

Editorial overview: Dialogues with the good, the bad, and the ugly

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Plants as well as their biotic partners range in diversity in terms of their size, complexity, and lifestyles. In their natural and agricultural habitats plants are constantly interacting with a plethora of organisms, which in turn may affect them positively, negatively, or neutrally. The interaction partners are also communicating with the plant as well as with each other. These multi-tiered interactions occur at physical, chemical, and biological levels. In recent years, exciting progress has been made towards understanding the molecular, biochemical, and structural underpinnings of these interactions. This issue of Current Opinion in Plant Biology compiles the recent major findings in plant biotic interaction at organismal, cellular, molecular, and biochemical levels. The biotic partners covered in this issue range from beneficial microbes to biotrophic and necrotrophic fungal pathogens, bacteria, oomycetes, nematodes, and insect pests on a wide variety of hosts from Arabidopsis to cereal crop plants to trees. Besides highlighting state-of-the-art developments in the field, this issue also identifies knowledge-gaps and future areas of promising research. Increased understanding of plant biotic interaction will facilitate ecologically sustainable and environmentally friendly co-existence of plants, microbes and humans in both natural and agricultural settings.

Meet the neighbors

In the first line of dialogue, plants sense their biotic partners because of their signature patterns, leading to pattern-triggered immunity (PTI). Pathogens have evolved multiple strategies to escape recognition by the plant's pattern-recognition receptors. [Sanguankiatichai et al.](#) discuss various strategies for how pathogenic bacteria evade recognition of flagellin patterns by plants, including polymorphisms in the amino acid sequences of elicitor peptides, post-translational modification and masking of the flagellin proteins, modulation of flagellin transcription levels, apoplastic effectors targeting flagellin recognition as well as modulation of signal transduction by intracellular effectors. [Sanguankiatichai et al.](#) note that this is just the tip of the iceberg, as much of the current understanding of flagellin recognition in plant-bacteria interactions comes from experiments involving artificial inoculation with synthetic peptides or individual bacterial strains, while dynamic interactions occurring in the plant-microbiome will be much more complex.

Wilson and McDowell *et al.* highlight the recent findings of the diverse host targets of oomycete intracellular effectors such as ROS homeostasis, ethylene signaling, antimicrobial autophagy, and plasmodesmatal trafficking that affect plant regulatory networks to the pathogen's advantage. It is interesting to find that different fungi and oomycetes have evolved independently to challenge common targets such as the ethylene response pathway in ways suitable to each pathogen's lifestyle.

Pathogens are classified as biotrophs, hemi-biotrophs or necrotrophs based on their nutrition acquirement strategies. Most of the knowledge in plant immunity is based on the biotrophic and to some extent hemi-biotrophic pathogens and their hosts. However, resistance and susceptibility mechanisms in context of necrotrophic pathogens, which have a broader host range with limited major-effect resistance genes, are not as well understood. Liao *et al.* highlight the commonalities and differences between necrotrophs and biotrophs, ranging from their virulence strategies to sensing of microbe-associated molecular patterns (MAMPs) and the downstream signaling cascade that determines the final outcome of the interaction. Liao *et al.* conclude that better understanding of virulence strategies of necrotrophic pathogens and resistance and susceptibility mechanisms of their hosts will be critical in designing better disease control strategies in crop plants.

Crystal clarity

Tremendous progress has been made in the structural characterization of pathogen effectors and their interaction with the corresponding host immunoreceptors. Outram *et al.* emphasize that several different effectors may have similar structural folds in spite of having highly diverse sequences, indicating a shared function. Förderer *et al.* conclude that the structural resolution of several intracellular immune receptor nucleotide-binding and leucine-rich repeat (NLR) proteins in their active and inactive states has provided clarity on the biochemical function of the resistosome complexes. This knowledge opens unprecedented avenues for targeted engineering of these NLRs to make plants resistant to a broad range of pathogens.

Bernoux *et al.* highlight the recent findings on the connection between cell surface- and intracellular-triggered immune pathways in plants, which were earlier considered separate. They hypothesize that PTI and effector-triggered immunity (ETI) may potentiate each other through a transcriptional feed forward loop involving receptors and signaling components. Alternatively, PRR- and NLR-induced responses may be connected via physical interactions between proteins involved in the two pathways. They further point out

that most of the structural and biochemical level details have been discovered in a few model plant species, and how PTI and ETI connect to confer robust immunity in crop plants will be an exciting future research area with applications in precise breeding of resistant crop varieties.

