

Battle for survival: plants and their allies and enemies

Editorial overview

Xinnian Dong and Regine Kahmann

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Xinnian Dong

Department of Biology, Duke University, Box 90338, Durham, NC 27708-0338, USA
 e-mail: xdong@duke.edu

Xinnian Dong's main research goal is to understand the interactions between microbes and their hosts. She uses *Arabidopsis thaliana* as a model organism to perform genetic and genomic studies of plant immune responses. Dr Dong is especially interested in the response known as SAR, which when induced can provide plants protection against a broad spectrum of pathogens. The Dong laboratory has identified several key components in this inducible defence response. Amongst them, NPR1 has been shown to play a central role. A loss of NPR1 function results in hypersensitivity to disease, whereas over-expression of NPR1 leads to enhanced, broad-spectrum resistance. Currently, the Dong laboratory is using new genetic and genomic tools to construct the plant immune network and to investigate how SAR, a short-term immune response, is mechanistically linked to the plants' long-term survival strategies during evolution.

Regine Kahmann

Max Planck Institute for Terrestrial Microbiology, Dept. Organismic Interactions, Karl-von-Frisch-Strasse, D-35043 Marburg, Germany
 e-mail: kahmann@mpi-marburg.mpg.de

Regine Kahmann's main research goal is to understand how biotrophic plant pathogenic fungi establish a compatible interaction with their hosts. She uses the *Ustilago maydis*/maize system as a model. Her work focuses on two areas. One is how the fungus perceives the plant surface. Her laboratory has identified the primary cues for fungal differentiation on the leaf surface and is currently pursuing how these cues are perceived and how they connect to the conserved underlying signalling network. Her second main area of research centres on a large class of novel secreted effector proteins. In the *U. maydis* genome many of the respective genes are organized as clusters that are upregulated during the biotrophic stage. Her group could show that several of these novel effectors suppress plant defence responses at discrete stages of biotrophic development. Currently, the Kahmann laboratory is determining the localization of these effectors as well as their site and mode of action. In addition her group is using comparative genomics of related fungal species to study effector gene evolution and to identify determinants for host specificity.

The recent discovery that there are approximately 10–100 trillion microorganisms associated with a single human body prompted some scientists to make the outrageous claim that we are 90% microbial! Lacking the mobility of animals, plants probably have even more intimate relationships with microbes. Studies of plant–microbe interactions were initially driven by agriculture, but the striking parallels found in innate immune responses between plants and animals have brought plant pathology to the forefront of basic biology. Nevertheless, it was the use of monocultures that led to the detection of genetic variations in plant immune responses and resulted in the cloning of the polymorphic resistance (R) genes 15 years ago. What great progress has been made in 15 years! Studies of plant–biotic interactions have moved from mindless ‘spray and pray’ to a highly integrated field of molecular biology, cellular genetics, genomics, biochemistry, metabolomics, as well as evolution and ecology. Here we present a collection of reviews summarizing some of the recent exciting findings. A common theme in these reviews is that each host's immune mechanism often encounters a counter-attack strategy in the pathogen.

The first two reviews in this series, ‘Fungal phytotoxins as mediators of virulence’ by Möbius and Hertweck and ‘Recent progress in discovery and functional analysis of effector proteins of fungal and oomycete plant pathogens’ by Ellis *et al.* highlight the diversity of mechanisms used by fungal and oomycete pathogens to establish a compatible/incompatible interaction. They range from toxic compounds produced by the pathogen or even by pathogen-hosted bacteria, which are designed to distress, weaken or kill the host, to a multitude of secreted effector proteins. For this latter class, Ellis *et al.* describe the immense impact of genomics and transcriptomics on their identification and localization based on specific motifs used for translocation into host cells. They also survey the current status of ascribing avirulence/virulence functions to these mostly novel proteins, touching on the problems encountered by redundancy, the possible translocation mechanism in light of new data from studies of *Plasmodium*, as well as the ongoing search to identify virulence targets.

On the topic of plant immunity, in ‘Host–pathogen warfare: the plant cell wall’ Hématy *et al.* use the fortress walls of medieval cities as a metaphor to describe the functions of plant cell walls against pathogens that must pass through the wall to gain access to water and nutrients in the host. The authors first discuss the possible mechanisms that plants employ to monitor cell wall integrity, based on what is known in yeast. Various plant cell wall elicitors are then described. In addition to these chemical signals, assault on the cell wall by structures such as haustoria can generate physical pressure on the membrane. The various receptors involved in the perception of these signals, both chemical and mechanical, are summarized in Figure 2 of their

review. Because plant cell wall associated defences are similar to those triggered by pathogen-associated molecular patterns (PAMPs), the authors propose to use PAMP signalling as a model to study cell wall integrity sensing.

