Journal of General Plant Pathology (2019) 85:468–470
https://doi.org/10.1007/s10327-019-00880-8

AWARD

Plant interactions with parasitic and beneficial *Colletotrichum* fungi under changing environmental conditions

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Received: 27 May 2019 / Accepted: 2 June 2019 / Published online: 29 August 2019

Introduction

Plants are naturally associated with a great diversity of fungi. Plant-colonizing fungi are considered to have evolved from saprotrophic fungi via the acquisition of a capacity to colonize plant tissues and to obtain nutrients from the host. A transition from saprotrophic to plant-associated life forms provided a new niche without high competition among fungi. However, once fungi began to associate with plants, they had to contend with plant defense responses that aim to detect and eliminate anything that is "non-self". To overcome or evade plant defense responses, parasitic fungi had to develop diverse infection strategies. Instead of a parasitic habit, some fungi had to adopt a mutualistic habit that provided benefits to hosts in exchange for benefits from the hosts. It is crucial to note that the degree of plant responses to such parasitic or mutualist fungi would vary depending on the environmental and host conditions (Hiruma et al. 2018). However, since most studies on plant–microbe interactions are done in relatively stable laboratory conditions, little is known regarding the factors influencing fungal infection strategies in a changing environment.

Colletotrichum, an ascomycete genus with numerous species, is one of the most economically important groups of plant pathogens. *Colletotrichum* species cause anthracnose diseases in a wide range of economically important crops (Kubo and Takano 2013). Notably, various *Colletotrichum* species have reportedly been isolated from healthy plants after surface disinfection, suggesting that the fungi are endophytes that colonize plant tissues without disease symptoms (García et al. 2013). Therefore, species of *Colletotrichum* provide key fungal strain resources for the study of diverse infection strategies ranging from parasitic to potentially mutualistic strategies. Here, I summarize recent findings on the unique infection strategies of both parasitic and mutualistic *Colletotrichum* fungi during colonization in *Arabidopsis thaliana*.

This article is an abstract of the paper presented by a winner of the Young Scientist Award at the 2019 Annual Meeting of the Phytopathological Society of Japan in Tsukuba.

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Strategies for plant invasion by parasitic *Colletotrichum* species

Asexual spores (conidia) of *Colletotrichum* species germinate to form a germ tube that differentiates a specialized infection structure (appressorium) that is highly pigmented with melanin, which is critical for appressorium function (Kubo and Takano 2013). The formation of a melanin layer facilitates the generation of high turgor pressure within the appressorium that is required for mechanical penetration of the plant cuticle and cell wall (Kubo and Takano 2013). Although the appressorium-mediated entry mode is effective during host invasion, parasitic *Colletotrichum* species that are adapted to specific host plants usually fail to invade other plant species outside their host ranges because plants mount non-host resistance responses against non-adapted parasites, which typically results in the termination of early stages of pathogenesis (Hiruma et al. 2011, 2013). Studies on *A. thaliana* nonhost resistance against *Colletotrichum gloeosporioides* have revealed that the non-adapted anthracnose fungus adopts a previously undocumented hyphal tip-based entry (HTE) in *A. thaliana* mutants exhibiting defective pre-invasive resistance (Hiruma et al. 2010). HTE is regulated by the presence of carbohydrate nutrients such as glucose and seems to be negatively regulated by the fungal mitogen-activated protein kinase (MAPK) cascade that is required for appressorium formation. In addition, HTE is predominantly selected around wound sites from which sugars might leak (Hiruma et al. 2010). The results above imply that the non-adapted *Colletotrichum* perceive plant status via wound sites and have the ability to adopt the new entry mode instead of the appressorium-mediated entry. Currently, it remains unclear whether non-host pre-invasive resistance can be attenuated in plants grown in the field. Such an alternative invasion strategy could also facilitate the colonization of plant species outside their original host ranges under shifting field conditions, which could ultimately be associated with the acquisition of new host plants.

