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Current Opinion in Plant Biology

# Common threads amid diversity

## Editorial overview

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**Current Opinion in Plant Biology** 2008, **11**:357–359

This review comes from a themed issue on
Biotic Interactions
Edited by Murray Grant and Sophien Kamoun

1369-5266/$ – see front matter
Published by Elsevier Ltd.

**DOI** 10.1016/j.pbi.2008.06.005

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Reserach in Murray Grant's laboratory focuses predominately on three key themes of the interaction between *Pseudomonas syringae* and *Arabidopsis thaliana*: (i) how bacterial type III effectors suppress basal defense and promote nutrition, (ii) establishment of systemic immunity, and (iii) the mechanisms underlying function of the RPM1 disease resistance protein. Central to this research is the need for a better understanding of the contribution of small molecules, in particular phytohormones to defense responses.

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Research in Sophien Kamoun's laboratory focuses on effector biology in filamentous plant pathogens, particularly oomycetes such as the Irish famine organism *Phytophthora infestans*. Current activities aim at understanding how pathogen effectors function, how they evolve, and how they traffic into host cells. Also, the lab continues to be actively involved in several genome sequencing projects and in exploiting genomics resources to improve understanding of plant pathosystems.

A multitude of microorganisms, including bacteria, fungi, oomycetes, and nematodes, have evolved the ability to grow in plant tissue and have had a tremendous impact on shaping natural and managed plant diversity across the globe. The study of plant–microbe interactions is a very active and fast paced area of plant and microbial sciences. In this issue of *Current Opinion in Plant Biology*, we sought 15 articles to provide timely updates on a selection of topics. We selected subject matters that illustrate the wide diversity of research in the field. Diversity is apparent not just in the taxonomic breadth of the organisms that interact with plants, but also in the mode and site of action of pathogen and plant molecules that directly participate in the interactions. However, despite the fact that the articles report on findings and concepts on a variety of pathosystems and mechanisms, some common threads can be noted and are highlighted in this overview.

Plant parasitic lifestyles have evolved repeatedly in eukaryotes suggesting unique molecular processes for host infection. The articles by Davis *et al.*, Egan and Talbot, and Birch *et al.* discuss nematodes, fungi, and oomycetes, respectively. Although these major parasites belong to three phylogenetically distinct lineages of eukaryotic plant parasites, some commonalities are evident. A notable observation is that the concept of effectors has now extended beyond Gram-negative bacteria to these eukaryotic plant parasites. Each one of these articles discusses how these parasites secrete proteins to perturb plant processes and facilitate colonization. A mechanistic understanding of how these effectors contribute to parasitism is a major current research theme on these organisms.

A highlight of the comprehensive Davis *et al.* article is the revelation that a multitude of nematode-secreted proteins mimic plant molecules leading the authors to coin the phrase 'imitation is the sincerest form of parasitism'. Fascinating examples of plant mimics include secreted nematode proteins with similarity to expansins and CLAVATA3 signalling peptides. Additional nematode-secreted proteins with similarity to components of the proteasome might target host proteins for degradation, while others localize to the plant cell nucleus, suggesting a role in transcriptional regulation.

The completion of over 40 fungal genome sequences in recent years has greatly impacted our understanding of the biology of plant-associated fungi. The article by Egan and Talbot highlights among other topics the extraordinary diversity of G-protein-coupled receptors encoded in phytopathogenic fungal genomes, which provides insights into how these pathogens respond

and adapt to the dynamic environment created by the host. The impact of genomics is also obvious in the article by Birch *et al.* on the oomycete RXLR class of effectors that are translocated from haustoria inside plant cells. Long considered untractable organisms by fungal genetic research standards, the oomycetes have recently moved to center stage of research on plant–microbe interactions. The genome sequences of several oomycetes, such as the potato late blight pathogen *Phytophthora infestans*, revealed several hundred candidate effector genes. RXLR effectors are remarkable in sharing conserved host-translocation signals with malaria parasites of mammals. Birch *et al.* discuss the extent to which effector translocation relies on host- or pathogen-derived machinery and propose a model that evokes the exploitation of host endocytosis machinery, perhaps receptors analogous to the plant pattern recognition receptors described below.

