

Plant–microbe interactions: manipulating signals to enhance agricultural sustainability and environmental security

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Microorganisms are involved in many functions which impact plant growth, productivity and tissue quality and the signals that control this interaction with plants is critical. These interactions have global implications for the ecology of natural ecosystems and food security through impacts on crops. Some plant–microbe interactions are beneficial, such as those with nitrogen fixing bacteria or mycorrhizal fungi, while others are detrimental such as those with pathogenic bacteria and fungi. The presence of microorganisms in some cases (i.e. mycorrhizal fungi) is critical in order for plants to survive under extremely P-deficient conditions. For these and other reasons, the impact of plant signals on the survival, success, community behavior and function of species of microorganisms and vice versa is of great interest. Study of impacts on the biodiversity and functionality of the microbial biomass in soils and on plant surfaces such as root and leaves yields insight into such systems. If we can gain understanding into how plants and microorganisms communicate with each other, or how their individual signaling pathways interfere with one another at a biochemical, protein and transcriptional level, then we may be able to manipulate both beneficial and detrimental interactions. If we can do this successfully, we may have a range of opportunities to improve agricultural sustainability and environmental security into the future. This special issue will concentrate on the cutting-edge research in this field of plant–microbe interactions with a view to making

recommendations that will enhance agricultural sustainability and food security.

In this special issue we present eight papers, which demonstrate how specific individual and communities of microorganisms, including bacteria and fungi, have profound effects on the traits expressed by, biosynthetic pathways regulated by and transcriptional responses of the host plant. We then go on to present some research which harnesses this understanding to enhance plants resistance to pathogens. The papers present research which is focused on both pathogenic and beneficial microorganisms interacting with a range of host plants including ornamentals, those which produce pharmaceuticals, agricultural plants, both legume and cereals, and model plants. The research also covers the role of microorganisms in general growth promotion and tolerance to biotic stress, disease and fungal infection resistance, and abiotic stress including salt tolerance and promotion of nitrogen fixation. Collectively, this research demonstrates that it is possible to develop a fundamental understanding of the biochemical and molecular signals involved in plant responses to microorganisms and translate this into a predictable plant trait response, which has the potential to enhance a plants tolerance to stress.

With respect to how plant traits respond to microbial signals we present two papers (Patil et al. 2016; Tsavkelova et al. 2016). In Patil et al. (2016), 136 *Pseudomonas* isolates were classified based on plant growth promoting (PGP) traits (production of indole acetic acid and siderophore, phosphate solubilisation, biofilm formation and cyanogenesis) and the 12 best isolates were used for further studies on induction of resistance by seed priming. The isolate JUP121 showed the best disease protection against ragi blast disease. The elevated level of resistance in susceptible ragi plants observed through seed priming was similar to that of the resistant variety. They conclude that

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this can be adopted as a simple strategy to induce resistance in susceptible varieties. Similarly, Tsavkelova et al. (2016) aimed to select the plant growth promoting rhizobacteria (PGPR) for orchid seed germination. By the isolation of rhizoplane and endophytic rhizobacteria from *Dendrobium moschatum* roots, the known PGPR (*Azospirillum*, *Enterobacter*, *Streptomyces*) and less well known (*Roseomonas*, *Agrococcus*) strains were tested for the production of biologically active auxin. It was demonstrated that some isolates (*Streptomyces* and *Azospirillum*. Endophytic *Agrococcus* and *Sphingomonas*) provide significant promotion of orchid germination. Altogether, the data confirms that selection provides a good strategy for choosing the active strains of PGPR for germination of seeds.

We go on to present three papers that demonstrate the influence of microbes on plant biosynthetic pathways (Zheng et al. 2016; Islam et al. 2016; Garg and Singla 2016) associated with accumulation of valuable metabolites and enhanced tolerance to salinity. Zheng et al. (2016) culture *Artemisia annua* with endophytic *Penicillium oxalicum* B4 to explore endophyte-mediated effects on artemisinin biosynthesis, an important ingredient used in anti-malarial pharmaceuticals. Under certain conditions the endophyte enhanced growth and artemisinin content of the host plant. The endophyte induced oxidative stress in regenerated plantlets through the generation of reactive oxygen species (ROS) including $O_2\bullet$ and H_2O_2 , which was then accompanied by the activation of antioxidant enzymes such as peroxidase, catalase and superoxide dismutase during the later stages of the stress. There was a significant increase in amorphaadiene synthase (ADS) and amorpha-4,11-diene monooxygenase (CYP71AV1) transcripts in dual culture of endophyte-plantlets. It is suggested that the induced ROS modulates the expression of those key genes for artemisinin biosynthesis and may be responsible for conversion of artemisinin acid into artemisinin. In another stream of research, Islam et al. (2016) conducted a study to evaluate the ability of PGPR *Bacillus cereus* Pb25, isolated from soil irrigated with saline water, to promote *Vigna radiata* (mungbean) growth in the absence and presence of salt stress. Inoculations with PGPR improved plant growth, and increased root and shoot fresh and dry biomass and yield as compared to plants with no bacterial treatment. Furthermore, PGPR inoculation significantly increased the antioxidant enzymes (POD, SOD and CAT) activities and enhanced the accumulation of proline, potassium, nitrogen and phosphorus as well as decreased sodium accumulation in saline stressed plants. These results suggest that *B. cereus* signals interfere with the plants biosynthetic pathways and this knowledge can be used to develop a bio-inoculant to help tolerate saline environments. Similarly, Garg and Singla (2016) look at impacts of plant–microbe interactions on salinity tolerance

