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Review

Stop and smell the fungi: Fungal volatile metabolites are overlooked signals involved in fungal interaction with plants

Ningxiao LI[a], Alsayed ALFIKY[b,c], Martha M. VAUGHAN[d], Seogchan KANG[a,b,*]

[a]Intercollege Graduate Degree Program in Plant Biology, Pennsylvania State University, University Park, PA, 16802, USA
[b]Department of Plant Pathology & Environmental Microbiology, Pennsylvania State University, University Park, PA, 16802, USA
[c]Genetics Department, Faculty of Agriculture, Tanta University, Egypt
[d]Mycotoxin Prevention and Applied Microbiology Research Unit, National Center for Agricultural Utilization Research, United States Department of Agriculture, Agricultural Research Service, 1815 N University St, Peoria, IL, 61604, USA

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ABSTRACT

Diverse fungi are intimately associated with plants, and molecules secreted from both the plant and fungal sides play critical roles in the establishment of their associations and affect plant growth and health. Through evolutionary arms races or strategic alliances with plants, fungi and other microbes have invented a bewildering array of secreted molecules to parasitize or communicate with plants. Research empowered by omics data and tools has greatly advanced understanding of the nature, role and mechanism of action of many secreted fungal proteins that affect plants directly or indirectly. However, available information about fungal volatile metabolites with similar functions is quite limited. Through this review, we aim to stimulate expeditions to this vastly under-explored frontier of fungal chemical ecology.

1. Introduction

In a rather simplistic and anthropocentric manner, plant-associated microbes can be classified as 'beneficial, detrimental, or unknown' based on their effects on plant growth and health. Microbes secrete diverse classes of molecules that directly or indirectly affect plant growth, development, productivity and overall health (Bednarek *et al.*, 2010). Characterization of the nature, synthesis, function and mechanism of action of such molecules is critical for understanding how

* *Corresponding author*. 311 Buckhout Lab, Pennsylvania State University, University Park, PA, 16802, USA. Tel.: +1 814 863 3846.
E-mail address: sxk55@psu.edu (S. Kang).
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plants and microbes interact and how their interactions have evolved. One well documented class of secreted molecules includes phytohormones, such as indole-3-acetic acid, cytokinins and gibberellins (Chanclud *et al.*, 2016; Gutierrez-Manero *et al.*, 2001; Loper and Schroth, 1986; Macdonald *et al.*, 1986; Timmusk *et al.*, 1999), and molecules that mimic phytohormones, such as coronatine produced by *Pseudomonas syringae* (Zheng *et al.*, 2012) and methylated cytokinins released by *Rhodococcus fascians* (Radhika *et al.*, 2015). Diverse and often inter-connected roles of the hormones in regulating many physiological and developmental processes, including defense responses, likely presented evolutionary opportunities for plant-associated microbes to hijack or manipulate such processes in plants by releasing one or more hormones or their structural or functional analogs. Plant pathogens secrete assorted virulence factors (e.g., proteins, small RNAs, and metabolites) into the plant–pathogen interface and plant cells to disarm or manipulate plant defense machineries so as to facilitate pathogenesis (Chanclud *et al.*, 2016; Collemare and Lebrun, 2011; Deslandes and Rivas, 2012; Rovenich *et al.*, 2014; Weiberg *et al.*, 2014; Zheng *et al.*, 2012). The manipulation of plant defense *via* the secretion of such molecules is not limited to pathogens. Establishment of the symbiotic associations with rhizobia and mycorrhizal fungi also requires suppression of host defense responses, because like pathogens, these beneficial microbes also display pathogen-associated molecular patterns (PAMPs), which activate basal defense responses termed PAMP triggered immunity (PTI) (Evangelisti *et al.*, 2014; Jones *et al.*, 2007; Plett and Martin, 2011). These symbiotic associations also involve specific secreted signals, from both the plant and microbe sides, in order to initiate and coordinate appropriate developmental and growth changes required for the establishment of their partnership (Harrison, 2005; Jones *et al.*, 2007; Perret *et al.*, 2000; Venturi and Keel, 2016). Plant growth-promoting rhizobacteria (PGPR) and fungi (PGPF) enhance plant growth and defense by influencing the plant physiology *via* the use of diverse secreted molecules (Bakker *et al.*, 2013; Kundan *et al.*, 2015; Pieterse *et al.*, 2014; Shoresh *et al.*, 2010; Venturi and Keel, 2016).

