal Chem 387:445–453 doi:10.1007/s00216-006-0761-2

Molina L, Constantinescu F, Michel L, Reimmann C, Duffy B, Défago G (2003) Degradation of pathogen quorum-sensing molecules by soil bacteria: a preventive and curative bilogical control mechanism. FEMS Microbiol Ecol 1522:1–11

Morris CE, Monier J-M (2003) The ecological significance of biofilm formation by plant-associated bacteria. Annu Rev Phytopathol 41:429–453 doi:10.1146/annurev.phyto.41.022103.134521

Mougel C, Cournoyer B, Nesme X (2001) Novel tellurite-amended media and specific chromosomal and Ti plasmid probes for direct analysis of soil populations of *Agrobacterium* biovars 1 and 2. Appl Environ Microbiol 67:65–74 doi:10.1128/AEM.67.1.65-74.2001

Mukhopadhyay A, Gao R, Lynn DG (2004) Integrating input from multiple signals: The VirA/VirG two-component system of *Agrobacterium tumefaciens*. ChemBioChem 5:1535–1542 doi:10.1002/cbic.200300828

Nagahama K, Yoshino K, Matsuoka M, Sato M, Tanase S, Ogawa T et al (1994) Ethylene production by strains of the plant-pathogenic bacterium *Pseudomonas syringae* depends upon the presence of indigenous plasmids carrying homologous genes for the ethylene-forming enzyme. Microbiology 140:2309–2313

Nishijyo T, Haas D, Itoh Y (2002) The CbrA-CbrB two-component regulatory system controls the utilization of multiple carbon and nitrogen sources in *Pseudomonas aeruginosa*. Mol Microbiol 40:917–931 doi:10.1046/j.1365-2958.2001.02435.x

Oberhansli T, Defago G, Haas D (1991) Indole-3-acetic acid (IAA) synthesis in the biocontrol strain CHA0 of *Pseudomonas fluorescens*—role of tryptophan side-chain oxidase. J Gen Microbiol 137:2273–2279

Olesen MR, Jochimsen BU (1996) Identification of enzymes involved in indole-3-acetic acid degradation. Plant Soil 186:143–149 doi:10.1007/BF00035068

Pappas KM, Winans SC (2003) The RepA and RepB autorepressors and TraR play opposing roles in the regulation of a Ti plasmid *repABC* operon. Mol Microbiol 49:441–455 doi:10.1046/j.1365-2958.2003.03560.x

Paterson E, Gebbing T, Abel C et al (2006) Rhizodeposition shapes rhizosphere microbial community structure in organic soil. New Phytol 173:600–610 doi:10.1111/j.1469-8137.2006.01931.x

Patten CL, Glick BR (1996) Bacterial biosynthesis of indole-3-acetic acid. Can J Microbiol 42:207–220

Patten CL, Glick BR (2002) Role of *Pseudomonas putida* indoleacetic acid in development of the host plant root system. Appl Environ Microbiol 68:3795–3801 doi:10.1128/AEM.68.8.3795-3801.2002

Peck MC, Fisher RF, Long SR (2006) Diverse flavonoids stimulate NodD1 binding to *nod* gene promotors in *Sinorhizobium meliloti*. J Bacteriol 188:5417–5427 doi:10.1128/JB.00376-06

Penrose DM, Glick BR (2001) Levels of ACC and related compounds in exudate and extracts of canola seeds treated with ACC deaminase-containing plant growth-promoting bacteria. Can J Microbiol 47:368–372

Penrose DM, Glick BR (2003) Methods for isolating and characterizing ACC deaminase-containing plant growth-promoting rhizobacteria. Physiol Plant 118:10–15 doi:10.1034/j.1399-3054.2003.00086.x

Perley JE, Stowe BB (1966) Production of tryptamine from tryptophan by *Bacillus cereus*. Biochem J 100:169

Perrig D, Boiero ML, Masciarelli OA, Penna C, Ruiz OA, Cassan FD et al (2007) Plant-growth-promoting compounds produced by two agronomically important strains of *Azospirillum brasilense*, and implications for inoculant formulation. Appl Microbiol Biotechnol 75:1143–1150 doi:10.1007/s00253-007-0909-9

Phillips DA, Joseph CM, Maxwell CA (1992) Trigonelline and stachydrine released from alfalfa seeds activate NodD2 in *Rhizobium meliloti*. Plant Physiol 99:1526–1531

