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Review

A review: Quorum sensing in *Bradyrhizobium*

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ABSTRACT

Quorum sensing (QS) systems are an important form of cellular communication in bacteria. QS systems are based on the synthesis and secretion of a chemical signal (autoinducer) that accumulates as a function of population growth until reaching a threshold concentration that permits coordinated expression of certain genes that regulate bacterial physiology and behavior. A wide variety of soil bacteria (rhizobia) capable of establishing symbiotic associations with plants produces small chemical signaling molecules to communicate among themselves for physiological adaptation to environmental changes. Most species of rhizobia associated with legume plants have QS systems that regulate their behavior in a variety of soil microhabitats, including the establishment of symbiosis with the host plant. Species of the large, complex genus *Bradyrhizobium* are ecologically and agriculturally important, but present knowledge is limited and fragmentary regarding their QS communication systems, types of autoinducer produced, and biological processes regulated by QS. Therefore, the objective was to review findings to date on QS mechanisms in *Bradyrhizobium*, and the role of these mechanisms in symbiosis development and bacterial survival strategies. Bacteria of genus *Bradyrhizobium* produce a variety of QS signaling molecules, some of which are not found in any other bacterial genus. Of particular interest are the synthesis of bradyoxetin by *Bradyrhizobium* japonicum and its role in symbiosis regulation, and the synthesis of various branched homoserine lactones (HSLs) by other *Bradyrhizobium* species. In peanut-nodulating strains, these HSLs are associated with the processes of biofilm formation, motility, and autoaggregation. A proposed model is presented of QS mechanisms in *Bradyrhizobium* strains and the physiological processes regulated. The findings reviewed here provide a basis for future studies of QS communication systems in rhizobia and of regulatory mechanisms in bacterial behavior and ecophysiology.

Contents

1. Introduction

The high level of organization achieved by many bacterial species is reflected by their ability to synthesize molecules that play important roles in cell signaling mechanisms or regulate the expression of specific genes in response to changes in population

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density. Such processes, termed quorum sensing (QS) (Fuqua and Greenberg, 2002), allow bacteria to coordinate their behavior in response to dynamic changes in the environment (Dong et al., 2008; Bernard et al., 2007). Through QS, bacterial populations are capable of regulating a variety of physiological processes, including bioluminescence, motility, symbiosis, plasmid transfer, antibiotic production, virulence factors, and biofilm formation (González and Marketon, 2003; Sanchez-Contreras et al., 2007; Pierson and Pierson, 2007). The common characteristic is that each of these processes are performed only if the bacterial cell population density is sufficiently high to ensure the success of the communication (Winzer et al., 2002; Atkinson et al., 2007).

QS mechanisms are common in soil bacteria that form associations with plants, and help regulate various aspects of the mechanisms whereby the bacteria–plant interaction is established (Bernard et al., 2007; Parsek and Greenberg, 2005; Whitehead et al., 2001; Dong et al., 2007; White and Winans, 2007). Communication within bacterial populations or communities that are in direct contact with the roots of plants is crucial in determining the physiological status of rhizosphere communities. Thus, QS mechanisms are important for bacterial survival, diversity maintenance, and interactions with plants.

Most rhizobial species have been found to produce one or more molecules associated with a QS system that regulates some aspect of the rhizobia–legume symbiosis (González and Marketon, 2003; Zheng et al., 2006; Sanchez-Contreras et al., 2007). QS mechanisms are involved in numerous symbiosis-related rhizobial functions, including exopolysaccharide (EPS) production, motility, nitrogen fixation, and nodulation (Rinaudi and Giordano, 2010). Despite the clear connection between QS and symbiosis, various rhizobial species with QS gene mutations are capable of establishing effective symbioses with their legume hosts, suggesting that the primary role of the QS system is to promote full development of symbiosis through enhancement of rhizobia–legume interactions. Better understanding of linkages between QS and symbiosis is therefore a valuable tool for improvement of rhizobia–legume interactions at the agroproductive level. Some studies indicate that QS regulatory systems mediated by *N*-acyl-homoserine lactones (acyl-HSLs) are present in rhizobia and regulate various aspects of symbiotic interactions (Sanchez-Contreras et al., 2007). Such acyl-HSLs may serve as signaling molecules between rhizobia and legume hosts. In some cases, the host produces acyl-HSL-mimicking compounds that activate or disrupt rhizobial communication and thereby affect the symbiosis (Sanchez-Contreras et al., 2007; Gao et al., 2003). Acyl-HSL production by the plant-associated genera *Bradyrhizobium*, *Sinorhizobium*, *Rhizobium*, and *Mesorhizobium* is of particular interest in terms of its effect on rhizobia–legume symbiotic interactions.

