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Editorial overview: Biotic interactions – from single molecules to complex ecosystems

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Benjamin Schwessinger studied biochemistry in Leipzig Germany before becoming fascinated by plants. Benjamin switched to plant science half way through his degree and graduated from the beautiful University of Glasgow with a first-class honours Bachelor of Science. He obtained his PhD from the University of East Anglia working at the Sainsbury Laboratory with Dr Cyril Zipfel investigating receptor kinase mediate immune signaling in Arabidopsis. He move to sunny California to work with Prof Pamela Ronald at the University of California, Davis. During this time, he mostly worked on immune signalling in rice while being supported by EMBO and HFSP postdoctoral fellowships. Looking for new frontiers, Benjamin moved to work on the genome biology and evolution of plant pathogenic rust fungi at the Australian National University, Canberra. His initial move was support by an Australian Research Council DECRA award to work in the laboratory of Prof John Rathjen. In 2018, Benjamin became fully independent supported by an Australian Research Council Future Fellowship and he is currently a Senior Lecturer at the Australian National University. His team focuses on genome evolution and host adaptation of rust fungi in addition to other aspects of plant and fungal biology. <http://teamschwessinger.com/>.

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The year 2019 delivered major advancements in our understanding of Plant–Biotic interactions on multiple scales. Many of these fundamental discoveries are driven by applying the latest technological advances. This includes solving the first structure of a plant Nucleotide binding Leucine-rich Repeat (NLR) immune receptor protein by Cryo-EM, which revealed a wheel-shaped resistosome complex as described by [Xiong *et al.*](#) Similarly, the first complete haplotype-phased chromosome-level genome assembly of a rust fungus revealed unambiguously the origin of the deadly Ug99 wheat stem rust strain via somatic hybridization as outlined by [Figuroa *et al.*](#) At the same time, research on Plant–Biotic interactions now strives to go beyond the simplified one-to-one systems based on single reference accession and genome. Both plant and pathogen population studies aim to uncover the true diversity of interactions. For eukaryotic plant pathogens, the progress in our understanding of *Zymoseptoria tritici* described by [Badet *et al.*](#) has been remarkable from the discovery of agriculturally important Avrs to the first eukaryotic pathogen pan-genomes. The impact of multiple to thousands of microbes on plant disease outcomes is now much more appreciated with high-throughput microbiome studies leading to the discovery of ever more biological diversity and highlighting the importance of biogeography. We are only starting to scratch the surface of the vast ocean of life associated with plants on a global scale. Our understanding of the biological world will be further driven by the integration of diverse approaches and systems while working openly and collaboratively.

This issue of COPB includes reviews contributed by diverse researchers from each continent, except Antarctica. The collection of articles does not include every recent breakthrough and we apologize to those authors and topics that could not be covered. With this issue, we invite you to celebrate the diversity of scientists and a breadth of topics that span various scales, from single molecules to networks, and from amenable study systems to complex ecosystems.

One molecule – many forms and functions

We continue to learn a lot in Plant–Biotic interactions by studying amenable systems and individual proteins. Along this line, [Xiong *et al.*](#) describe recent Cryo-EM structures of inactive and active forms of the NLR immune receptor ZAR1. Although this is the only plant NLR structure published to date, it answers several long-standing questions supported by biochemical analyses of NLRs. The inactive NLRs are held together by intramolecular interactions and activation leads to dramatic intra- and intermolecular structural changes. The active oligomeric resistosome complex formed by ZAR1 is strikingly similar to apoptosome and inflammasome formed by

Berkeley where she studied plant–microbe interactions as well as genomic and computational biology focusing on Arabidopsis as a model pathosystem in laboratory of Prof Brian Staskawicz. During her postdoc with Prof Jorge Dubcovsky at University of California Davis, she focused on wheat genomics. Supported by USDA NIFA Postdoctoral Fellowship, she led the development of wheat exome capture and sequenced over 3000 mutant wheat lines cataloguing mutations in an openly available reverse genetics database. Krasileva started her own group in 2014 at Earlham Institute and The Sainsbury Laboratory in the United Kingdom continuing work on wheat genomic and starting an independent research program on the evolution of plant immune system. Krasileva is the first recipient of the international Carlotta award for her contribution to wheat research. Currently, she is an Assistant Professor in the Department of Plant and Microbial Biology at UC Berkeley. Krasileva Lab at Berkeley maintains research interests in the biology of genomes, including both plants and microbes, as well as evolution and function of plant innate immunity. <https://krasilevalab.org>.

