4.1 Introduction

In the last 15 years microbiologists have become aware that in most bacteria a major level of regulation exists which involves intercellular communication via the production and response to signal molecules. The concentration of the signal molecules increases alongside the bacterial population density and when it reaches a critical level, when a sufficient number of cells are present, bacteria respond and modulate gene expression. This cell-density-dependent modulation of gene expression has been termed quorum sensing (QS) (Fuqua et al. 1994). This allows bacteria to modify their behavior and act as multicellular entities; it is believed that in natural ecosystems bacteria are always aiming at establishing communities rather than choosing to exist as solitary cells. The reason being that intercellular communication provides significant advantages to a group of bacteria such as improving access to environmental niches, enhancing its defense capabilities against other microorganisms or eukaryotic host-defense mechanisms, and facilitating the adaptation to changing environmental conditions.

Bacterial QS signaling compounds at present can be broadly divided in two main classes, one being produced by Gram-positive bacteria and the other by Gram-negative bacteria. Gram-positive bacteria produce short, usually modified peptides processed from precursors which are then exported out of the cell and are then sensed by the bacterium through a signal transduction cascade (Bassler 2002; Sturme et al. 2002). A typical Gram-negative QS system, on the other hand (Fig. 4.1), involves the production of an acylated homoserine lactone (AHL) which was first described in the marine bioluminescent bacterium *Vibrio fischeri* in which QS regulates light production (Ruby 1996). Other types of less common signaling molecules have also been identified (Barber et al. 1997; Flavier et al. 1997a), including a furanosyl borate diester which appears to be employed by bacteria for interspecies communication (Chen et al. 2002).
Several AHL QS systems have been described for Gram-negative plant-associated bacteria, including *Pseudomonas putida*, *P. chlororaphis/P. aureofaciens*, *P. syringae*, *Burkholderia cepacia*, *B. glumae*, *Erwinia carotovora*, *E. chrysanthemi*, *E. stewartii*, *Ralstonia solanacearum*, *Agrobacterium tumefaciens*, *Rhizobium etli*, *R. leguminosarum*, and *Sinorhizobium meliloti*. Among them, QS is involved in the regulation of antibiotic biosynthesis, extracellular enzymes, antifungal production, plasmid conjugation, biofilm formation, virulence factors, and rhizosphere gene

**Fig. 4.1 a** A typical N-acyl homoserine lactone (AHL) dependent quorum sensing (QS) system in Gram-negative bacteria. The LuxI-type proteins are the main class of enzymes capable of synthesizing AHLs and they use the cellular metabolites S-adenosyl-methionine (SAM) and acetylated acyl carrier proteins (ACP) to form AHLs. At high cell density, the AHL signal accumulates and interacts directly with the LuxR-type protein, inducing a conformational change (usually allowing multimerization) altering the affinity for specific DNA sequences (known as *lux* boxes) at target gene promoters changing gene expression (see text for all details).

**Fig. 4.1 b** Some common AHL signal molecules