In 'Early molecular events in PAMP-triggered immunity' Zipfel first summarizes recent studies of PAMP recognition by pattern recognition receptors (PRRs) in various plant species and points out the main distinction between PRRs and R proteins. The former are receptors of molecules that are conserved amongst a given class of microbes whereas the latter detect (often indirectly) highly variable microbial effectors. Zipfel also clarifies that the programmed cell death response is not unique to R-mediated immunity; some PAMPs can also trigger cell death in plant hosts. Recent studies show that the earliest event after PAMP recognition is multimerization between PRRs and other membrane-associated proteins. The author believes that these proteins are either signal adaptors or amplifiers for PRRs. The importance of this PAMP-triggered immunity (PTI) is demonstrated by the various strategies that bacterial pathogens use to inhibit PRR and adaptor functions.

It is known that MAPK cascades are involved in various plant responses to biotic and abiotic stresses. In 'MAPK cascade signalling networks in plant defence' Pitzschke *et al.* report new insights into the roles of MAPK cascades in PTI, phytoalexin biosynthesis and stomatal immune responses. Even though plant genomes encode large numbers of MAPK pathway components (110 in *Arabidopsis*), only a few of them have been studied in detail. In this review the authors focus on the role of two positive immune mediators, MPK3 and MPK6, and one negative regulator, MPK4, and present an interesting example of how *Agrobacterium* can hijack the host MAPK system to aid infection.

In contrast to the small number of PRR and MAPK cascades studied in plant immune responses, over 40 R proteins have been cloned and functionally studied so far. In 'STANDing strong, resistance proteins instigators of plant defence' Lukasik and Takken delve deep into the structure and function of R proteins, which are STAND (signal transduction ATPase with numerous domains) family proteins. Table 1 and Figures 1–3 of this review nicely summarize the huge amount of information on the functional domains of R proteins and their interacting partners.

Pathogen infection can often trigger wholesale changes in host cellular functions. In 'Trafficking vesicles: pro or contra pathogens?' Frey and Robatzek provide an overview on the inward and outward host membrane traffic redirected upon pathogen challenge and their key roles in pre-invasion defence, PTI, systemic acquired resistance

(SAR) as well as in pathogen effector uptake. Because this is a new direction for plant immune studies, Frey and Robatzek also update the current knowledge in animal systems. The authors point out that understanding the driving force for this pathogen-targeted vesicle traffic and identification of the cargos carried by these vesicles will be the next challenge.

Autophagy, the process controlling the degradation of a cell's own components, is emerging as an integral component of infection-related development in several plant pathogenic fungi as well as during the hypersensitive plant response. In 'The emerging role of autophagy in plant pathogen attack and host defence' Talbot and Kershaw give an overview of macroautophagy as well as selective autophagy systems and describe the newly uncovered significance of these starvation-induced processes in appressorium-mediated plant infection by fungal pathogens. They also highlight the role of autophagy for the spatial restriction of programmed cell death triggered by specific avr/R gene interactions and speculate that autophagy could be the mechanism of plant cell death during the plant immune response or provide for cell survival when other pro-death signals spread.

There are several stress-induced signals in plants. Amongst these, nitric oxide (NO) is a particularly difficult one to work with. This is reflected in the title of the review by Leitner *et al.*, 'NO signals in the haze: nitric oxide signalling in plant defence'. Even though NO has been implicated in many physiological processes, including immune responses, NO production, turnover and mode of action are still poorly understood in plants. One of the reasons, as the authors point out, is that the pleiotropic phenotypes of NO-related mutants often complicate genetic studies. However, the authors are more optimistic about the recent progress in understanding NO-dependent protein modifications, especially S-nitrosylation, during plant defence. Identification of these target proteins, which are involved in controlling gene regulation, multiple hormonal signalling pathways as well as cell death, will provide us with valuable molecular markers to support future studies on NO signalling in plants.

Identification of the mobile signal(s) for SAR has also been a long and difficult endeavour. In 'Plants under attack: systemic signals in defence' Shah discusses the various metabolites that have been reported to be possible long distance signals in plant defence and entertains the possible advantages of having multiple systemic signals for SAR.

