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Authors

Ronald, Pamela C

Shirasu, Ken

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Front-runners in plant–microbe interactions

Editorial overview

Pamela C Ronald and Ken Shirasu

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Pamela C Ronald^{1,2}

¹ Plant Pathology Faculty, The Genome Center, University of California, Davis, CA 95616, USA

² Joint Bioenergy Institute, Emeryville, CA 94608, USA

e-mail: pcronald@ucdavis.edu

Pamela Ronald is professor, Department of Plant Pathology and the Genome Center at the University of California, Davis. She also serves as Director of Grass Genetics at the Joint Bioenergy Institute.

Ronald's laboratory has engineered rice for resistance to disease and tolerance to flooding, which seriously threaten rice crops in Asia and Africa. Ronald led the isolation of the rice XA21 immune receptor, the bacterial Axx21 quorum sensing factor and the rice Sub1A submergence tolerance transcription factor. In 1996, she established the Genetic Resources Recognition fund, a mechanism to recognize intellectual property contributions from less developed countries.

She and her colleagues were recipients of the USDA 2008 National Research Initiative Discovery Award for their work on rice submergence tolerance. Ronald was awarded a Guggenheim Fellowship, the Fulbright–Tocqueville Distinguished Chair and the National Association of Science Writers Science in Society Journalism Award. She is an elected fellow of the American Association for the Advancement of Science.

Ronald has written opinion pieces for the Boston Globe, The Economist, and the New York Times and is a blogger for National Geographic's ScienceBlogs. She is coauthor with her husband, Raoul Adamchak, an organic farmer, of 'Tomorrow's Table: Organic Farming, Genetic, and the Future of Food'. Bill Gates calls the book 'a fantastic piece of work'. In 2011, Ronald was selected as one of the 100 most creative people in business by Fast Company Magazine.

Ken Shirasu

Plant Immunity Research Group, RIKEN Plant Science Center, 1-7-22 Suehiro-cho, Tsurumi-ku, Yokohama 230-0045, Japan

The Ken Shirasu laboratory investigates the molecular mechanisms underlying plant immunity, with a focus on signaling proteins that are modified upon infection. The Shirasu lab also studies *Striga* spp., parasitic plants that cause devastating agricultural damages especially in Africa, using genomic tools to understand how plants infect other plants.

Plants and microbes, abundant in the environment, can peacefully coexist or battle for survival. Plants must determine if the associated microbes are friends or foes, while microbes attempt to manipulate the plant host to access nutrients and/or create shelter. In this volume of Current Opinions in Plant Biology, we highlight multiple topics in the field, including immune receptor biology, metabolomics, signal transduction, symbiosis biology, and microbial genomics.

Receptors mediating immunity

For over 100 years, genes for resistance have been used in breeding. However, until recently the molecular basis of this immunity was unknown. Advances in the last 15 years has revealed that plant and animal innate immune systems depend on a diverse assortment of cell surface and cytoplasmic receptors that detect and respond to invading pathogens.

In plants, these receptors are commonly classified into a group that recognizes conserved microbial signatures (called pattern recognition receptors, PRRs) and a group that recognizes highly variable effectors (nucleotide binding-leucine rich repeat receptors, NB-LRRs). The first group contains both extracellular membrane bound receptors and intracellular receptors that frequently contain (or associate with) non-arginine–aspartate (non-RD) kinases. The second group includes intracellular NB-LRRs, which are often fused to additional domains but typically lack kinase domains. These two systems of microbial perception in plants are commonly referred to as Pathogen Associated Molecular Pattern [PAMP] Triggered Immunity (PTI) and Effector Triggered Immunity (ETI), respectively. Understanding how microbial signals are converted into PTI or ETI remains a fundamentally important issue.

Four reviews in this volume address these issues. First the mechanism of action of three well-characterized PRRs, rice Xa21 and Arabidopsis FLS2 and EFR, are addressed. Monaghan *et al.* discuss the important role of multiprotein complexes at the plasma membrane that interact with PRRs. The authors describe the molecular interactions and protein modifications that have been uncovered and shown to occur between PRRs and their regulatory proteins. These studies have provided important mechanistic insight into how plants avoid infection and achieve immunity.

Dardick *et al.* note that the non-RD subclass of kinases is associated with PRR-mediated immunity. For example, of the approximately 75 plant receptor-like kinases (RLKs) that have been functionally characterized, nearly one dozen of these are non-RD kinases, all of which have known or

putative functions in the recognition of conserved microbial signatures characteristic of PRRs. Unlike their more common RD counterparts, non-RD kinases do not generally auto-phosphorylate the activation loop, presenting a potential mechanistic difference in their activation and/or function. Such changes to the RD motif may reflect distinctive properties of PRR-mediated signaling. Determining the precise role of kinases in PRR signaling and their mechanism(s) of activation will require further biochemical and structural studies to identify how non-RD kinase catalytic activity is regulated, what role (if any) non-RD catalytic activity plays in signaling, and the relationship between non-RD kinases and their RD regulatory partners.