Mutualism of *Colletotrichum* species that contributes to plant fitness in nutrient-limiting conditions

As outlined above, several *Colletotrichum* species have been isolated or detected from healthy plants in nature. However, it is difficult to determine whether a particular fungal association with a healthy plant is merely the result of a stochastic encounter or has ecological significance. *Colletotrichum tofieldiae* (*Ct*), for example, has been isolated from healthy wild *A. thaliana* after surface disinfection. *Ct* is closely related to other parasitic *Colletotrichum* species, such as *Colletotrichum incanum*, that cause disease on several Brassicaceae species (Hiruma et al. 2016; Sato et al. 2005). Surveys have revealed the prevalent distribution of the fungus in wild populations of *A. thaliana* in central Spain, suggesting a close relationship with hosts in specific environmental conditions. In addition, infection experiments in the laboratory have revealed that *Ct* colonizes the roots of several Brassicaceae species including *A. thaliana* without causing visible symptoms. During *Ct* root infection, *Ct* forms stable biotrophic hyphae that are surrounded by the host plasma membrane in cortical cells. *Ct* biotrophic hyphae seem to be similar to those of parasitic *Colletotrichum* species that transiently form before entering the necrotrophic phase, when host cells are actively killed. In the case of *Ct*, a clear transition to the necrotrophic phase is not observed. The lack of transition to a necrotrophic phase could be related to the fungal infection strategy, which does not result in severe damage in the host. Notably, *Ct* facilitates plant growth and fitness under low-phosphate conditions via the transfer of phosphorus to the hosts, which has been demonstrated using ^{33}P radioisotope tracing experiments. In contrast, *Ct*-mediated phosphorus translocation and plant growth promotion are not observed when nutrient levels are adequate. Therefore, *Ct* establishes specific beneficial interactions with host plants under low-nutrient conditions via the provision of “a second root” to host plants (Hiruma et al. 2016).

Arbuscular mycorrhizal fungi (AMF) promote plant growth under nutrient-deficient conditions by facilitating the transfer of macronutrients such as phosphorus to hosts (Bonfante and Genre 2010). Despite the benefits of AMF in plants, 10–20% of land plants, particularly Brassicaceae species including *A. thaliana*, do not form mutualistic interactions with AMF (Bonfante and Genre 2010). Until very recently, it was not clear how the Brassicaceae species, most of which do not have specialized root architecture, adapt to low-nutrient soil conditions without the assistance of AMF. However, the results of the identification and characterization of *Ct* suggest that the Brassicaceae species establish beneficial interactions with a facultative endophyte that is closely related to parasitic fungi. To obtain benefits from *Ct*, Brassicaceae species have to regulate *Ct* growth via tryptophan-derived secondary metabolites such as indole glucosinolates, some of which are antifungal. *Ct* causes severe symptoms in *Arabidopsis cyp79B2 cyp79B3* mutant plants, which lack most of the tryptophan-derived secondary metabolites (Hiruma et al. 2016). In addition, low phosphate concentrations partially reduce the expression of several genes associated with the generation or regulation of tryptophan-derived secondary metabolites (Hacquard et al. 2016). Considering that the secondary metabolite pathway is highly developed in the Brassicaceae lineage, Brassicaceae species could have acquired and developed a metabolitic pathway regulated by phosphate status to establish a beneficial interaction with facultative endophytes. The establishment of beneficial interactions could have facilitated adaptation to low-nutrient conditions such as soils in central Spain, where *Ct* was originally isolated.

Conclusion

I presented an example where plant-associated parasitic fungi have two distinctive infection strategies, from which one is activated based on the carbohydrate nutrient status on the surface of plant leaves. I also showed that a facultative endophyte closely related with parasitic fungi could behave similar to mutualistic fungi under specific environmental and host conditions. To control plant-associated fungi with diverse infection strategies effectively, it is critical to elucidate the molecular mechanisms underlying the selection of such diverse infection strategies under changing environmental conditions.

Acknowledgements I am deeply grateful to Dr. Yoshitaka Takano and Dr. Tetsuro Okuno, Dr. Kazuyuki Mise and Dr. Masanori Kaido at Kyoto University, Dr. Paul Schulze-Lefert at Max Planck Institute, Dr. Richard O’Connell at INRA, and Dr. Yusuke Saijo at NAIST for their valuable suggestions, support, and warm encouragement. I also appreciate my collaborators for their help and encouragement. I am supported by Japan Society for the Promotion of Sciences (JSPS) KAKENHI Grant (18H04822), the Japan Science and Technology Agency (JST) Grant (JPMJPR16Q7).

Compliance with ethical standards

Conflict of interest The author has no conflict of interest to declare.

Human and animal rights statement This article does not contain any experiments performed with human participants or animals.

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