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MEETING REVIEW

12th Japan-US Seminar in Plant Pathology Meeting Report

Yumino Sasaki,[1,†] Juliana González-Tobón,[1] Yuta Hino,[2] Chujia Jin,[3] Tianrun Li,[4] Tan Anh Nhi Nguyen,[5] Blake Oakley,[6] and Danielle Stevens[4]

[1] Plant Pathology and Plant-Microbe Biology Section, School of Integrative Plant Science, Cornell University, Ithaca, NY 14853, U.S.A.
[2] Graduate School of Bioagricultural Sciences, Nagoya University, Nagoya, Japan
[3] Laboratory of Plant Pathology, Graduate School of Agriculture, Kyoto University, Kyoto, Japan
[4] Department of Plant Pathology, University of California, Davis, Davis, CA 95616, U.S.A.
[5] Department of Life Sciences, Graduate School of Arts and Sciences, The University of Tokyo, Tokyo, Japan
[6] Department of Plant Pathology, University of Georgia, Athens, GA 30602, U.S.A.

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The 12th iteration of the Japan-US Seminar in Plant Pathology was held in Ithaca, New York at Cornell University in the fall of 2022. Presentations covered a range of topics under the theme "Remodeling of the Plant-Microbe Environment During Disease, Defense, and Mutualism," and the meeting included a panel discussion of best practices in science communication. This report presents highlights of the meeting, from the perspective of early career participants of the seminar.

Keywords: effectors, mutualism, NLR, plant immunity, PRR

The 12th Japan-US Seminar in Plant Pathology, "Remodeling of the Plant-Microbe Environment During Disease, Defense, and Mutualism", was convened August 28 through September 2, 2022, at Cornell University. Since the last Japan-US Seminar in 2015, there have been profound leaps in our understanding of both sides of plant-microbe interactions. Approximately 100 scientists from various institutions shared the latest developments toward understanding the multi-layered interactions that occur at the interface of the plant and microbe. A poster session, a panel discussion on science communication, and networking activities supplemented the presentations. In this report, we, early career scientists, highlight presented studies that, in our view, are addressing critical knowledge gaps in the molecular interactions of plants with pathogens and mutualists. We also present key takeaways from the science communication panel and propose questions for future investigation.

Defense

Plants carry two major classes of immune receptors, cell surface pattern-recognition receptors (PRRs) and intracellular nucleotide-binding leucine-rich repeat (LRR) receptors (NLRs). PRRs with or without a kinase domain, receptor-like kinases (RLKs) or receptor-like proteins (RLPs), respectively, have various ectodomains to detect diverse ligands, including microbe-, plant cell damage–, and herbivore-associated molecular patterns, to induce pattern-triggered immunity (PTI) (Ge et al. 2022). NLRs recognize pathogen-secreted effectors or effector-mediated perturbations of host targets inside the plant cell, inducing effector-triggered immunity (ETI) that generally culminates in cell death via the hypersensitive reaction (HR) (Yuan et al. 2021). Characterizing the diversity of these immune receptors and their underlying molecular mechanisms is necessary for understanding the co-evolutionary plant-pathogen arms race and engineering disease resistance in crop plants.

Adam Steinbrenner (University of Washington) reported on an evolutionary trajectory through which novel immune receptor functions can emerge. Several phaseoloid legume species recognize the caterpillar-associated molecular pattern inceptin (In11) by the RLP Inceptin receptor (INR). By analyzing the INR locus, Dr. Steinbrenner showed that, over the course of about 53 million years, an initial insertion event followed by diversification gave rise to a subset of phaseoloid species evolving a functional INR. Reconstruction and functional analysis of ancestral and chimeric INRs showed that In11 detection is mediated by a few amino acid differences in the INR LRR domain (Snoeck et al. 2022). These findings provide a model of how plants can evolve detection of pathogen patterns through immune receptor diversification and localized mutation. Additionally, this advance serves as a promising foundation for engineering INRs in legume crops such as soybean and chickpea that do not carry a functional INR.