Beck *et al.* describe the importance of appropriate subcellular localization for PRR function. Localization and trafficking of PRRs play important roles in quality control and possibly in the number of active receptors at the plasma membrane. Because endocytosis has been observed for a number of PRRs, it is likely that this process represents a conserved mechanism across different plant-microbe interactions. Endocytosis may be important for increasing the number of PRR signaling platforms, distributing PRR signaling within the cell, triggering/promoting a subset of PRR-mediated responses, and limiting overactivation of PRR signaling. This would collectively enhance the accuracy of the receptor outputs, allowing the plant to efficiently defend itself against potential pathogens without detrimental effects to the host. Understanding the subcellular dynamics of PRRs will provide novel tools to dissect the signaling pathways and elucidate the interception between PRR trafficking and associated responses.

Takken describes progress in our understanding of the molecular mechanism underlying NB-LRR protein function. The elucidation of the first domain structures of NB-LRRs combined with computational modeling has facilitated the construction of 3D models of entire NB-LRR proteins. Studies linking the nucleotide binding state of NB-LRRs to intra-molecular and inter-molecular interactions have provided a mechanistic framework on how these proteins can act as sensors, switches and responders. Heidrich *et al.* also outline how and where NB-LRR proteins function by forming higher order signaling complexes. Because, activation of NB-LRRs often results in host cell death, tight regulation of these proteins is required to avoid inappropriate cell damage. Finally, Ti and Li further discuss ubiquitination, an emerging mechanism for rapid degradation of NB-LRR proteins.

Most plants are resistant to most pathogenic microbes. In other words, some pathogens are able to infect particular plants (host) but fail to overcome the barriers of other species (nonhost). Fan and Doerner summarize multiple mechanisms for 'nonhost resistance (NHR)'. For

example, some plants resist particular viruses by using gene silencing systems or block viral replication preventing viral translation. The two layered surveillance system governed by PRR and NB-LRR proteins is also likely to play an important role in NHR. These proteins can be a great resource for creating crop plants with durable resistance. Indeed, transgenic utilization of PRR and NB-LRR to accomplish NHR has been successful [1,2]. However, transfer of NB-LRR to achieve NHR in a different family has faced difficulties, representing a phenomenon called restricted taxonomic functionality [3,4]. Further technological breakthroughs to overcome this problem are urgently needed.

Chemical defense and diversity

Bednarek, as well as Fan and Doerner, provide excellent examples for NHR chemical defense. In particular, they highlight the role of glucosinolates (GSLs), which are produced upon pathogen infection or tissue damage of crucifers. For example, Arabidopsis plants produce aliphatic isothiocyanates (ITCs), derivatives of GSL, which inhibit the growth of certain *Pseudomonas syringae* pathovars. Significantly, *P. syringae* pv. *tomato* strain which contains the *saxA* enzyme to metabolize ITCs is able to colonize in Arabidopsis, suggesting that ITCs play an important role in NHR. Indole GSLs are also critical compounds produced when pathogens enter epidermal cells, triggering PAMP-induced callose deposition in Arabidopsis. Another phytochemical benzoxazinones also controls pathogen entry; however, understanding its precise mechanism requires further investigation.

The phytochemicals used to fight against or attract other organisms are highly diverse. How do plants establish this observed metabolic diversification during evolution? Diversification of individual enzymes can be driven by the gene duplication and subsequent mutation followed by natural selection. But how this is possible for apparent emergence of entire new pathways? Potential accumulation in a metabolic pathway intermediate could result in negative effects on growth. To answer this intriguing question, Kliebenstein and Osbourn provide a genomic view of how secondary metabolic pathways evolve. A central finding from recent genomic analyses is the identification of physical gene clusters for the metabolic pathways. The clustered gene sets may have an evolutionary advantage as these genes are often coordinately expressed, similar to the bacterial operon system. Such transcriptomics and metabolomics studies have begun to provide insights into how diverse networks of phytochemicals have evolved.

Signal transduction: redox change and activation of transcriptional factors

Immediately after plants perceive microbes, the cellular redox status dramatically changes. The main contributing factors for the change are reactive oxygen and

nitrogen intermediates (ROIs or RNIs). Although the sources of ROIs have been well documented, we still do not know how plants produce RNIs. Yu *et al.* describes the current view of the potential sources of RNIs. Bursts of RNIs, and to a lesser extent ROIs, lead to S-nitrosylation, the redox-based covalent attachment of a nitric oxide (NO) to a cysteine residue on a number of proteins. Yu *et al.* list S-nitrosylation targets which have been identified to control plant immunity. Notable targets are NPR1 and RBOHD, which are the key regulators of salicylic acid (SA)-based and ROI-based immunity pathways, respectively. S-nitrosylation acts like other post-translational modification such as phosphorylation to regulate protein functions. How the S-nitrosylated residues regulate immunity-related proteins is discussed in the review.