Various species of *Bradyrhizobium* have great agroecological importance; however, our knowledge of QS communication mechanisms in this group remains fragmentary and ambiguous. One problem in this regard is the complexity of the genus and the mechanisms whereby different species establish symbiosis with different legume hosts. In the soybean symbiont *B. japonicum*, QS mechanisms have been shown to be involved in symbiosis regulation through synthesis of bradyoxetin. Other novel molecules such as acyl branched-HSLs and aryl-HSLs have been isolated from *B. japonicum* and other *Bradyrhizobium* species, but their biological functions have not been studied. Production of acyl-HSLs (well-known signaling molecules) has been reported for peanut-nodulating *Bradyrhizobium* strains and shown to be associated with bacterial survival mechanisms such as biofilm formation, motility, and autoaggregation. QS mechanisms clearly play important agroecological roles in *Bradyrhizobium* species, but the connections between these mechanisms and the physiology of the bacteria are not well understood. In this review article, we summarize current knowledge of QS mechanisms in *Bradyrhizobium*, the biological processes affected by these mechanisms, and the production of novel QS signals. Theoretical models are presented that take into account the available data and provide a basis for future studies.

2. QS and symbiosis

Rhizobia–legume symbiosis is a very specific interaction between the bacteria and the plant that leads to the formation of nitrogen-fixing nodules in plant roots. The development of a successful symbiotic program involves several steps whereby the two partners exchange chemical signals (plant flavonoids/bacterial Nod factors) and various genes are differentially expressed. These processes result in activation of a nodulation program in the plant and coordination of bacterial invasion of the root with initial division of root cortical cells (Oldroyd and Downie, 2004). The symbiotic association is established when differentiated rhizobia inside the nodules (bacteroids) reduce atmospheric nitrogen to ammonium ions that the plant can utilize, and these compounds are exchanged for energy sources from the plant (Gage, 2004; Jones et al., 2007). Biological nitrogen fixation is a crucial process in agricultural food production and long-term productivity of crops under sustainable and environmentally sound programs. Improved understanding of the factors that control this process will help enhance the effectiveness of symbiotic development as a strategy in sustainable agriculture. The simple two-signal model (flavonoids/Nod factors) can be extended to more complex signaling systems that involve both plant and bacterial compounds to direct the course of root colonization (infection) (Cooper, 2007). A variety of physiological mechanisms are controlled by QS in various rhizobial species; these include surface polysaccharide production, growth inhibition, adaptation to stationary phase, nodulation efficiency, symbiosome development, and nitrogen fixation (Sanchez-Contreras et al., 2007). HSL molecules produced by rhizobia that communicate through QS can therefore be regarded as signals involved in the symbiotic programs of the rhizobia.

Bacterial invasion of the plant root in rhizobia–legume symbiosis may occur in two different ways. Plants provide to rhizobia a specific mechanism whereby the bacteria reach the nodule primordium. In most cases, the mechanism involves root-hair curling and the development of "infection threads" (Gage and Margolin, 2000). Another infection mechanism, termed "crack entry", observed in subtropical legumes such as *Arachis* and *Aeschynomene* sp., involves entry of bacteria into the root through epidermal injuries caused by the emergence of lateral roots (Boogerd and van Rossum, 1997). After entry, the rhizobia colonize intercellular spaces in root subepidermal tissue as small populations termed "infection pockets". The invasion process then continues through intercellular bacterial dissemination and entry from the infection pocket to cells of the nodule primordium for direct capture (Boogerd and van Rossum, 1997). Depending on the invasion mechanism, groups of bacteria accumulated in either root-hair curling or infection pockets are the last external populations prior to entry into plant tissues. Such groups may act as signaling centers from which the bacteria produce the amounts of chemical signals (*e.g.*, Nod factors, EPSs, HSLs) necessary to initiate plant responses (Goormachtig et al., 2004). The involvement of QS mechanisms at this stage of the invasion program presumably leads to physiological processes that determine subsequent infection and development of the rhizobia–legume symbiosis.

QS mechanisms have been identified and defined in many rhizobial species of agroecological importance, including *Sinorhizobium meliloti*, *Rhizobium leguminosarum*, *Rhizobium* etli, *Mesorhizobium* spp., and *Bradyrhizobium* spp. These rhizobial QS