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Short Communication

Shared weapons in fungus-fungus and fungus-plant interactions? Volatile organic compounds of plant or fungal origin exert direct antifungal activity *in vitro*

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ABSTRACT

Fungi emit a diverse blend of volatile organic compounds (VOCs) that mediate multiple fungus-fungus interactions. Plants emit VOCs as well, which can serve as resistance-inducing signals but might also act as direct resistance agents. We screened 22 VOCs that are emitted from infected plants for putative inhibitory effects on three fungal phytopathogens: *Colletotrichum lindemuthianum*, *Fusarium oxysporum* and *Botrytis cinerea*. The growth of all three fungi was significantly inhibited when the mycelia were exposed to an atmosphere containing nonanal, (+)-carvone, citral, *trans*-2-decenal, *L*-linalool, or nerolidol. Eugenol completely inhibited the growth of all three fungi, and 1-octen-3-ol, nonanal, 2,6-dimethyl-2,4,6-octatriene, citral, α-terpineol and *trans*-2-decanal inhibited at least one fungus completely. Most of these VOCs are also emitted from fungi. We conclude that antagonistic fungus-fungus and plant-fungus interactions might share common mechanisms and that plant VOCs can function as resistance agents that fungal pathogens must overcome for successful infection.

Fungi emit a diverse array of volatile organic compounds (VOCs): low-weight, lipophilic molecules that play multiple roles in fungus-fungus or fungus-plant interactions (Bennett and Inamdar, 2015; El Ariebi et al., 2016). On the one hand, fungal VOCs serve as 'chemical weapons' in antagonistic fungus-fungus interactions (Bennett and Inamdar, 2015). On the other hand, multiple fungi colonize plants (Partida-Martinez and Heil, 2011), and VOC-mediated growth promotion effects have been reported for various fungal species, particularly in the genus *Trichoderma* (Hung et al., 2013; Lee et al., 2016; Li et al., 2016). However, plants emit VOCs as well, for example in response to infection, and several of these compounds act as signals and trigger the expression of plant resistance genes (Scala et al., 2013; Heil, 2014). For example, nonanal and methyl salicylate primed pathogenesis-related (PR) genes in common bean (*Phaseolus vulgaris*) and lima bean (*Phaseolus lunatus*) (Yi et al., 2009; Quintana-Rodriguez et al., 2015), and the exposure to (*S*)-(−) limonene, *L*-linalool, nonanal, methyl salicylate, or methyl jasmonate, induced resistance in *P. vulgaris* to the fungal pathogen, *Colletotrichum lindemuthianum*. Interestingly, the same compounds inhibited the growth of the fungus *in vitro* (Quintana-Rodriguez et al., 2015), thereby supporting theoretical predictions that a direct defensive function of a compound should precede its signalling function in evolutionary trajectories (Maag et al., 2015; Veyrat et al., 2016).

However, the effects of plant-derived VOCs on fungi range from inhibition to promotion. *Trans*-2-hexenal inhibited the conidial germination of *Monilinia laxa* (Neri et al., 2007) and citral inhibited the growth of *Botrytis cinerea*, *Trichoderma viride* and *Penicillium digitatum* (Simas et al., 2017). By contrast, *Uromyces fabae* stimulated volatile emissions from its host plant and among the emitted

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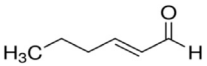
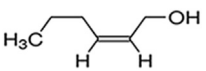
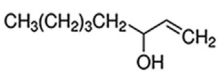
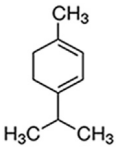
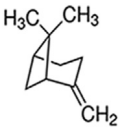
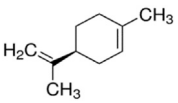
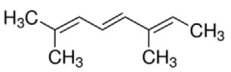
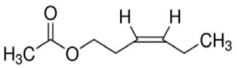
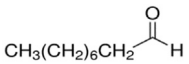
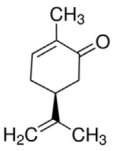
Table 1
Volatile organic compounds of fungal or plant origin with inhibitory effects on fungi.

Compound	CAS Nr.	Structure	Fungus inhibited[a]	Fungi and plants as source			
				Fungal source	Reference	Plant source	Reference
Ethanol	64-17-5		F	*Trichoderma* sp., *Tuber* sp., common in yeasts	Hung et al. (2013); Ebert et al. (2016) Lee et al. (2016); Li et al. (2016)		
trans-2-Hexen-1-al	6728-26-3		B			*Arabidopsis thaliana* infected with *Botrytis cinerea*	Matsui et al. (2012)
cis-2-Hexen-1-ol	928-94-9		F,B			*P. vulgaris* infected with *Pseudomonas syringae*	Croft et al. (1993)
1-Octen-3-ol	3391-86-4		F,B	"Possibly the most widespread fatty acid derived fungal volatile"	Müller et al. (2013); Li et al. (2016); Dickschat (2017)	*P. vulgaris* infected with *C. lindemuthianum*	Quintana-Rodriguez et al. (2015)
α-Terpinene	99-86-5		F,B	"Emitted from fungi"	Schmidt et al. (2016)	Tomato infected with *Tomato severe rugose virus*	Fereres et al. (2016)
(−) β-Pinene	18172-67-3		F,B	*Trichoderma* sp.	Lee et al. (2016)	*P. vulgaris* infected with *C. lindemuthianum*	Quintana-Rodriguez et al. (2015)
(S)-(−)-Limonene	5989-54-8		C	'Limonene': *Trichoderma* sp., interacting fungi	Hung et al. (2013); El Ariebi et al. (2016); Lee et al. (2016)	*P. vulgaris* infected with *C. lindemuthianum*	Quintana-Rodriguez et al. (2015)
2,6 − Dimethyl − 2,4,6 − octatriene	673-84-7		B			*P. vulgaris* infected with *C. lindemuthianum*	Quintana-Rodriguez (unpubl.)
cis-3-Hexenyl acetate	3681-71-8		F			*P. lunatus* (md or colonized with EF)	Navarro-Melendez and Heil (2014)
Nonanal	124-19-6		C,F,B	*Trichoderma* sp.	Hung et al. (2013); Lee et al. (2016)	*P. vulgaris* infected with *C. lindemuthianum*, *P. lunatus* treated with BTH	Yi et al. (2009); Quintana-Rodriguez et al. (2015)
(+)- Carvone	2244-16-8		C,F,B			*Brassica oleracea* treated with jasmonic acid, *Cucumis sativus* infested with spider mite	Bruinsma et al. (2009); Kappers et al. (2010)