activated mammalian Apaf-1 and NLR proteins, respectively. The striking re-arrangement of the coiled coil motif in ZAR1 and its association with membranes give a hint of how NLRs could induce cell death. [Aguilar *et al.*](#) review a different versatile molecule, — the Geminiviral genome. Roughly the same size as the coding sequence of NLRs, the Geminiviral genome encodes 3–4 ORFs that represent a minimal pathogen that is capable of eliciting a full spectrum of plant responses. The Cryo-EM structure of Geminivirus particles have been solved within the last few years as well. We look forward to the future insights from in-depth studies of single molecule systems, while being careful not to overgeneralize and appreciating the biological diversity in front of us.

No single point of failure — decentralized networks

In the last several years, we have learned to appreciate that both immune proteins as well as pathogen-derived molecules hardly ever work in isolation. They are rather part of intricate sensing and signalling networks. [Steinbrenner](#) summarizes research on networks of plasma membrane localized pattern recognition receptors, their co-receptors and downstream kinases. [Steinbrenner](#) emphasizes that these networks can evolve dynamically even within a species leading to nuanced differences in signal transduction as well as emergence of novel specificities. Consistently with plants monitoring the apoplast for pathogen molecules, the apoplast is an important early battle ground for eukaryotic plant pathogens. [Rocafort *et al.*](#) summarize the latest research on apoplastic effectors of plant-associated fungi and oomycetes. In this tit-for-tat, pathogens use effectors to shield molecules like chitin for being recognized by the plant immune system. Yet effectors themselves can be recognized by plasma membrane localized immune receptor proteins and kinases. Complementally, [Feehan *et al.*](#) highlight recent breakthroughs in intracellular NLR networks, the differentiation of receptors into sensors and helpers and a growing complexity of co-dependencies among them. Even with built-in redundancies, networks are not pathogen-proof. Well controlled responses to one pathogen can be exploited by another: [Faris and Friesen](#) summarize the ultimate ying and yang of plant–biotic interactions, how resistance to biotrophic pathogens can also lead to susceptibility to the necrotrophic pathogens that purposely induce and exploit cell death responses.

[Zanetti *et al.*](#) describe another fascinating network of signal amplification control: mRNA stability, uORFs and lncRNAs in root nodule symbiosis. The vast information accumulated in this system would be without doubt applicable to regulation of other plant–biotic interactions. [Zogli *et al.*](#) summarize the accumulated -omics data to decipher networks in plant–insect interactions.

The recurring theme is the robustness of distributed networks. They give rise to diversity of regulatory mechanisms and provide robust redundancy. In addition, the network structures display inherent plasticity for lineage- and species-specific expansions and evolution of new functions.

Form basic to applied — real world challenges

Never have we been so close to gaining molecular understanding of plant–biotic interactions in crop fields and natural ecosystems. [Karasov *et al.*](#) revisit a long-standing argument for the deployment of genetically and spatially heterogeneous populations of crops instead of stacking genes to maximize resistance and minimize genetic interference and incompatibilities. They summarize our current knowledge of heterogeneous genetic diversity in wild populations and provide compelling arguments that the plant immune

system might work best on the population level. However, intercropping is challenging and would need to be assisted by new technologies, including phenotyping. [Hu *et al.*](#) review the application of some of these technologies with specific focus on pathogen diagnostics. At import or export borders and in crop fields, early pathogen detection is essential. Novel approaches range from spectral imaging to precise molecular testing based on DNA using new portable sequencing devices and biosensors of protein molecules. [Tripathi *et al.*](#) summarize real world applications of genome editing with CRISPR-Cas9 with a focus on bananas. CRISPR editing is now prevalent in crops, and the reviewed focus crop banana, a clonal polyploid monoculture that is a major source of income to many developing countries, is a prime example where this technology is making a difference.