Phillips DA, Joseph CM, Yang GP et al (1999) Identification of lumichrome as a *Sinorhizobium* enhancer of alfalfa root respiration and shoot growth. Proc Natl Acad Sci USA 96:12275–12280 doi:10.1073/pnas.96.22.12275

Piper KR, Beck von Bodman S, Farrand SK (1993) Conjugation factor of *Agrobacterium tumefaciens* regulates Ti plasmid transfer by autoinduction. Nature 362:448–450 doi:10.1038/362448a0

Piper KR, Beck Von Bodman S, Hwang I, Farrand SK (1999) Hierarchical gene regulatory systems arising from fortuitous gene associations: controlling quorum sensing by the opine regulon in *Agrobacterium*. Mol Microbiol 32:1077–1089 doi:10.1046/j.1365-2958.1999.01422.x

Powell GK, Morris RO (1986) Nucleotide sequence and expression of a *Pseudomonas savastanoi* cytokinin biosynthetic gene—homology with *Agrobacterium tumefaciens tmr* and *tzs* loci. Nucleic Acids Res 14:2555–2565 doi:10.1093/nar/14.6.2555

Prinsen E, Chauvaux N, Schmidt J et al (1991) Stimulation of indole-3-acetic acid production in *Rhizobium* by flavonoids. FEBS Lett 282:53–55 doi:10.1016/0014-5793(91)80442-6

Proctor MH (1958) Bacterial dissimilation of indoleacetic acid—new route of breakdown of the indole nucleus. Nature 181:1345–1345 doi:10.1038/1811345a0

Prusty R, Grisafi P, Fink GR (2004) The plant hormone indoleacetic acid induces invasive growth in *Saccharomyces cerevisiae*. Proc Natl Acad Sci USA 101:4153–4157 doi:10.1073/pnas.0400659101

Pueppke SG, Broughton WJ (1999) *Rhizobium* sp. NGR234 and *R. fredii* USDA257 share exceptionally broad, nested host ranges. Mol Plant Microbe Interact 12:293–318 doi:10.1094/MPMI.1999.12.4.293

Qian W, Han ZJ, He CZ (2008) Two-component signal transduction systems of *Xanthomonas* spp.: a lesson from genomics. Mol Plant Microbe Interact 21:151–161 doi:10.1094/MPMI-21-2-0151

Rademacher W (1994) Gibberellin formation in microorganisms. Plant Growth Regul 15:303–314 doi:10.1007/BF00029903

Raskin I (1992) Salicylate, a new plant hormone. Plant Physiol 99:799–803

Rasmussen TB, Givskov M (2006) Quorum sensing inhibitors: a bargain of effects. Microbiology 152:895–904 doi:10.1099/mic.0.28601-0

Rasmussen TB, Skindersoe ME, Bjarnsholt T, Phipps RK, Christensen KB, Jensen PO, Andersen JB, Koch B, Larsen TO, Hentzer M, Eberl L, Hoiby N, Givskov M (2005) Identity and effects of quorum-sensing inhibitors produced by *Penicillium* species. Microbiology 151:1325–1340 doi:10.1099/mic.0.27715-0

Reddy PM, Rendón-Anaya M, de los Dolores Soto del Río M et al (2007) Flavonoids as signaling molecules and regulators of root nodule development. Dynamic Soil. Dyn Plant 1:83–94

Redfield RJ (2002) Is quorum sensing a side effect of diffusion sensing? Trends Microbiol 10:365–370 doi:10.1016/S0966-842X(02)02400-9

Reverchon S, Chantegrel B, Deshayes C, Doutheau A, Cotte-Pattat N (2002) New synthetic analogues of N-acyl homoserine lactones as agonists or antagonists of transcriptional regulators involved in bacterial quorum sensing. Bioorg Med Chem Lett 12:1153–1157 doi:10.1016/S0960-894X(02)00124-5

Riaz K, Elmerich C, Moreira D, Raffoux A, Dessaux Y, Faure D (2008) A metagenomic analysis of soil bacteria extends the diversity of quorum-quenching lactonases. Environ Microbiol 10:560–570 doi:10.1111/j.1462-2920.2007.01475.x

Riviere J, Laboureu P, Sechet M (1966) Bacterial degradation of indole-3-acetic acid and of gibberellin A3 in soil. Ann Physiol Vegetale 8:209

Robert-Seilaniantz A, Navarro L, Bari R et al (2007) Pathological hormone imbalances. Curr Opin Plant Biol 10:372–379 doi:10.1016/j.pbi.2007.06.003