Greg Martin (Cornell University) reported on an NLR, Ptr1, from a wild tomato relative that can detect the proteolytic activity of the type III effector AvrRpt2, present in *Pseudomonas syringae* pv. *tomato* race 1 strains. Race 1 strains lack effectors AvrPto and AvrPtoB that induce the widely used Pto/Prf-based resistance in cultivated tomatoes. No qualitative resistance to *P. syringae* pv. *tomato* race 1 had been identified. Remarkably, Ptr1 has convergently evolved with two other NLRs from *Arabidopsis* and apple to recognize the proteolytic activity of AvrRpt2, an effector widely distributed in phytopathogenic bacteria (Mazo-Molina et al. 2020). The discovery of Ptr1 and its addition to the list of NLRs detecting AvrRpt2 activity provides new insights into the selective pressures that drive NLR evolution and will pave the way for editing existing tomato cultivars,

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[†] Corresponding author: Y. Sasaki; ys494@cornell.edu

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which carry a pseudogenized Ptr1 ortholog, for resistance against emerging *P. syringae* pv. *tomato* race 1 strains (Mazo-Molina et al. 2019).

Instead of acting alone to detect pathogen effectors or effector perturbations, some NLRs function in pairs. NLR pairs consist of a sensor and a helper NLR, in which the sensor NLRs recognize pathogen effectors and interact with the cognate helper NLRs to cooperatively induce plant immune responses. Ryohei Terauchi (Kyoto University and Iwate Biotechnology Research Center) presented the latest findings on the molecular interactions between paired rice NLRs and their cognate *Magnaporthe oryzae* avirulence (AVR) genes. The rice genome contains almost 500 NLR-like genes, although how most of these NLRs work, individually or in pairs, is largely unknown (Baggs et al. 2017). Dr. Terauchi reported on the diverse non-canonical integrated domains (IDs) of rice sensor NLRs that bait *M. oryzae* effectors by mimicking their plant host targets (Fujisaki et al. 2017; Grund et al. 2019; Maqbool et al. 2015; Ortiz et al. 2017). Evidence was presented that *M. oryzae* effector AVR-Pik is capable of binding and stabilizing host small HMA (heavy metal–associated) proteins, some of which were shown to be susceptibility factors. The sensor NLR Pik-1, in turn, evolved an HMA ID that acts as bait for the effector. This finding provides new insight into the co-evolutionary arms race between rice and *M. oryzae* (Oikawa et al. 2020). Dr. Terauchi also expanded on recent work investigating how NLR pairs evolve. By comparing NLR pair alleles at the Pia/Pias locus across diverse *Oryza* species, a picture for divergent evolution of sensor and helper NLRs emerges, in which the helpers have undergone purifying and sensors have undergone balancing selection (Shimizu et al. 2022). These findings support a model in which the adoption of diverse IDs contributes to the evolution of sensor NLRs to keep pace with the rapid evolution of pathogen effectors that target host proteins. This understanding may enable engineering of sensor NLR IDs to expand AVR recognition specificity.

Immune responses from PRRs and NLRs must be strictly regulated to balance the tradeoff between defense and growth. Plant peptides called phytocytokines have recently been implicated in fine-tuning of immune responses (Rzemieniewski and Stegmann 2022). However, the molecular mechanisms of their regulatory functions remain unclear. Libo Shan (Texas A&M University) reported on a group of small phytocytokines regulating defense and water loss (SCREWs), recognized by the LRR-RLK plant screw unresponsive receptor (NUT). The perception of SCREWs by NUTs induces stomatal reopening after bacterial pathogen invasion, leading to reduced apoplastic water potential, which ultimately inhibits pathogen multiplication. SCREW and NUT expression is specifically upregulated after pathogen invasion and during PTI (Liu et al. 2022). These results suggest that precise and localized regulation of stomatal activity ensures a swift change of the host micro-environment to limit bacterial proliferation.

Plant-derived C-terminally encoded peptides (CEPs) are also known for modulating immune outputs (Fitrianti et al. 2022; Zhu et al. 2020). Kazuhiro Toyoda (Okayama University) reported that the exogenous application of the *Arabidopsis* CEP5 suppresses PTI. Pretreatment of *Arabidopsis* plants with purified CEP5 also enhances disease susceptibility to non-adapted and avirulent pathogens like *Colletotrichum tropicale* and *Pseudomonas syringae* pv. *tabaci* (Fitrianti et al. 2022). Furthermore, Chiaki Itoh and Haruka Hasegawa, students in Dr. Toyoda's lab, presented evidence for salicylic acid treatment– and PTI/ETI–induced expression of some CEPs. Although the CEP5 receptor and mechanism of CEP-mediated immunity attenuation remain unclear, these new data support a model in which CEPs modulate PTI/ETI pathways and prevent excessive immunity.

