

The Rise of Evolutionary Molecular Plant–Microbe Interactions (EvoMPMI)

Shigeyuki Betsuyaku ^{1,2,*}

¹Faculty of Life and Environmental Sciences, University of Tsukuba, 1-1-1 Tennodai, Tsukuba, Ibaraki, 305-8577 Japan

²Microbiology Research Center for Sustainability, University of Tsukuba, 1-1-1 Tennodai, Tsukuba, Ibaraki, 305-8572 Japan

*Corresponding author: E-mail, betsuyaku.shige.ge@u.tsukuba.ac.jp; Fax, + 81-29-853-6110.

(Received January 1, 2020; Accepted January 23, 2020)

With the elucidation of the *Marchantia polymorpha* genome sequence, this liverwort established a strong position as the latest novel model system in plants (Bowman et al. 2017). In addition to its unique phylogenetic placement, its relatively low genetic redundancy in many regulatory processes has attracted the attention of plant biologists interested in using *Marchantia* as a promising model system for various evolutionary studies of land plants. In particular, the phytohormone signaling pathways involving auxins, jasmonates, abscisic acid and cytokinins, which regulate various developmental processes in *Marchantia*, have been intensively studied and compared with knowledge obtained from other model plant systems such as *Arabidopsis thaliana* (Flores-Sandoval et al. 2015, Kato et al. 2015, Eklund et al. 2018, Monte et al. 2018, Aki et al. 2019). These evolutionary developmental biology studies have contributed considerably to understanding the origin and evolution of phytohormone signaling pathways in land plants. Moreover, comparative studies using *Marchantia* are not only limited to investigating plant developmental biology but also being expanded to understand evolutionary molecular plant–microbe interactions (EvoMPMI) (Upson et al. 2018). However, the establishment of novel *Marchantia* pathosystems for use in such EvoMPMI studies is a highly laborious process.

In this issue, Matsui et al. (2020) report on the isolation and characterization of novel pathogens that naturally infect *Marchantia*. They ‘hunted’ natural pathogens of *Marchantia* by exposing lab-grown thalli to the open air and harvested those exhibiting disease-like symptoms. In the end, four fungal isolates belonging to the Polyporales order were obtained and, of these, three isolates were found to cause disease symptoms in *Marchantia* thalli using their in vitro infection system. The authors further focused on one of these isolates designated *Marchantia* infectious 1 (MI1), derived from the well-known necrotrophic white rot fungus *Irpex lacteus* (Fig. 1).

In various seed plants, the jasmonic acid (JA) signaling pathway mediated by the JA receptor COI1 is known to function in defense responses against necrotrophic pathogens, herbivores and physical wounding, while the salicylic acid (SA) pathway is