Padmanabhan *et al.* show that besides proteins, phytohormones and certain metabolites, 'Host small RNAs are big contributors in plant innate immunity'. The review focuses on the role of pathogen-induced endogenous small RNAs, such as nat-siRNAs and lsiRNAs, in plant

defence and the strategies used by bacterial pathogens to suppress the host small RNA-mediated gene-silencing pathway through bacterial-silencing repressors (BSR). The authors point out that more than 30% of the *Arabidopsis* genome produces antisense transcripts, underlining the significant potential for small RNA production and regulation.

When plants are attacked by herbivores, they do not rely solely on their own defence mechanisms but recruit help from outside, that is predators and parasitoids. Two reviews deal with these issues. In 'Plant defence against herbivory: progress in identifying synergism, redundancy and antagonism between resistance traits' [Rasman and Agrawal](#) argue that in order to understand the complex and variable defences of plants against herbivore attack on the physiological as well as ecological level, genetic modification, quantitative genetics and phylogenetically controlled comparative studies are needed. They derive their conclusions from examples where major types of direct defences are compromised. Such experiments have revealed that redundancy, synergy and antagonism are not exceptions but the rule. They also pick up on the debate on the evolutionary and ecological significance of defence compounds and discuss the possibility that secondary metabolites do nothing but serve to increase the probability of producing a few biologically active compounds when defence is required or the alternative that phytochemical diversity is self-adaptive.

[Unsicker et al.](#) in 'Protective perfumes: the role of vegetative volatiles in plant defence against herbivores' evaluate the roles of plant volatiles that are emitted upon herbivore damage. They survey the diverse roles of such volatiles as herbivore repellents, attractants of herbivore enemies as well as attractants of plant enemies. They advocate more field-based research for a full evaluation of the defensive significance of volatiles and for the assessment of the effects of volatile production on plant fitness. Only such experiments in natural habitats will allow to distinguish between contributions of abiotic stresses and may eventually provide an answer as well as contributions by other trophic levels and may eventually allow an answer to the question of why herbivores induce the synthesis of a complex bouquet of volatiles rather than a single compound.

On a subject where herbivores act in service of the plant, [Brandenburg et al.](#) in 'The sweetest thing advances in nectar research' focus on nectar production in angiosperms which functions as a reward to visitors who transport pollen in return. They address the physiology and genetics of nectar sugar production and nectar composition, highlight new data showing that the driving selective force for

pollinator preference is not only nectar sugar composition but also sugar concentration and nectar volume. [Brandenburg et al.](#) also discuss alternative pollination strategies where the plant deceives the visitor by mimicking a mating partner or rewarding species. To answer the fundamental question whether plants with reduced nectar content or altered nectar composition will show reduced fitness (because of avoidance by pollinators) or whether their fitness will increase because of enhanced outbreeding, the authors propose to generate 'cheating plants' by genetic manipulation.

The last three reviews covered here all deal with symbiotic interactions. [Den Herder and Parniske](#) in 'The unbearable naivety of legumes (in symbiosis)' give an overview on the molecular events leading to rhizobial nodule symbiosis. They place special emphasis on those processes that are diversified and depend on the genotypes of both partners as this may offer new strategies towards increased nitrogen fixation in legumes. They coin the term 'naivety' to describe the fact that symbiotic nitrogen fixation is often suboptimal owing to an early partner choice that does not allow selection for the later benefits of the plant. [Bucher et al.](#) in 'Chasing the structures of small molecules in arbuscular mycorrhizal signalling' focus on the molecules that govern the interaction between arbuscular mycorrhiza fungi and their host plants. Compared to the molecular understanding of the rhizobial N-fixing root nodule symbiosis, this system suffers from the obligate biotrophy of the fungal partner, which currently prevents the application of reverse genetic approaches. Nevertheless, in recent years crucial molecules used for communication have been identified and ideas on their perception and functions are emerging. [Bucher et al.](#) give special emphasis to possible parallels in other systems that might lead to the identification of fungal receptors for plant signalling compounds.

[Martin and Nehls](#) describe the impact of genomics for elucidating which genes govern the interaction of ectomycorrhizal fungi with their respective host plant. In 'Harnessing ectomycorrhizal genomics for ecological insights' they discuss that the dual life style of such fungi that can either live in the soil as saprotrophs or as symbionts inside plant roots is reflected by specific features of their genome. They also describe the novel tools being developed for genotype-to-phenotype analysis and highlight how genomic information can be used to shed light on the mechanisms by which ectomycorrhizal fungi control biogeochemical cycles in forest soils.

Finally, we would like to thank the authors for sharing their insights and apologize for missing some of the exciting topics. Happy reading.