In addition to peptides that modulate specific responses to pathogens or inhibit immunity, NLRs themselves can regulate inappropriate activation of immunity. Hiroaki Adachi (Kyoto University) reported on an atypical NLR that plays this role in the context of an NLR network. NLR networks comprise multiple helper and sensor NLRs, often encoded throughout the host genome, that work together to induce immunity. Mismatches between helpers and sensors can lead to inappropriate expression, autoimmunity, and growth defects. In asterid plants, NLRs required for cell death (NRCs) are helper NLRs that form key nodes of the NLR network, typically harboring an N-terminal MADA motif associated with the ability to induce the HR (Adachi et al. 2019). Dr. Adachi described NRCX, a novel NRC that lacks a functional MADA motif and is unable to induce cell death like other NRCs do (Adachi et al. 2023). Interestingly, when NRCX is silenced, *N. benthamiana* shows a dwarf phenotype partially dependent on key network helpers NRC2 and NRC3, suggesting NRCX acts as a negative regulator of NRC2- and NRC3-mediated autoimmunity (Adachi et al. 2023). Building on the relatively recent discovery of sensor and helper NLRs and NLR networks, the findings on NRCX expand the diversity of known NLR functions to include maintaining network homeostasis and normal plant development. A better understanding of immune regulation will reveal how plants defend against a myriad of pathogen pressures and will be critical for future engineering of robust disease resistance in plants.

Responses downstream of immune receptor activation were also highlighted. Hirofumi Yoshioka (Nagoya University) reported on the dynamics of mitogen-activated protein kinase (MAPK) activity and reactive oxygen species (ROS) production in response to pathogen and insect attacks. After pathogen sensing, MAPKs phosphorylate WRKY transcription factors, master regulators of plant immunity. In *N. benthamiana*, defense-related MAPKs interact with NbWRKY8 dependent on its D domain and phosphorylate serine residues within the proline-directed serine (SP) cluster (Ishihama et al. 2011). The Yoshioka lab developed a FRET-based MAPK sensor using the D domain and SP cluster of NbWRKY8 and used it to visualize MAPK activity spatiotemporally. Dr. Yoshioka reported the exciting finding that MAPK activation propagates cell-to-cell in response to pathogen and chewing insect attacks. RBOH-dependent ROS production is also a crucial event for plant immunity. Activated NbWRKY8 induces gene expression of NbRBOHB and robust ROS production during ETI (Adachi et al. 2015). Hydrogen peroxide (H_2O_2) leads to sulfenylation, an oxidative post-translational modification, of cysteine residues of ROS sensor proteins (Kimura et al. 2017). Dr. Yoshioka also described the identification, through proteomic screening of sulfenylated proteins, of a candidate ROS sensor protein that positively regulates immune responses. Altogether, the findings presented support the model that the interplay between the MAPK-WRKY pathway and ROS production is a pivotal signaling event in plant immunity, and they provide a view of the complex downstream responses of immune receptor activation.

Disease

PRRs and NLRs are key components of the multilayered plant defense system pathogens face during infection. Throughout the co-evolutionary arms race, pathogens have acquired diverse effectors to overcome immunity mediated by these receptors (Jones and Dangl 2006). In addition to effector proteins, small RNAs (sRNAs) and secondary metabolites (e.g., phytotoxins, phytohormones) play key roles in virulence (Zhang et al. 2022).

Hailing Jin (University of California, Riverside) reported on fungal sRNAs delivered by extracellular vesicles that can hijack plant RNA interference (RNAi) machinery to repress host immune responses (Weiberg et al. 2013). Interestingly, sRNA trafficking is bidirectional; *Arabidopsis* sRNAs can be transferred to pathogenic *Botrytis cinerea* to silence *B. cinerea* virulence genes (Cai et al. 2018). The Jin group successfully expressed modified sRNAs in *Arabidopsis* to silence specific genes of the pathogen responsible for sRNA generation and virulence (Wang et al. 2016). These findings point to custom anti-fungal sRNAs as a promising tool for disease control .