The key hubs of the transcriptional network in plant immunity are the WRKY transcription factors. There are 72 WRKY encoding genes in the Arabidopsis genome, and most of them respond to pathogen infection transcriptionally and/or post-translationally. Ishihama and Yoshioka summarize recent findings on various WRKYs, focusing mainly on their post-translational regulations. For example, several groups have shown that the group-I WRKY proteins, which contain a serine–proline (SP) cluster, are substrates of mitogen activated protein kinases (MAPKs). The phosphorylation of a WRKY by MAPKs enhances its DNA binding and transactivation activities. It is not yet known how different MAPKs choose the right WRKYs at the right time to trigger a specific effect. Systematic interaction and phosphorylation analyses will help sort out the complicated substrate specificities.

Symbiosis biology

Most higher plants are able to form symbiotic associations with certain microbes to obtain necessary nutrients. In the rhizosphere, the most well-characterized symbiotic interactions are nitrogen fixing rhizobium with legumes and Arbuscular mycorrhizal fungi (AMF) with non-Brassicaceae plants. Geurts *et al.* summarize recent findings in this field of research, comparing rhizobium and AMF symbiotic signaling networks. Signaling molecules (Nod factor) from rhizobium and AMF (Myc factor) are strikingly similar and the perception of the compounds are likely to be mediated by LysM-type receptor kinases. The downstream also contains common signaling modules that are required for both rhizobium and AMF symbiosis. From an evolutionary stand point, rhizobium nodule formation is much younger than AMF symbiosis; it is probable that the nitrogen fixing bacteria hijacked AMF symbiosis signaling networks. Some plants, such as Legumes, can accommodate both rhizobium and AMF. How do they differentiate the two? The secrete codes may be written in Ca²⁺ oscillation and the key Enigma machine to decode is calcium and calmodulin-dependent

protein kinase (CCaMK). Here, Singh and Parniske discuss how CCaMK functions in symbiosis and provide a mechanistic model.

Microbial genomics and beyond

Lanfranco and Young report on our first look into the genomes and transcriptomes of AMF. Although all known AMF have long been classified into the phylum Glomeromycota, based on new genome sequence information, this classification now requires revision. This will be a complicated task because AMF are multinucleate and nuclei can be transferred to a genetically different strain by hyphal fusions. Genome-wide transcriptomic analysis of an AMF reveals a metabolic complexity but little gene loss. The review also discusses the exchange of resource, especially carbon and phosphate, between the host and symbiotic fungi as predicted by the genome data analyses.

Certain fungi living in the aerial tissues can also form mutualistic symbiotic associations with plants. Tanaka *et al.* summarize progress on the studies of Epichloë endophytes that live in temperate grasses. Epichloë endophytes provide the host plants with secondary metabolites that serve a bioprotective function. To maintain this mutualistic interaction, the Epichloë endophytes restrict the fungal growth through synchronized intercalary division and extension. The reactive oxygen species produced by NADP oxidase are required for this synchronized growth. Genome-wide transcriptomic analysis of the endophyte is ongoing, identifying key genes important for the symbiotic state.

A current paradigm in the field is that plant-associated microbes secrete ‘effectors’, molecules that manipulate host cell processes for their own benefit. As genome studies advance in an astonishing rate, the number of potential effectors is exponentially increasing. In this volume, three papers review effectors from bacteria, fungi, and oomycetes. Feng and Zhou focused on bacterial effectors secreted via the type III system. The targets of the well-characterized type III effectors are mainly PTI signaling modules. A number of interesting biochemical properties of the effectors have been discovered and beautifully supported by the structural analyses. By contrast, the identified effectors from fungi and oomycetes are relatively small, and understanding the precise mechanisms of how these proteins function is challenging. Rafiqi *et al.* discuss progress toward understanding the role of effectors in plant–fungal interactions. They describe how the recent genome sequencing of rust and powdery mildew obligate biotrophs has provided insight into the repertoires of potential effectors of these highly specialized pathogens. Identification of the first host-translocated effectors from mutualistic fungi has revealed that these fungi also manipulate host cells through effectors. The biological activities of some fungal effectors are just beginning to be revealed, and much uncertainty still surrounds the mechanisms of

transport into host cells. This is also the case for oomycete effectors as Boxkurt *et al.* highlight the novel insights from structural and functional analyses and discuss important questions of oomycete effector biology.

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