Robinette D, Matthysse AG (1990) Inhibition by *Agrobacterium tumefaciens* and *Pseudomonas savastanoi* of development of the hypersensitive response elicited by *Pseudomonas syringae* pv *phaseolicola*. J Bacteriol 172:5742–5749

Rosa-Putra S, Nalin R, Domenach A-M et al (2001) Novel hopanoids from *Frankia* spp. and related soil bacteria. Eur J Biochem 268:4300–4306 doi:10.1046/j.1432-1327.2001.02348.x

Saenkham P, Eiamphungporn W, Farrand SK, Vattanaviboon P, Mongkolsuk S (2007) Multiple superoxide dismutases in *Agrobacterium tumefaciens:* functional analysis, gene regulation, and influence on tumorigenesis. J Bacteriol 189:8807–8817 doi:10.1128/JB.00960-07

Sakakibara H, Takei K (2002) Identification of cytokinin biosynthesis genes in *Arabidopsis*: A breakthrough for understanding the metabolic pathway and the regulation in higher plants. J Plant Growth Regul 21:17–23 doi:10.1007/s003440010043

Sakakibara H, Kasahara H, Ueda N, Kojima M, Takei K, Hishiyama S, Asami T, Okada K, Kamiya Y, Yamaya T, Yamaguchi S (2005) *Agrobacterium tumefaciens* increases cytokinin production in plastids by modifying the biosynthetic pathway in the host plant. Proc Natl Acad Sci USA 102:9972–9977 doi:10.1073/pnas.0500793102

Sanguin H, Remenant B, Dechesne A, Thioulouse J, Vogel TM, Nesme X, Moënne-Loccoz Y, Grundmann GL (2006) Potential of a 16S rRNA-based taxonomic microarray for analyzing the rhizosphere effects of maize on *Agrobacterium* spp. and bacterial communities. Appl Environ Microbiol 72:4302–4312 doi:10.1128/AEM. 02686-05

Savka MA, Dessaux Y, Oger P et al (2002) Engineering bacterial competitiveness and persistence in the phytosphere. Mol Plant Microbe Interact 15:866–874 doi:10.1094/MPMI.2002.15.9.866

Schaefer AL, Greenberg EP, Oliver CM, Oda Y, Huang JJ, Bittan-Banin G, Peres CM, Schmidt S, Juhaszova K, Sufrin JR, Harwood CS (2008) A new class of homoserine lactone quorum-sensing signals. Nature. doi:10.1038/nature07088

Schmelz EA, Engelberth J, Alborn HT, O'Donnell P, Sammons M, Toshima H et al (2003) Simultaneous analysis of phytohormones, phytotoxins, and volatile organic compounds in plants. Proc Natl Acad Sci USA 100:10552–10557 doi:10.1073/pnas.1633615100

Schmidt PE, Broughton WJ, Werner D (1994) Nod factors of *Bradyrhizobium japonicum* and *Rhizobium* sp. NGR234 induce flavonoid accumulation in soybean root exudate. Mol Plant Microbe Interact 7:384–390

Schuhegger R, Ihring A, Gantner S, Bahnweg G, Knappe C, Vogg G, Hutzler P, Schmid M, Van Breusegem F, Eberl L, Hartmann A, Langebartels C (2006) Induction of systemic resistance in tomato by N-acyl-L-homoserine lactone-producing rhizosphere bacteria. Plant Cell Environ 29:909–918 doi:10.1111/j.1365-3040.2005.01471.x

Schwalm K, Aloni R, Langhans M, Heller W, Stich S, Ullrich CI (2003) Flavonoid-related regulation of auxin accumulation in *Agrobacterium tumefaciens*-induced plant tumors. Planta 218:163–178 doi:10.1007/s00425-003-1104-6

Schwessinger B, Zipfel C (2008) News from the frontline: recent insights into PAMP-triggered immunity in plants. Curr Opin Plant Biol 11:1–17 doi:10.1016/j.pbi.2008.06.001

Sekine M, Watanabe K, Syono K (1989) Nucleotide sequence of a gene for indole-3-acetamide hydrolase from *Bradyrhizobium japonicum*. Nucleic Acids Res 17:6400–6400 doi:10.1093/nar/17.15.6400

Shah S, Li JP, Moffatt BA, Glick BR (1998) Isolation and characterization of ACC deaminase genes from two different plant growth-promoting rhizobacteria. Can J Microbiol 44:833–843 doi:10.1139/cjm-44-9-833