Effector proteins and sRNAs may contribute generally to virulence by suppressing host immune responses, but they can also determine host specificity, as is the case for some bacterial type III effectors (Angot et al. 2006; Bocsanczy et al. 2012; Poueymiro et al. 2009). Through comparative genomic analysis of putative effector content, Danielle Stevens (University of California, Davis) identified candidate determinants of host specificity across several *Clavibacter* spp., which cause severe diseases in crop plants with high host-specificity. The ability of candidates to elicit the HR in non-host plants was tested, implicating the serine proteases ChpG and Pat-1 of *Clavibacter michiganensis* as determinants. This finding suggests that the non-host recognition of these effectors underlies host specificity (Verma and Teper 2022). The work also highlights the power of comparative "effectoromics" to elucidate host range determinants of pathogenic bacteria, which may serve as a foundation for pathogen control strategies. Yoshitaka Takano and Ru Zhang (Kyoto University) reported on host-determining effectors and transcription factors of *Colletotrichum orbiculare.* This pathogen can infect cucurbits as well as distantly related Solanaceae such as *N. benthamiana*. The newly identified effectors, named EPC1 to EPC4, are regulated by the transcription factor TFV1 as well as its closest homolog TVL1 and are critical for full virulence toward the cucurbits but not *N. benthamiana*. The distinct ways effectors can contribute to host specificity, illustrated by the findings shared in these two presentations, raise the interesting question of how different selective forces shape effector evolution and distribution.

Mutualism

Presentations on mutualism delved into mechanisms and co-evolution. Of particular interest was a presentation by Kei Hiruma (The University of Tokyo) that highlighted the dynamic and environmentally dependent nature of some interactions. The ascomycete *Colletotrichum tofieldiae* has been described as a beneficial endophyte that transfers phosphorus to *Arabidopsis*, enhancing plant growth under phosphate-starved conditions (Hiruma et al. 2016). Dr. Hiruma reported on a pathogenic *Colletotrichum tofieldiae* strain isolated in Japan, Ct3, that is closely related to a previously isolated endophytic strain but inhibits *Arabidopsis thaliana* growth by producing abscisic acid (ABA) under phosphate-limited conditions. The Ct3 ABA biosynthesis genes are clustered and co-activated with those for botrydial (BOT), a secondary metabolite that promotes virulence in *B. cinerea* (Hiruma et al. 2022; Siewers et al. 2005). By perturbing ABA signaling, Ct3 represses genes related to nutrient uptake in the host. Interestingly, knock-out of the ABA-BOT cluster or its silencing by increased temperature renders Ct3 beneficial for plant growth in low phosphate conditions (Hiruma et al. 2022). This modulation of the plant host metabolism by Ct3, which occurs only in certain environmental conditions, serves as an example of the dynamic interactions that can exist between fungi and their hosts, ranging from pathogenicity to mutualism. The results also suggest a potential method for redirecting pathogenic fungi toward mutualistic relationships through targeted modulation of secondary metabolite biosynthesis.

New findings on interactions involving multiple microbes and a host plant in field contexts were also reported. Tan Anh Nhi Nguyen (The University of Tokyo) described another interesting strain of *Colletotrichum tofieldiae*, Ct4, which enhances the growth of *Brassica* plants in nitrogen-limited (unfertilized) fields in Japan. The results of 16S metagenomic analysis of the rhizosphere microbiome revealed that Ct4 attracts beneficial bacteria onto Ct4-colonized roots, providing insight into a mechanism through which mutualists could benefit plants. This finding also highlights the importance of understanding the complexity of interactions within the plant-associated microbiome in the native context in order, for example, to use fungal endophytes for plant growth enhancement.