All too often technological solutions advance much faster than regulatory frameworks. This is especially obvious for laboratory-based genetic crop improvements and novel disease diagnostics. Hence scientists need to promote the applications of these technologies at the same time as they develop them. Concomitantly, open data sharing, data standards, and reproducible data handling will be important to maximize the impact of many novel big data technologies.

Multitudes of interactions – plant–pathogen populations and ecosystems

Plant–Biotic interactions are often reduced to binary study systems happening in isolation. [Afkhami *et al.*](#) describe the initial step beyond the classic one-to-one pathogen–host interaction and review tripartite mutualism. They highlight that the more complex interactions often display non-additive and synergistic effects on host fitness as for example observed for arbuscular mycorrhizal fungi and rhizobia in legumes. Bacterial symbionts of fungi can be seen as an extension of these tripartite interactions and are reviewed by [Bastias *et al.*](#) Here endosymbiotic bacteria of fungi often show net benefits for the host interaction while the effect of ectosymbionts depends on their role as helpers or pathogens of fungi. [Baltrus](#) looks beyond the tripartite interactions and explores the influence of dispersal and biogeography on phytobiomes. Despite being sessile, plants use chemoattractants and repellants to actively recruit their own microbiome communities which are influenced by the biogeography of pre-existing microbial diversity in soil and air. [Baltrus](#) raises the important point that diversity goes beyond metabarcodes. The actual microbiome–plant interactions are really defined by the diversity of biochemical pathways encoded within these communities. One of the next frontiers will be to assemble stable communities that expresses the desired biochemical

properties to increase crop productivity. The biggest challenge will be the maintenance of these communities in the presence of stiff competition from other microbes including pathogens. This is an idea [McCann](#) also explores in her review on the emergence of plant diseases. Spillover of pathogens from natural ecosystems present a real risk to agriculture, especially to large scale monocultures. Engineering crop microbiomes could lead to changed selection pressures facilitating these spillover events. Once novel pathogens are established on crop plants, host adaptation via mutation and recombination can lead to rapid epidemics as seen for the kiwi fruit disease in New Zealand. After long-term adaptation, the pathogen population can display various levels of genetic diversity depending on multiple factors including biogeographic and genetic barriers, gene flow between species, recombination and modes of reproduction. The resulting genetic diversity of a species at the global population level can be captured with pan-genomes as reviewed by [Badet *et al.*](#) In the short term, host-adaptation can also be expressed via host-specific infection mechanism. [Petre *et al.*](#) review host-specialized transcriptomes in eukaryotic pathogens and reach the conclusion that specialized transcriptomes are usually restricted to a limited set of genes. These include effectors, control of nutrient assimilation, and the maintenance of cellular homeostasis. It is clear that plants are situated in a large ocean of microbial biodiversity which encompasses even bigger biochemical complexity. While we are starting to map out the ocean, we ultimately have to move beyond descriptive studies and gain an in-depth understanding of the underlying mechanistic and evolutionary pathways. This will close the gap between descriptive studies and mechanistic understanding of Plant–Biotic interactions at different ecosystem scales.

Outlooks

Flor's gene for gene conceptualization of plant–biotic interactions in the mid 20th century occurred side by side with Alan Turing's test of a machine's ability to exhibit intelligent behavior. Future breakthroughs in Plant–Biotic interactions will require to combine well-designed sampling regimes with the latest algorithms. Only meaningful and carefully curated datasets will facilitate the advances promised by statistical analyses and machine learning. These precise spatial and temporal maps of plant/pathogen co-occurrence will enable us to decipher the complexity of interactions between host genotypes, microbiomes, and the environment with temporal resolution. We should also aim to move from understanding the biology of single molecules and networks to targeted modifications, utilizing the newest genome editing tools, breakthroughs in DNA sequencing and construction of synthetic circuits. One of the biggest

challenges that awaits us is ensuring robust standards of information sharing including rich and meaningful metadata, reaching from cryEM images to high-throughput images and large genomic datasets. The future looks bright and interdisciplinary. The skills that enable future breakthroughs will require new adapted university curriculums while building on our past strengths. To have tangible societal impact, we must not forget that science requires us to communicate our advances in an accessible

dialogue with the public. This will enable us to harvest the fruits of our research labor. A computer won against a human in Go in 2016, we hope that a team of computers and humans can soon outcompete plant pathogens and improve plant health.

Conflict of interest

None.