FOCUS ON THE GOOD, THE BAD AND THE UNKNOWN: GENOMICS-ENABLED DISCOVERY OF PLANT-ASSOCIATED MICROBIAL PROCESSES AND DIVERSITY

MPMI Focus Issue Overview

MPMI has played a leading role in disseminating new insights into plant-microbe interactions and promoting new approaches. Articles in this Focus Issue highlight the power of genomic studies in uncovering novel determinants of plant interactions with microbial symbionts (good), pathogens (bad), and complex microbial communities (unknown). Many articles also illustrate how genomics can support translational research by quickly advancing our knowledge of important microbes that have not been widely studied.

The outcome of microbial interactions can range from beneficial to detrimental. To explore the molecular mechanisms that lead to different outcomes, Eaton et al. compare the global gene expression profiles of a wild-type mutualistic fungus, *Epichloë festucae*, with three antagonistic mutants on the host *Lolium perenne*. Their results provide evidence that this mutualist-to-antagonist transition was accompanied by an increased potential for utilizing host nutrients, suggestive of traits acquired by phytopathogenic fungi. Such global gene expression studies also provide insight into the adaptation of mutualists to their hosts. By characterizing the transcriptome of an ectomycorrhizal fungus (ECF) during multiple developmental stages on two hosts, a gymnosperm and an angiosperm, Plett et al. identify gene sets that are conserved and variable across hosts. Moreover, by simultaneously profiling gene expression in ECF and its angiosperm host, they elegantly demonstrate a coordinated and shifting transcriptomic landscape during this symbiosis.

Host specificity has long been known as a hallmark of the *Rhizobium*-legume mutualism. Jorin and Imperial are the first to apply population genomics to address the question of whether distinct host species select distinct rhizobial genotypes. The sequences from pools of *Rhizobium leguminosarum* bv. *viciae* “trapped” by the nodules of four distinct hosts clearly demonstrate host-specific selection based on single nucleotide polymorphism patterns both in the *nod* gene cluster and genomewide. Their results illustrate the power this new methodology to better understand plant mutualisms.

Microbes also benefit plants by producing secondary metabolites (SM) that are antagonistic to pathogens. Two studies explore genome sequencing to help in identifying biocontrol-active SM. Following a comprehensive analysis of SM-encoding genes in the genome of *Pseudomonas chlororaphis*, Calderon et al. demonstrate that an antifungal compound specific to this organism, 2-hexyl, 5-propyl resorcinol, is critical to its biocontrol activity. Similarly, Takeuchi et al. compare the genome sequences of two *Pseudomonas* sp. strains that differed in their antagonism to the oomycete *Pythium ultimum* to identify the SM rhizoxin as a critical factor in biocontrol.

This focus issue also highlights how genomic approaches are being used to study all classes of plant pathogens. Burkhardt et al. use RNA-seq to reveal that 55% of intron-containing genes of the oomycete pathogen *Pseudoperonospora cubensis* are alternatively spliced, with approximately 1% of the alternatively spliced genes encoding predicted effector proteins. This study suggests that alternatively splicing may play a crucial role in pathogenesis and emphasizes the importance of transcriptome analyses for high-quality genome annotations. Besides protein effectors, pathogens also produce suites of SM during infection that can be harmful not only to their plant host but also to mammals that eat the infected plant products. Excellent examples are the neurotoxin patulin and

the nephrotoxin citrinin produced by the postharvest fungal pathogen of pome fruits *Penicillium expansum*. Using comparative genome and transcriptome analyses, Ballester et al. demonstrate that, despite a significant genome contraction, *P. expansum* possesses an extensive potential for SM production. However, patulin and citrinin are dispensable for apple infection. In another mycotoxin study, Brown et al. use comparative genomics of three pathogenic *Fusarium* spp. to complete the identification of a cluster of genes required for producing fusaric acid. Deletions of this cluster disrupt fusaric acid production but do not affect the virulence of two *Fusarium* spp. Both studies raise the question of the biological role of these fungal SM.

On the host side, plants have evolved both conserved and unique countermeasures to thwart pathogen or pest infestation. Martel et al. demonstrate the divergence of spider mite-induced responses in tomato and *Arabidopsis*, highlighting how genomic approaches help reveal the molecular diversity and evolution of such countermeasures across plant species. As part of their defense arsenal, plants produce numerous small molecules that pathogens must contend with, including antimicrobial phenolic compounds such as hydroxycinnamic acids (HCA). The ability to degrade HCA is required for early stages of infection, root colonization, and HCA resistance by *Ralstonia solanacearum*. A comparative genomics analysis of the *R. solanacearum* species complex by Lowe et al. demonstrates that the HCA degradation pathway is conserved, supporting a critical role in pathogenesis.

Considering the vast diversity of microbial species in nature, our current knowledge represents the very tip of the proverbial iceberg, and many novel microbes and their products await discovery. Seidl et al. show that a saprophytic species of the fungal genus *Verticillium* shares a large repertoire of effectors found in its pathogenic relatives. Since saprophytes feed on dead plant tissue, they presumably do not require these effectors to contend with host defenses, suggesting that they may confer alternative ancestral functions that evolved into pathogenic weaponry. The structure and function of the plant microbiome is likely affected by complex biotic and abiotic factors. Rapidly increasing sequencing capacity has enabled comprehensive surveys of microbial communities associated with diverse organisms and ecosystems and their changes in response to various factors. Copeland et al. investigated seasonal changes of the phyllosphere bacterial community in multiple crop species to identify key factors underpinning their dynamics, thus providing new insights and questions that require further studies. A review by Schlaeppi and Bulgarelli guides us through the current status and future directions of plant microbiome research as well as providing an overview of key concepts and approaches in this exponentially growing field.

We would like to thank all of the authors who elegantly illustrated the use of genomics to better understand the biology, ecology, and evolution of plant-associated microbes, the microbial products that facilitate pathogenesis and symbiosis, and the interconnectedness between microbial communities and the function and evolution of plants. We also greatly appreciate the input from our reviewers.

Guest Editors

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