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Highlight

What gets turned on in the rhizosphere?

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The rhizosphere, the soil fraction closely associated with plant roots, consists of a complex environment conditioned by plant exudates and abiotic conditions. This zone is rich in microbial activity which takes part in biological and ecological processes important for plant health. As a result, many studies dealing with the rhizosphere focus on microbial ecology and physiology and more specifically on beneficial or pathogenic plant–microbe interactions. Likewise, increasing efforts are being dedicated to understanding the involvement of the rhizosphere in the environment such as its participation in biogeochemical processes (Drigo *et al*., 2008) and in the remediation of environmental contaminants, e.g. rhizoremediation (Böltner *et al*., 2008).

To understand the role of microbes in the panoply of processes and interactions which take place in the rhizosphere, it is essential to know which genes are expressed. The ever-increasing availability of plant and bacterial genome sequences and the development of 'omic' technologies permit genome-wide approaches to unveil either microbial or plant functioning in the rhizosphere. Indeed, much has been done to investigate the global gene expression or transcriptomes of various plants when confronted with pathogens, symbiotic nitrogen-fixing bacteria, plant growth-promoting rhizobacteria (PGPR), or environmental conditions. However, the gene expression of microbes in the rhizosphere is much less studied largely due to the difficulty to obtain sufficient material under controlled conditions in this otherwise highly variable and irregular niche. In this regard, most advances in this area have been made using derivatives of *in vivo* expression technology (IVET) (Ramos-González *et al*., 2005; Rediers *et al*., 2005) while most microbial transcriptomic studies rely on synthetic medium (Mark *et al*., 2005; Yuan *et al*., 2008) or bacteria in plant compartments (i.e. in nitrogen-fixing nodules) (Ampe *et al*., 2003; Becker *et al*., 2004). Thus, global gene expression of rhizobacteria interacting with live roots which would highlight the physiological functioning of microbial cells in the rhizosphere remains to a large extent a 'black box'. Therefore, the recent reports by Matilla and colleagues (2007) and Attila and colleagues (2008a) represent a major step forward to increase our understanding of microbial life in the rhizosphere.

The report by Matilla and colleagues (2007) constitutes the first report on bacterial genomics in the rhizosphere. The authors describe the whole transcriptome analyses of the PGPR *Pseudomonas putida* KT2440 in the rhizosphere of maize. The data obtained suggest that two opposing forces act simultaneously to drive adaptation of this PGPR to life in the rhizosphere: nutrient availability as reflected by the increased expression of genes involved in the uptake of certain carbon and nitrogen sources, and stress adaptation as indicated by the induction of genes coding for stress responses and detoxification proteins. Moreover, plant–bacterial signalling may be reflected by another relevant group of genes induced in the rhizosphere, comprising signal transduction sensors and response regulators, as well as transcriptional regulators. Interestingly, several mutants of genes induced in the rhizosphere were shown to be affected in competition against the wild-type strain to colonize maize roots, indicating that the transcriptome indeed provides insight into genetic expression patterns required for bacterial survival and proliferation in the rhizosphere.

The report by Attila and colleagues (2008a) is of interest for various reasons. First, the report deals with the global gene expression in the rhizosphere not only of the pathogen *Pseudomonas aeruginosa* but also of the model woody plant, poplar, when they interact. Second, the report describes novel plant assays which can be used to test the virulence of animal pathogens, and finally, the authors succeeded in identifying new virulence factors of the bacteria. With regard to the transcriptome analyses, the parallel approach used by the authors advances our knowledge on the complex interactions which take place in the field. Specifically, the authors identified 1770

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differentially expressed genes in poplars exposed to *P. aeruginosa*. Among the functions affected differentially included pathogenesis-related genes, components of signal transduction and transcription factors and plant hormone-responsive genes related to pathogenic attack. On the other hand, Attila and colleagues (2008a) found more than 600 differentially expressed genes of *P. aeruginosa* when colonizing poplar trees. The differentially expressed genes included those involved in type III secretion, metabolism and biosynthesis, motility, adaptation, protection, cell division, transport, transcription and translation regulation, chaperons and membrane proteins. To better understand the role of these genes in the interaction between *P. aeruginosa* and poplar plants, a number of mutants of upregulated genes were tested using the novel poplar wilting and barley germination assays. These assays constitute a useful addition to plant assays used for testing the virulence of animal pathogens (Prithiviraj *et al*., 2005) and have been employed recently to study the role of ion transporters in *P. aeruginosa* virulence (Ueda and Wood, 2008). The battery of mutants of induced genes found by Attila and colleagues (2008a) were also tested for their behaviour in competition, motility, biofilm formation and growth. In this way, seven novel genes involved in plant pathogenesis could be identified including a gene involved in quorum sensing and a haemolysin with haemolytic and cytotoxic effects. Another of these virulence genes was later shown to increase biofilm formation and stimulate virulence by activating pyoverdine synthesis and quorum-sensing phenotypes (Attila *et al*., 2008b).

These seminal reports pave the way for additional studies of gene expression in the rhizosphere which undoubtedly will have major repercussions in the future. Their importance lies not only in the fact that they show that it is possible to study whole transcriptome bacterial gene expression in the rhizosphere but also in the fact that they improve on previous data on the importance of motility, biofilm formation, nutrient acquisition, stress adaptation and complex signalling and regulatory processes in this zone. Predictably, additional bacterial transcriptome studies will be used to study the induction of catabolic pathways in polluted soils undergoing rhizoremediation. Likewise, parallel transcriptomic studies of the plant in plant–microbe interactions will highlight how plants adapt to or actively adjust the microbial populations in the rhizosphere. Together, these studies could lead to assigning functions to unannotated genes and down the road provide applications for improving plant health by protecting against pathogens and improving crop production.

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