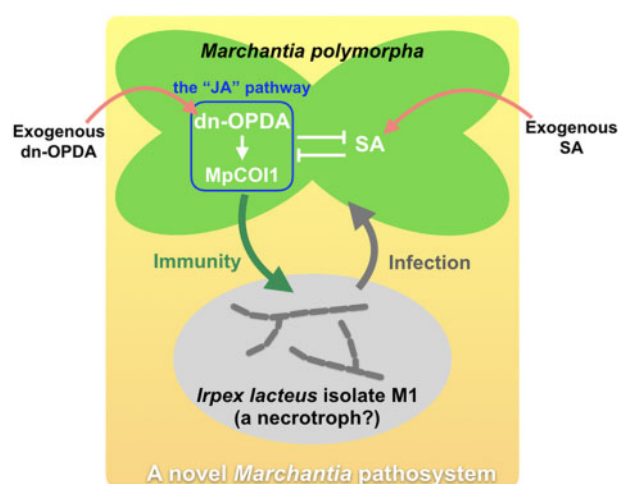


Fig. 1 The dn-OPDA (JA)/SA cross talk found in the *M. polymorpha*–*I. lacteus* M1 pathosystem. In *Marchantia*, the COI1 ortholog MpCOI1 recognizes dn-OPDA isomers other than JA. The dn-OPDA pathway that is regulated by MpCOI1 is required for resistance to *I. lacteus* M1, a newly isolated potential necrotrophic pathogen of *Marchantia*. While exogenous application of SA promotes *Marchantia* disease development caused by *I. lacteus* M1, addition of dn-OPDA suppresses SA-mediated disease promotion in the *Marchantia*–*I. lacteus* M1 pathosystem, suggesting that the SA–JA cross talk that is widely observed in seed plants is also conserved albeit in a slightly different form in *Marchantia*, which utilizes dn-OPDA as the bioactive jasmonate.

responsible for immunity against biotrophic pathogens (Thaler et al. 2012). Generally, these two phytohormone pathways act antagonistically to each other, with SA–JA antagonism being observed widely among seed plants (Thaler et al. 2012). A comparative and evolutionary study using *Marchantia* has recently revealed that the *Marchantia* COI1 ortholog, MpCOI1, recognizes dinor-12-oxo-phytodienoic acid (dn-OPDA) isomers other than JA, highlighting the co-evolution of phytohormone synthesis and receptor specificity in land plants (Monte et al. 2018). However, whether the dn-OPDA signaling pathway mediated by MpCOI1 functions in immunity against

necrotrophic pathogens, by analogy to JA in seed plants, remained to be resolved.

Matsui et al. (2020) examined the roles of the JA (dn-OPDA) and SA pathways in resistance to the newly isolated *I. lacteus* MI1, a potential necrotrophic pathogen of *Marchantia*. First, exogenous application of SA was found to promote *Marchantia* disease development caused by *I. lacteus* MI1, resembling the activation of the SA pathway that compromises JA-mediated immunity in many seed plants (Fig. 1). Although exogenous application of dn-OPDA did not obviously promote immunity against *I. lacteus* MI1, co-treatment with SA and dn-OPDA suppressed SA-mediated disease promotion, suggesting the antagonistic action of dn-OPDA and SA in *Marchantia* immunity against *I. lacteus* MI1 (Fig. 1). Using the *Mpcoi1* mutant, they further demonstrated that the endogenous dn-OPDA pathway regulated by *MpCOI1* was required for *Marchantia* resistance against *I. lacteus* MI1 (Fig. 1). The notion that SA–JA cross talk in seed plants is conserved in a slightly different form in *Marchantia*, which utilizes dn-OPDA as the bioactive jasmonate, was also reported in another recent study describing *Marchantia* immunity to *Pseudomonas syringae* pv. *tomato* DC3000, a model bacterial pathogen used widely to study immunity in seed plants such as *Arabidopsis* and tomato (Gimenez-Ibanez et al. 2019). Taken together, EvoMPMI studies using different pathosystems are providing clues as to how the well-known SA–JA cross talk that regulates plant immunity may have evolved from its ancestral form.

To understand in evolutionary terms the complex cross talk among phytohormones involved in plant–microbe interactions, a variety of *Marchantia*-based pathosystems ranging from biotrophic to necrotrophic interactions is required (Carella and Schornack 2018, Upson et al. 2018). While the innovative isolation of novel natural pathogens of *Marchantia* by Matsui et al. (2020) has undoubtedly contributed to strengthening the field of EvoMPMI, further molecular characterization of the *Marchantia*–*I. lacteus* MI1 pathosystem, as well as pathological and ecological studies, is needed. Nevertheless, studies using *Marchantia* are proving extremely powerful as exemplified by many phytohormone studies published in the last few years (Flores-Sandoval et al. 2015, Kato et al. 2015, Eklund et al. 2018, Monte et al. 2018, Aki et al. 2019). In addition to the report by Matsui et al. (2020), a growing number of other pathogens and endophytes of *Marchantia* are being reported (Carella et al. 2018, Nelson et al. 2018, Gimenez-Ibanez et al. 2019), while conventional defense marker genes are also being identified (Gimenez-Ibanez et al. 2019). Thus, the time for EvoMPMI research is here and now.