Rapid progress in the discovery and functional genomics of diverse resistance genes in crop plants has revealed wide diversity in the type and their mechanisms of action, beyond the quintessential R-Avr-mediated ETI. Taking the case of wheat, an important cereal crop plant, Sinha *et al.* discuss the recent discoveries made in the identification of several atypical resistance genes and conclude that these findings may enable the development of crop plants that are resistant to diverse pathogens for years to come.

Chemical warfare

Plants and their microbiome affect each other, and as such both plant fitness and the composition and function of their microbial community depend on efficient back and forth communication between them and among them. Koprivova and Kopriva present the recent updates on the identification of plant secondary metabolites that affect microbiome function and composition. Rangel and Bolton complete the picture by highlighting the roles of pathogens' secondary metabolite effectors that influence microbial community to outcompete proximal microbes. Rangel and Bolton also describe the self-resistance mechanisms that these pathogens employ to escape the toxic effects of such SMEs to themselves.

Plants and microbes both produce various phytohormones, some of which share the same biosynthetic pathways while others are unique. Nakano *et al.* communicate the complexity of phytohormone interaction between plant-microbe, microbe-microbe and microbe-plant level. They also highlight the opportunities to explore more about the microbial phytohormone synthesis pathways; effect of these inter-organismal phytohormone networks on community assembly; and origin of phytohormone biosynthesis and signaling, which will be useful in developing better agricultural production systems.

Endogenous signaling peptides known to have growth-regulatory functions are increasingly being recognized as immune-modulatory agents that fine-tune PTI. Similarly, several peptides called phytocytokines, which are actively released as immunogenic factors, are known to be involved in plant growth and development. Rzemieniewski and Stegmann present recent progress made on the comprehension of phytocytokines in simultaneously regulating growth and PTI, highlighting

the complex interplay of peptide signaling pathways regulating multiple aspects of a plant's life.

Distinguishing foes from friends

The plant rhizosphere contains a plethora of organisms, many of which provide life-supporting services to the plant, as they enhance nutrient acquisition, stimulate root architecture, or boost plant immunity. [Redkar et al.](#) discuss recent progress in understanding the role of secreted effectors as compatibility determinants in root-colonizing fungi. Using two broad host range root-infecting fungi with similar modes of colonization but opposite outcomes (pathogenic or beneficial) during the later colonization stages in the host the authors speculate on why these associations ultimately result in contrasting outcomes for the host.

[Pradhan and Requena](#) highlight the role of small RNAs (smRNAs), including microRNAs, as mobile signals that plants use for cross-kingdom communication with their microbial neighbors. They hypothesize that plants may use smRNAs as regulatory tools helping plants to discriminate between friends and foes.

From micro to macro

In spite of their tremendous importance in climate change mitigation, food security, timber trade, biodiversity, ecology, landscape interventions, culture and survival of humans on the planet, tree–microbe interaction research faces challenges of a different magnitude altogether. In light of recent literature, [Rabiey et al.](#) bring attention to the importance, challenges and opportunities in scaling up tree-microbe/microbiome interactions research.

[Kloth and Dicke](#) present the current molecular understanding of herbivory-induced rapid systemic signaling in the framework of insect–plant interactions. Various molecular mechanisms are orchestrated in the host, minutes after the insect attack. [Kloth and Dicke](#) discuss how various types of signaling mechanisms including

electrical signaling, Ca^{2+} waves, hydraulic signals, chemical signals, and reactive oxygen species signaling are used by plant hosts in their rapid defense response against herbivory-induced damage.

[Goverse and Mitchum](#) discuss recent advances in the field of molecular plant–nematode interactions that have improved our mechanistic understanding of this pathosystem. The authors describe the several commonalities of this host–parasite interaction to traditional plant–microbe interaction knowledge, such as the role of cell surface receptors and NLR-mediated defense response. They also highlight the fascinating distinctiveness of the plant–nematode interactions, such as exploitation of the host's post-translational trafficking mechanism to mediate feeding site formation and non-canonical resistance, which will have significant implications in not only improving plants resistance to parasitic nematodes but also to other pathogens in a multi-trophic context.

With the unprecedented recent progress made in our understanding of the depth, width and complexity of plant–biotic interactions, we are strategically at a point where we can develop enabling strategies for designing crop plants and trees that successfully resist diverse pathogenic organisms, while at the same time maximize profitable functions of beneficial organisms in the root microbiome. Breakthroughs in protein structure determination, microscopic and biochemical analysis, and gene editing are allowing us to analyze, visualize, and utilize the plant–biotic interaction to the benefit of plants, crops and the planet.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.