

Plant–microbe symbiosis

Plant pathologists (that is, students of plant diseases and of the microbes that cause them) have contributed greatly to the understanding of plant–microbial symbiosis. It was Heinrich Anton de Bary (a plant pathologist) who in 1879 offered a definition of symbiosis (“*the living together of unlike organisms*”) which is favoured by many to this day, and not just plant pathologists. It was another plant pathologist, George McNew, who in the 1960s formalized the disease triangle, a simple but highly effective conceptual tool to explain infectious diseases as the outcome of a three-way interaction between a pathogen (that is, a disease-causing infectious agent), its host (plant or otherwise), and the environment that the pathogen and host share. Then there was Curt Leben (also a plant pathologist), who in 1965 made the case that the disease triangle felt too ‘flat’ and should feature a ‘fourth dimension’, one that represents the non-pathogenic members of what he called the plant “*microflora*”. Leben argued that the size, composition and function of these plant-associated non-pathogenic microbial communities are likely to impact the abundance and activity of cohabiting pathogens and so by extension would be able to influence the manifestation of disease. This sounds like a pre-omics premonition of what we have come to accept as the essential role of host microbiomes in relation to host health. Interesting to note here is that one of the earliest definitions of the term ‘microbiome’ was actually coined by (you guessed it) a plant pathologist: in 1988, John Whipps used it to refer to a “*characteristic microbial community*” occupying a physico-chemically

distinct habitat that serves as a “*theatre of activity*” where members of the microbiota (pathogens as well as non-pathogens) interact.

Typically, plant pathologists define themselves and each other along distinct dividing lines: for example, they may study either foliar, trunk or root diseases, they are experts on either bacterial, fungal or viral pathogens, or they specialize in tree, fruit or vegetable crops. There is no line that separates plant pathologists who study pathogens from those who study non-pathogens, because such a line would mark, in the traditional sense of plant pathology, the boundary of the discipline. However, plant pathologists have been known to cross into non-pathogen territory on occasion. A classic example is the case of ‘biocontrol’, which in this context is the exploitation of microbe–microbe interactions such as antagonism and competition to protect plants from harmful pathogens. Indeed, many research labs in academia and the agro-industry are heavily invested in prospecting Leben’s ‘fourth dimension’ for bacteria, fungi and other microorganisms with traits that have practical potential for mitigation of pathogen establishment on plants. Other highly sought-after microbial traits are those that aid plants in the acquisition of essential nutrients such as phosphorus or in dealing with environmental stresses such as drought. These so-called plant-growth promoting microorganisms, together with the aforementioned biocontrol agents, can be thought of as “*probiotics for plants*”, capable (in theory, greenhouse or sometimes field setting) of keeping plants healthy in the face of one or more biotic and abiotic challenges.



As plant pathologists entered the -omics era, they came into possession of tools to explore the structure and function of plant-associated microbiota in ways that would have left Leben with envy, excitement or probably both. These tools are bringing many new advances to the understanding of the role of the environment (for example, soil and air) as a source of pathogenic and non-pathogenic microorganisms that colonize surfaces and internal tissues of plants. Also, much has been learned about the types and numbers of plant genes that underlie the selection for or against associations with microbial beneficials, commensals or pathogens. The field has gained enormously from the use of model plants such as *Arabidopsis thaliana*, the lab mouse of the plant world, for which extensive resources, including a genome sequence, gene knockouts and model pathogens are available. The comparison of whole-genome sequences from pathogenic and non-pathogenic microorganisms has not only helped the search for genes and gene products that contribute to pathogenicity and virulence, but also created a greater appreciation for the types of genes that contribute to microbial survival on roots, leaves and other plant parts. These may or may not be compartment specific, for example, genes that are enriched in leaf surface colonists to deal with damage from UV exposure and the dangers of desiccation, or genes that maximize survival in the face of shared access to limited nutrient sources and that code for high-affinity uptake systems,

synthesis of plant hormones to stimulate nutrient release from the host or the production of antimicrobial compounds. Lastly, these plant microbial genomes also provide first clues about the genes and gene clusters that pathogens need for survival when they are not (yet) realizing their pathogenic potential, or when plant symbionts (pathogenic or not) find themselves dissociated from their plant host.

For sure, these are exciting times for plant pathologists. Many are intrigued by or already pursuing the prospect of a fuller mastery of 'their' pathosystem through closer acquaintance with all microorganisms that cohabit 'their' plant host and may interact with 'their' plant pathogen. In doing so, they continue the tradition of making impactful contributions to the field of plant-microbial symbiosis and to our understanding of the incentives, outcomes and applications of the microbe-microbe interactions that play out in the 'theatre' known as the plant microbiome.



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