Acknowledgements

The author would like to thank Japan Science and Technology Agency (JST) for his position within JST Exploratory Research for Advanced Technology (ERATO) Nomura Microbial Community Control project (ERATOJPMJER1502).

References

- Aki, S.S., Mikami, T., Naramoto, S., Nishihama, R., Ishizaki, K., Kojima, M., et al. (2019) Cytokinin signaling is essential for organ formation in *Marchantia polymorpha*. *Plant Cell Physiol.* 60: 1842–1854.
- Bowman, J.L., Kohchi, T., Yamato, K.T., Jenkins, J., Shu, S., Ishizaki, K., et al. (2017) Insights into land plant evolution garnered from the *Marchantia polymorpha* genome. *Cell* 171: 287–299.e15.
- Carella, P., Gogleva, A., Tomaselli, M., Alfs, C. and Schornack, S. (2018) *Phytophthora palmivora* establishes tissue-specific intracellular infection structures in the earliest divergent land plant lineage. *Proc. Natl. Acad. Sci. USA* 115: E3846–E3855.
- Carella, P. and Schornack, S. (2018) Manipulation of bryophyte hosts by pathogenic and symbiotic microbes. *Plant Cell Physiol.* 59: 656–665.
- Eklund, D.M., Kanei, M., Flores-Sandoval, E., Ishizaki, K., Nishihama, R., Kohchi, T., et al. (2018) An evolutionarily conserved abscisic acid signaling pathway regulates dormancy in the liverwort *Marchantia polymorpha*. *Curr. Biol.* 28: 3691–3699.e3. p
- Flores-Sandoval, E., Eklund, D.M. and Bowman, J.L. (2015) A simple auxin transcriptional response system regulates multiple morphogenetic processes in the liverwort *Marchantia polymorpha*. *PLoS Genet.* 11: e1005207–26.
- Gimenez-Ibanez, S., Zamarreño, A.M., García-Mina, J.M. and Solano, R. (2019) An evolutionarily ancient immune system governs the interactions between *Pseudomonas syringae* and an early-diverging land plant lineage. *Curr. Biol.* 29: 2270–2281.e4.
- Kato, H., Ishizaki, K., Kouno, M., Shirakawa, M., Bowman, J.L., Nishihama, R., et al. (2015) Auxin-mediated transcriptional system with a minimal set of components is critical for morphogenesis through the life cycle in *Marchantia polymorpha*. *PLoS Genet.* 11: e1005084–26.
- Matsui, H., Iwakawa, H., Hyon, G.-S., Yotsui, I., Katou, S., Monte, I., et al. (2020) Isolation of natural fungal pathogens from *Marchantia polymorpha* reveals antagonism between salicylic acid and jasmonate during liverwort–fungus interactions. *Plant Cell Physiol.* 61: 265–275.
- Monte, I., Ishida, S., Zamarreño, A.M., Hamberg, M., Franco-Zorrilla, J.M., García-Casado, G., et al. (2018) Ligand-receptor co-evolution shaped the jasmonate pathway in land plants. *Nat. Chem. Biol.* 14: 480–488.
- Nelson, J.M., Hauser, D.A., Hinson, R. and Shaw, A.J. (2018) A novel experimental system using the liverwort *Marchantia polymorpha* and its fungal endophytes reveals diverse and context-dependent effects. *New Phytol.* 218: 1217–1232.
- Thaler, J.S., Humphrey, P.T. and Whiteman, N.K. (2012) Evolution of jasmonate and salicylate signal crosstalk. *Trends Plant Sci.* 17: 260–270.
- Upson, J.L., Zess, E.K., Białas, A., Wu, C.-H. and Kamoun, S. (2018) The coming of age of EvoMPMI: evolutionary molecular plant–microbe interactions across multiple timescales. *Curr. Opin. Plant Biol.* 44: 108–116.