and present a study which investigates the potential of naringenin (Nar), a flavonoid thought to play a role as a signal in such interactions, and mycorrhizal fungi (*Funneliformis mosseae*) in enhancing nodulation and nitrogen fixation in *Cicer arietinum* L. (chickpea) genotypes (PBG 5, DCP 92-3) under a range of salt stress. The data show that exogenous Nar partly restored nodulation and mycorrhization indicating its involvement as signal molecule in symbiosis. Mycorrhization and Nar enhanced salt-induced trehalose 6-P-synthase and phosphatase and reduced trehalase activity, leading to greater trehalose biosynthesis and nodule function.

We also present three papers which investigate the plant transcriptome response to microbial interactions and translate this into validation of the impact of these transcripts on the beneficial trait (Shen et al. 2016; Sun et al. 2016; Luo et al. 2016). Shen et al. (2016) investigate plant responses to *Phytophthora parasitica*, a broad spectrum fungal pathogen, by quantifying differential gene expressions between inoculated and mock-treated *Nicotiana benthamiana* leaves using RNA-Seq approaches. A total of 5375 and 3614 genes were found to be upregulated and downregulated, respectively. Infection with *P. parasitica* triggered massive metabolic reprogramming in the inoculated tissues. Genes related to photosynthesis, starch biosynthesis, and nitrogen assimilation were suppressed while sucrose degrading genes were induced. Notably, plant defence responses were activated, reflected by a larger number of upregulated jasmonic acid (JA) and ethylene (ET) signalling genes, receptor-like kinases, pathogenesis-related genes, and transcription factors. These types of studies allow the selection of candidate genes and traits for further research, which will translate this understanding to better tolerance to pathogens. Taking this approach to the next level of translation, Sun et al. (2016) studied the roles of JA and ET pathways in mediating defence against wheat Fusarium head blight (FHB), the expression patterns of genes in the *Fusarium graminearum*-challenged spikes between the cultivar Wangshuibai and its susceptible mutant NAUH117 at the Fhb1 locus were compared using wheat microarray. The results showed that most of JA-associated genes were induced in Wangshuibai while only a few were induced in NAUH117, and most ET-associated genes were up-regulated in both genotypes. A lipid transfer protein gene, which is a representative gene for JA pathway, was selected for functional analysis in *Arabidopsis* system using a T-DNA insertion mutant line for *LTP* gene. It was found that the mutant showed compromised FHB resistance compared with its wildtype, thereby validating the predicted function. Finally another example of how a specifically identified transcript can be validated as having a beneficial function in stress tolerance is given by Luo et al. (2016), who investigate the role of a rice SNARE

(soluble N ethylmaleimide-sensitive-factor attachment protein receptor). *OsSNAP32*, a SNAP25-type SNARE protein encoding gene, is shown to be ubiquitously expressed in the various tissues of blast-resistant rice landraces and is induced in rice seedlings inoculated by the blast pathogen (*Magnaporthe oryzae*). *OsSNAP32*-overexpressing transgenic lines increased resistance to blast, whereas *OsSNAP32* RNAi transgenic lines decreased resistance to blast. These results suggest that this specific transcriptional signal in rice is involved in resistance to blast fungus infection and could be deployed to enhance biotic stress tolerance in rice.

We hope that this special issue, focusing on plant–microbe interactions and the signals used and perceived by both, will act as a platform to stimulate more research in the area. It is clear that there is detailed understanding, in some specific cases, of the how plant–microbe interactions play out with respect to traits, biosynthetic pathways and the transcriptome, with some of the signals involved already known. Research that will translate this detailed understanding into interventions, which will allow us to manage systems more effectively, is starting to happen but should become a priority in the future. The research presented here suggests that we are on the cusp of being able to translate our detailed understanding in plant–microbe interactions and the signals involved into biological tools with the aim of achieving agricultural sustainability and environmental security. We thank the contributors and reviewers for their contributions and Plant Growth Regulation for the opportunity to present, what we hope will be, an impactful special issue on this hot topic.

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