Shaw LJ, Morris P, Hooker JE (2006) Perception and modification of plant flavonoid signals by rhizosphere microorganisms. Environ Microbiol 8:1867–1880 doi:10.1111/j.1462-2920.2006.01141.x

Shelp BJ, Bown AW, Faure D (2006) Extracellular gamma-aminobutyrate mediates communication between plants and other organisms. Plant Physiol 142:1350–1352 doi:10.1104/pp.106.088955

Skorpil P, Saad MM, Boukli NM et al (2005) NopP, a phosphorylated effector of *Rhizobium* sp. NGR234, is a major determinant of nodulation of the tropical legumes *Flemingia congesta* and *Tephrosia vogelii*. Mol Microbiol 57:1304–1317 doi:10.1111/j.1365-2958.2005.04768.x

Smadja B, Latour X, Faure D, Chevalier S, Dessaux Y, Orange N (2004) Involvement of N-acylhomoserine lactones throughout the plant infection by *Erwinia carotovora* subsp. *atroseptica* (*Pectobacterium atrosepticum*). Mol Plant Microbe Interact 17:1269–1278 doi:10.1094/MPMI.2004.17.11.1269

Smith AM (1973) Ethylene as a cause of soil fungistasis. Nature 246:311–313 doi:10.1038/246311a0

Somers E, Vanderleyden J, Srinivasan M (2004) Rhizosphere bacterial signalling: a love parade beneath our feet. Crit Rev Microbiol 30:205–240 doi:10.1080/10408410490468786

Spaepen S, Vanderleyden J, Remans R (2007) Indole-3-acetic acid in microbial and microorganism-plant signalling. FEMS Microbiol Rev 31:425–448 doi:10.1111/j.1574-6976.2007.00072.x

Stachel SE, Messens E, Van Montagu M et al (1985) Identification of the signal molecules produced by wounded plant cells that activate T-DNA transfer in *Agrobacterium tumefaciens*. Nature 318:624–629 doi:10.1038/318624a0

Staehelin C, Forsberg LS, D'Haeze W et al (2006) Exo-oligosaccharides of *Rhizobium* sp strain NGR234 are required for symbiosis with various legumes. J Bacteriol 188:6168–6178 doi:10.1128/JB.00365-06

Steidle A, Sigl K, Schuhegger R, Ihring A, Schmid M, Gantner S, Stoffels M, Riedel K, Givskov M, Hartmann A, Langebartels C, Eberl L (2001) Visualization of N-acylhomoserine lactone-mediated cell—cell communication between bacteria colonizing the tomato rhizosphere. Appl Environ Microbiol 67:5761–5770 doi:10.1128/AEM.67.12.5761-5770.2001

Steidle A, Allesen-Holm M, Riedel K, Berg G, Givskov M, Molin S, Eberl L (2002) Identification and characterization of an N-acylhomoserine lactone-dependent quorum-sensing system in *Pseudomonas putida* strain IsoF. Appl Environ Microbiol 68:6371–6382 doi:10.1128/AEM.68.12.6371-6382.2002

Streit WR, Joseph CM, Phillips DA (1996) Biotin and other water-soluble vitamins are key growth factors for alfalfa root colonization by *Rhizobium meliloti* 1021. Mol Plant Microbe Interact 9:330–338

Suzuki S, He YX, Oyaizu H (2003) Indole-3-acetic acid production in *Pseudomonas fluorescens* HP72 and its association with suppression of creeping bentgrass brown patch. Curr Microbiol 47:138–143 doi:10.1007/s00284-002-3968-2

Sykes LC, Matthysse AG (1986) Time required for tumor induction by *Agrobacterium tumefaciens*. Appl Environ Microbiol 52:597–598

Szurmant H, Ordal GW (2004) Diversity in chemotaxis mechanisms among the Bacteria and Archaea. Microbiol Mol Biol Rev 68:301–319 doi:10.1128/MMBR.68.2.301-319.2004

Szurmant H, White RA, Hoch JA (2007) Sensor complexes egulating two-component signal transduction. Curr Opin Struct Biol 17:706–715 doi:10.1016/j.sbi.2007.08.019

Tepfer D, Goldmann A, Pamboukdjian N et al (1988) A plasmid of *Rhizobium meliloti* 41 encodes catabolism of two compounds from root exudate of *Calystegium sepium*. J Bacteriol 170:1153–1161

Teplitski M, Robinson JB, Bauer WD (2000) Plants secrete compounds that mimic bacterial N-acyl homoserine lactone signal activities and affect population density-dependent behaviours in associated bacteria. Mol Plant Microbe Interact 13:637–648 doi:10.1094/MPMI.2000.13.6.637