Accordingly, there have been concerted efforts to identify and functionally characterize microbial secretomes (Bednarek *et al.*, 2010; Chisholm *et al.*, 2006; Hogenhout *et al.*, 2009). In addition to the fundamental significance, increasing need to sustain crop growth and health without relying so heavily on pesticides and fertilizers has also driven research in this field (Bednarek *et al.*, 2010). Enhanced knowledge on the microbial secretomes and their mechanisms of action should help facilitate the development of bio-based strategies for enhancing crop production and protection. However, in comparison to the copious available data on secreted microbial proteins, relatively little is known about the nature and role of secreted microbial metabolites, especially those that are volatile, in plant–microbe interactions. Both fungi and bacteria produce diverse volatile (or semi-volatile) organic compounds (VOCs), which comprise multiple classes of low-molecular weight lipophilic metabolites and their byproducts that vaporize at normal temperatures and pressures (Lemfack *et al.*, 2014). VOCs produced by fungi appear to have similar functions as those emitted from animals and plants, and play a critical role in ecological fitness, such as inhibition of competing organisms, coordination of growth and development within species, and communication with other neighboring organisms (Bailly and Weisskopf, 2012; Bitas *et al.*, 2013; Morath *et al.*, 2012; Rohlfs and Churchill, 2011). However, key questions such as which fungal VOCs confer such functions, how they manipulate other organisms, and how their synthesis occurs and is regulated, remain mostly unanswered. Systematic exploration of the diversity and function of fungal VOCs and their mechanisms of action will advance understanding of fungal biology and ecology in association with plants, animals and other microbes. This review focuses on the role of fungal VOCs in affecting plant growth, development, stress resistance, or combinations of these traits. Our goal is to emphasize critical knowledge gaps with hopes to stimulate concerted efforts to address them. We also discuss several technical challenges, which must be overcome in order to expedite explorations of VOC-mediated plant–fungal interactions.

2. Volatile signals play vital roles within and across multiple kingdoms

Considering that water is not consistently readily available in nature, it is unlikely that microbes would rely on water as the sole medium for secreted molecule-mediated interactions with neighboring organisms. Because volatile metabolites can travel through water, air and porous soils, they are more versatile than water-soluble signals and can function as both short- and long-range signals. Animals, plants and microbes have evolved the ability to produce and recognize volatile metabolite signals as a means of communication, and volatile-mediated signaling processes serve vital ecological functions (Bitas *et al.*, 2013; Herrmann, 2010; Li and Liberles, 2015; Schenkel *et al.*, 2015). In the absence of plant VOCs that function as homing cues to pollinators and seed dispersers (Baldwin, 2010; Herrmann, 2010), the terrestrial landscape and its inhabitants would look quite different. Some plants even mimic fungi by releasing a mixture of VOCs that are commonly emitted by mushrooms to attract certain insects for pollination (Kaiser, 2006). Without volatile cues released from plants parasitized by pests, neighboring plants would not receive an advanced warning of imminent threats, and parasitoids of insect herbivores would struggle to find their preys (Baldwin, 2010). If animals could not associate specific volatile compounds with food, mates or threats, they would not likely have survived very long or prospered. Similarly, microbial communities would likely become disfunctional in the absence of volatile communications, as microbial VOCs are thought to be involved in antagonism, mutualism, and intra- and inter-species regulation of cellular and developmental processes (Bitas *et al.*, 2013; Schmidt *et al.*, 2015). However, relatively little information is available regarding bacterial VOCs as signals, and even less is known about fungal VOCs.

Diversity of fungal VOCs and their potential functions

Although some fungi, such as truffles (*Tuber* spp.), have received a lot of attention and have a long history of volatile research (Splivallo *et al.*, 2011), studies on the nature and