Not all pathogen effectors are translocated inside host cells. The apoplast is an oft-overlooked site of conflict between pathogen and plants. Misas-Villamil and van der Hoorn propose that apoplastic effectors evolved in pathogens before host translocation processes suggesting that the apoplast is an ancient battlefield. Their article illustrates a diversity of apoplastic defense and counterdefense mechanisms that result from the antagonistic arms race taking place between plants and pathogens. Many elegant examples of attacking enzymes and counteracting inhibitors are described.

The apoplast is more commonly associated with primary induced defense responses orchestrated by plant pattern recognition receptors. Strategic deployment of receptor domains in the apoplast interdicts conserved invariant patterns associated with pathogens and microbes (PAMPs) and activates PAMP triggered immunity (PTI). The discovery that the brassinosteroid-associated kinase BAK1 is also associated with the archetypal pattern recognition receptor FLS2 was a major breakthrough during the past year. This increased connectivity in proximal signalling processes associated with PTI is explored by Schwessinger and Zipfel, who also examine emerging evidence suggesting components mediating effector-triggered immunity (ETI) may target repressors of PTI. The mechanisms by which PTI and ETI are suppressed are of outstanding interest in plant pathology. Remarkable progress has been made in unravelling the virulence strategies employed by bacterial type III effector proteins (T3E). Block *et al.* discuss three host processes targeted by T3Es, alteration of host protein turnover, alteration of host RNA homeostasis (transcription or stability), and modification of phosphorylation pathways. In addition, and in a twist to the molecular mimicry examples described by Davis *et al.* they explore the concept that plants have evolved both DNA and protein 'decoy' targets to conceal real host virulence targets from T3E activities.

Nonhost resistance is evoked when a plant species is resistant to all genetic variants of a pathogen. The article by Lipka *et al.* points out that genetic dissection of nonhost resistance of Arabidopsis to non-adapted powdery mildew fungi revealed distinct but functionally redundant layers of pre-invasion and post-invasion immune responses. The extent to which nonhost resistance is the result of ineffective pathogen effectors (lack of PTI or ETI suppression) or recognition of effectors from the non-adapted pathogen (ETI) remains to be determined.

The co-evolutionary interactions described in the articles above leave genetic footprints, which can provide informed insight into plant–microbe interactions. Ma and Guttman use comparative effector genomics to infer how plant pathogen interactions have been shaped by a combination of diversifying and positive selection. They hypothesize that selective pressures have differentially molded bacterial versus eukaryotic pathogens. Diversifying selection appears the primary evolutionary process modifying eukaryotic effectors, leading to the generation and maintenance of multiple alleles. By contrast, T3Es have evolved under positive selection resulting in rapid turnover and diversification of the T3E complement through gene-loss and acquisition. An emerging process driving evolution of novel T3Es appears to be terminal reassortment and understanding the mechanism driving this process is a major key challenge.

The importance of hormonal control in plant pathogen interactions is highlighted in four contributions in this issue. Lopez *et al.* comprehensively review the role of hormones in defense responses and scrutinize how modulation of relative hormone abundance can impact signalling pathway that effect other processes intrinsic to defense such as resource reallocation, water availability, and plant architecture.

The global ability of hormones to de-repress signalling pathways that are normally constitutively suppressed is a powerful feature utilized by both pathogen and host. A highlight of the past year was the discovery and characterization of a class of negative regulators of jasmonic acid signalling, the JAZ proteins. JA regulates a range of defense responses to both herbivores and necrotrophic pathogens, but till now the molecular basis of this regulation was elusive. Katsir *et al.* first review evidence that ubiquitin-dependent degradation of JAZ proteins is mediated through the interaction of the JA-isoleucine amino acid conjugate and the F-box protein COI-1 and then analyze the role for amino acid conjugation in jasmonate perception. These discoveries provide a fascinating mechanistic understanding of how the bacterial toxin and JA-Ile mimic, coronatine, have evolved to exploit hormone signalling pathways to promote virulence. Katsir *et al.*, finally provide insight into the outstanding questions facing this field and key immediate challenges.