Teyssier-Cuvelle S, Mougel C, Nesme X (1999) Direct conjugal transfers of Ti plasmid to soil microflora. Mol Ecol 8:1273–1284 doi:10.1046/j.1365-294X.1999.00689.x

Teyssier-Cuvelle S, Oger P, Mougel C, Groud K, Farrand SK, Nesme X (2004) A highly selectable and highly transferable Ti plasmid to study conjugal host range and Ti plasmid dissemination in complex ecosystems. Microb Ecol 48:10–18 doi:10.1007/s00248-003-2023-6

Theunis M, Kobayashi H, Broughton WJ et al (2004) Flavonoids, NodD1, NodD2, and *nod*-box NB15 modulate expression of the y4wEFG locus that is required for indole-3-acetic acid synthesis in *Rhizobium* sp. strain NGR234. Mol Plant Microbe Interact 17:1153–1161 doi:10.1094/MPMI.2004.17.10.1153

Tsavkelova EA, Klimova SY, Cherdyntseva TA, Netrusov AI (2006) Hormones and hormone-like substances of microorganisms: a review. Appl Biochem Microbiol 42:229–235 doi:10.1134/S000368380603001X

Tsubokura S, Sakamoto Y, Ichihara K (1961) Bacterial decomposition of indoleacetic acid. J Biochem 49:38

Ulrich LE, Koonin EV, Zhulin IB (2005) One-component systems dominate signal transduction in prokaryotes. Trends Microbiol 13:52–56 doi:10.1016/j.tim.2004.12.006

Uroz S, Dangelo C, Carlier A, Faure D, Petit A, Oger P, Sicot C, Dessaux Y (2003) Novel bacteria degrading N-acyl homoserine lactones and their use as quenchers of quorum-sensing regulated functions of plant pathogenic bacteria. Microbiology 149:1981–1989 doi:10.1099/mic.0.26375-0

Uroz S, Chhabra SR, Cámara M, Williams P, Oger P, Dessaux Y (2005) N-Acylhomoserine lactone quorum-sensing molecules are modified and degraded by *Rhodococcus erythropolis* W2 by both amidolytic and novel oxidoreductase activities. Microbiol 151:3313–3322 doi:10.1099/mic.0.27961-0

Uroz S, Oger PM, Chapelle E, Adeline MT, Faure D, Dessaux Y (2008) A *Rhodococcus qsdA*-encoded enzyme defines a novel class of large-spectrum quorum-quenching lactonases. Appl Environ Microbiol 74:1357–1366 doi:10.1128/AEM.02014-07

Vande Broek A, Lambrecht M, Eggermont K, Vanderleyden J (1999) Auxins upregulate expression of the indole-3-pyruvate decarboxylase gene in *Azospirillum brasilense*. J Bacteriol 181:1338–1342

Vandeputte O, Oden S, Mol A, Vereecke D, Goethals K, El Jaziri M et al (2005) Biosynthesis of auxin by the gram-positive phytopathogen *Rhodococcus fascians* is controlled by compounds specific to infected plant tissues. Appl Environ Microbiol 71:1169–1177 doi:10.1128/AEM.71.3.1169-1177.2005

Vogel J, Normand P, Thioulouse J, Nesme X, Grundmann GL (2003) Relationship between spatial and genetic distance in *Agrobacterium* spp. in 1 cubic centimeter of soil. Appl Environ Microbiol 69:1482–1487 doi:10.1128/AEM.69.3.1482-1487.2003

von Bodman SB, Bauer WD, Coplin DL (2003) Quorum sensing in plant-pathogenic bacteria. Annu Rev Phytopathol 41:455–482 doi:10.1146/annurev.phyto.41.052002.095652

von Rad U, Klein I, Dobrev PI, Kottova J, Zazimalova E, Fekete A, Hartmann A, Schmitt-Kopplin P, Durner J (2008) Response of *Arabidopsis thaliana* to N-hexanoyl-DL: -homoserine-lactone, a bacterial quorum sensing molecule produced in the rhizosphere. Planta 229:73–85

Wächter R, Langhans M, Aloni R, Götz S, Weilmünster A, Koops A, Temguia L, Mistrik I, Pavlovkin J, Rascher U, Schwalm K, Koch KE, Ullrich CI (2003) Vascularization, high-volume solution flow, and localized roles for enzymes of sucrose metabolism during tumorigenesis by *Agrobacterium tumefaciens*. Plant Physiol 133:1024–1037 doi:10.1104/pp.103.028142