Science Communication

Student moderators Juliana González-Tobón, Yuta Watanabe, and Yumino Sasaki moderated a panel discussion on "Best Practices for Sharing Science" with Maria Fernanda Alvarez (Rice Program Leader, Crops for Nutrition and Health, Alliance of Biodiversity International and International Center for Tropical Agriculture), Morgan Carter (Assistant Professor of Biology, University of North Carolina at Charlotte), Jeanne Harris (Professor of Plant Biology, University of Vermont and Editor-in-Chief of *Molecular Plant-Microbe Interactions*), Sophien Kamoun (Group Leader, The Sainsbury Laboratory), Laura Boykin Okalebo (Senior TED Fellow and Senior Scientific Consultant and Computational Biologist at Bioteam), Yoshitaka Takano (Professor of Plant Pathology, Kyoto University), and Mary Williams (Features Editor at Plant Cell and Plant Physiology, Developer of Teaching Tools in Plant Biology) as panelists.

Discussions focused on the role of social media in science and how it has spurred a "nonstop academic conference for all" (Foell 2021). Panelists illustrated the potential of social media as an educational tool and a gateway for collaboration and professional development. Social media can also expand and diversify networks, draw attention to inequities, and amplify research contributions and ideas from members of underrepresented groups, serving as a powerful tool for marginalized communities in the sciences (Polk and Diver 2020). The usefulness of academic social networks (ResearchGate, Google Scholar, ORCID), especially to early career scientists, was also emphasized. Panelists expressed a preference for open source, public platforms to guard against paywalls that could give rise to unequal access. Panelists also advocated for scientists to establish a searchable and transparent presence on the internet.

For-profit publishers, journal impact factors, and the rise of open science and preprints were also discussed. Importantly, "gatekeeping" by journals and the "publish or perish" model of scientific funding that has led to increased research misconduct were discussed and decried. Panelists praised open access and increasing implementation of preprints by journals, expressing how incorporation of preprints into science policy and research practices could promote open data and easier accessibility to new findings.

Knowing what to share in science was emphasized as being as important as knowing how to share. Audience member Fumiaki Katagiri (University of Minnesota) proposed that scientists should share searchable, organized metadata for each experiment to accurately compare results between labs working on highly context-dependent systems. Literature corrections and retractions were also addressed. Panelists spoke about how publishing a correction or retracting a paper should be normalized. Corrections and retractions should not be viewed as the consequence of "bad" science, but rather, a product of "good" science, i.e., the continued effort of multiple scientists, including the original authors, to validate and build on previous results.

Scientific journals communicate research findings to a specialized audience in a way that is often inaccessible to scientists from outside the field and to the lay audience. Panelists emphasized the value of science communication skills and ability to share information formatted for diverse audiences. In an increasingly connected world, effective science communication is vital, not only to engage more broadly with other scientists but to promote equitable participation in science, to combat misinformation, and to help people make informed decisions in their daily lives. If science is communicated effectively, the benefits of our research will be better understood and realized, and will ensure science is responsive to societal needs.

A recording of the panel can be found on the Cornell University website (https://vod.video.cornell.edu/media/20220831_Best%20practices%20for%20sharing%20science/1_240bsitm).

Status and Future Directions of Molecular Plant-Microbe Interaction Research

Since its inception in the 1960s, the Japan-US Seminars in Plant Pathology have encapsulated the latest developments in the field and have led to many fruitful international collaborations (Ouchi 2006). This seminar, the 12th in the series, highlighted recent progress across a diversity of exciting topics, only a selection of which we have highlighted here. Further, and new to the seminar, the panel discussion illustrated how effective science communication can facilitate better research, establish connections between scientific fields, reduce misinformation, and foster equity in science. The presentations at this seminar give rise to new questions for the field of molecular plant-microbe interactions. How do the diverse array of characterized immune receptors induce downstream physiological responses? How do PRRs and NLRs cooperate to induce these responses, and do effectors interfere at that step? How are effectors shaping pathogen host specificity, and how are host selective pressures in turn shaping effectors? If plants are reprogramming components of their metabolic pathways for beneficial organisms, how do they simultaneously balance inhibition of pathogens? How can this knowledge of plant-microbe interactions be applied to agriculturally relevant plants? Addressing these questions will benefit from international collaborations fostered through meetings such as the Japan-US Seminar. We look forward to its continuation and to work presented at future seminars addressing these questions.

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