Hormonal regulation is also central to activation of systemic immunity in plants. The past 12 months have witnessed the identification of an elusive mobile signal that can activate systemic acquired resistance, as well as the emergence of other potential candidate molecules. Vlot *et al.* first discuss the identification of methyl salicylate as the mobile SAR signal then crucially access new evidence linking participation of small peptides and other hormone derivatives in SAR. These data are summarized in a model that elegantly encapsulates our current understanding of components that contribute to signal generation, translocation, perception, or amplification.

The role of beneficial organisms in the agricultural environment is being accorded more attention with the inevitable realization that these mutualistic associations can contribute significantly to crop production. van Wees *et al.* further extend the efficacy of hormonal signalling as a global defense regulator to priming for enhanced defense. They review how MAMP recognition of rhizobacteria and certain growth promoting fungi such as *Trichoderma* is translated into effective systemic immunity via ethylene and jasmonate dependent signalling networks. Crucially, this systemic MAMP signalling is not associated with costly direct activation of defense but rather priming for enhanced defense.

Two articles further highlight the diversity of interactions at the plant microbe interface. Hogenhout and Loria review the virulence mechanisms of Gram-positive bacteria, a phylogenetically distinct group that diverged early from the better known Gram-negative bacteria. Many Gram-positive species are pathogenic on plants and are known to secrete various adhesins, toxins, plant hormones, and other virulence proteins. Here again, genomics is having a major impact. Genome sequences of several Gram-positive bacteria revealed the importance of horizontal gene transfer in the evolution of phytopathogenicity. Felton and Tumlinson overview our current knowledge of the volatile vocabulary associated with plant–insect interactions. While the recognition of herbivore associated molecular patterns and effectors (e.g. glucose oxidase) parallel scenarios discussed above, they also stress the need to consider resident foliar microbes, which can profoundly influence the outcome of this dialog. Indeed, it is likely that this will be an emerging theme in future plant–microbe–insect interaction studies.

Historically, the field of plant–microbe interactions has played a key role in the birth and development of RNA-silencing or RNAi, one of the hottest current topics in biology. RNAi is a universal gene regulation mechanism in eukaryotes that also functions in cellular defense against pathogens. Voinnet describes how in plants RNAi contributes to not just viral defense but also basal and race-specific resistance to other pathogens. Voinnet postulates that RNAi provides a high degree of flexibility in regulation of gene expression that further enhances the ability of plants to adapt to their environment. The Davis *et al.* article describes how RNAi technology is playing a key role in research on plant–nematode interactions. First, RNAi 'knockdown' of nematode genes can be achieved by hairpin dsRNA soaking enabling functional analyses of parasitism genes. Second, host-derived RNAi can be used to target parasitic nematode genes and engineer disease resistance presumably via ingestion of small interfering RNA (siRNA).

In conclusion, despite the staggering diversity of interactions between plant and microbes illustrated by this collection of articles, some guiding principles are clearly perceptible and will undoubtedly continue to drive research in the field.

Also, genome sequences will continue to become available for species that represent the diverse lifestyles and phylogenetic spectrum of plant-associated microbes. This will enable significant discoveries in organisms that are traditionally difficult to study and narrow the gap between traditional model systems and other organisms. Nonetheless, despite the enormous wealth of genomic resources and significant recent success in defining core host signalling nodes, a mechanistic understanding of the individual and collective contribution of effectors to pathogen nutrition and suppression of basal defense remains a considerable challenge. Progress will require embracing even more integrated functional approaches, including recognition of spatiality and an appreciation of the role of small molecules in defense responses.