Wang LL, Wang ET, Liu J, Li Y, Chen WX (2006) Endophytic occupation of root nodules and roots of Melilotus dentatus

by *Agrobacterium tumefaciens*. Microb Ecol 52:436–443 doi:10.1007/s00248-006-9116-y

Waters CM, Bassler BL (2005) Quorum sensing: communication in bacteria. Annu Rev Cell Dev Biol 21:319–346 doi:10.1146/annurev.cellbio.21.012704.131001

Weingart H, Ullrich H, Geider K, Volksch B (2001) The role of ethylene production in virulence of *Pseudomonas syringae* pvs. *glycinea* and *phaseolicola*. Phytopathology 91:511–518 doi:10.1094/PHYTO.2001.91.5.511

Whitehead NA, Barnard AML, Slater H, L SNJ, Salmond GPC (2001) Quorum-sensing in Gram-negative bacteria. FEMS Microbiol Rev 25:365–404 doi:10.1111/j.1574-6976.2001.tb00583.x

Wood DW, Setubal JC, Kaul R, Monks DE, Kitajima JP, Okura VK, Zhou Y et al (2001) The genome of the natural genetic engineer *Agrobacterium tumefaciens* C58. Science 294:2317–2323 doi:10.1126/science.1066804

Yamada T, Palm CJ, Brooks B, Kosuge T (1985) Nucleotide sequences of the *Pseudomonas savastanoi* indoleacetic acid genes show homology with *Agrobacterium tumefaciens* T-DNA. Proc Natl Acad Sci USA 82:6522–6526 doi:10.1073/pnas.82.19.6522

Yang CC, Crowley DE (2000) Rhizosphere microbial community structure in relation to root location and plant iron nutritional status. Appl Environ Microbiol 66:345–351

Yang SH, Zhang Q, Guo JH, Charkowski AO, Glick BR, Ibekwe AM et al (2007) Global effect of indole-3-acetic acid biosynthesis on multiple virulence factors of *Erwinia chrysanthemi* 3937. Appl Environ Microbiol 73:1079–1088 doi:10.1128/AEM.01770-06

Yoneyama K, Xie X, Kusumoto D et al (2007) Nitrogen deficiency as well as phosphorus deficiency in sorghum promotes the production and exudation of 5-deoxystrigol, the host recognition signal for arbuscullar mycorrhizal fungi and root parasites. Planta 227:125–132 doi:10.1007/s00425-007-0600-5

Yuan ZC, Edlind MP, Liu P et al (2007) The plant signal salicylic acid shuts down expression of the vir regulon and activates quormone-quenching genes in *Agrobacterium*. Proc Natl Acad Sci USA 104:11790–11795 doi:10.1073/pnas.0704866104

Yuan ZC, Haudecoeur E, Faure D, Kerr KF, Nester EW (2008a) Comparative transcriptome analysis of *Agrobacterium tumefaciens* in response to plant signal salicylic acid, indole-3-acetic acid and gamma-amino butyric acid reveals signalling cross-talk and *Agrobacterium*-plant co-evolution. Cell Microbiol 10:2339–2354 doi:10.1111/j.1462-5822.2008.01215.x

Yuan ZC, Liu P, Saenkham P et al (2008b) Transcriptome profiling and functional analysis of *Agrobacterium tumefaciens* reveals a general conserved response to acidic conditions (pH 5.5) and a complex acid-mediated signaling involved in *Agrobacterium*-plant interactions. J Bacteriol 190:494–507 doi:10.1128/JB.01387-07

Zhang XS, Cheng HP (2006) Identification of *Sinorhizobium meliloti* early symbiotic genes by use of a positive functional screen. Appl Environ Microbiol 72:2738–2748 doi:10.1128/AEM.72.4.2738-2748.2006

Zhang HB, Wang LH, Zhang LH (2002) Genetic control of quorum-sensing signal turnover in *Agrobacterium tumefaciens*. Proc Natl Acad Sci USA 99:4638–4643 doi:10.1073/pnas.022056699

Zipfel C (2008) Pattern-recognition receptors in plant innate immunity. Curr Opin Immunol 20:10–16 doi:10.1016/j.coi.2007.11.003

Zipfel C, Kunze G, Chinchilla D et al (2006) Perception of the bacterial PAMP EF-Tu by the receptor EFR restricts *Agrobacterium*-mediated transformation. Cell 125:749–760 doi:10.1016/j.cell.2006.03.037