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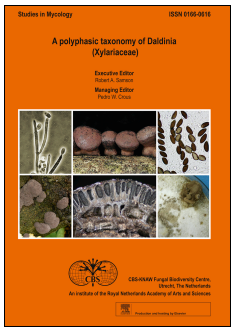

Fungus wars: basidiomycete battles in wood decay

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Fungus wars: basidiomycete battles in wood decay

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Running head: Fungus wars

Abstract: Understanding the mechanisms underlying wood decay basidiomycete community dynamics is crucial for fully understanding decomposition processes, and for modelling ecosystem function and resilience to environmental change. Competition drives community development in decaying woody resources, with interactions occurring at a distance, following physical contact, and through specialised relationships such as mycoparasitism. Outcomes of combative interactions range from replacement, where one mycelium displaces another, to deadlock, where neither combatant captures territory from the other; and a spectrum of intermediate outcomes (i.e. partial or mutual replacement) lie between these extremes. Many wood decay basidiomycetes coexist within a resource, in a complex and dynamic community, and new research techniques are focusing on spatial orientation of interactions in 3 dimensions, as opposed to historical two-dimensional research. Not only do interactions drive changes in species composition and thus wood decomposition rate, they also may have industrial applications in biocontrol of pathogenic or nuisance fungi, enzyme production, and in the production of novel antifungals and antibiotics. Altogether, fungal interactions are a fascinating and important field of study.

BACKGROUND TO INTERACTIONS

Wood decay basidiomycetes are central to the decomposition of recalcitrant lignocellulose, and thus to global carbon cycling. With approximately 80 Tg of carbon sequestered in woody biomass annually (Luyssaert *et al*. 2010; Bellassen & Luyssaert 2014), understanding the mechanisms underlying basidiomycete community dynamics is crucial for fully understanding decomposition processes, and for modelling ecosystem function and resilience to environmental change (Bardgett *et al*. 2008; Chapin *et al*. 2009; McGuire & Treseder 2010). Competition appears to be the most common type of interaction between wood decay basidiomycetes (Boddy 2000), and this drives community development in decaying woody resources. The distinction between interference competition, where one organism inhibits another, and exploitation competition, where one organism uses a resource and consequently reduces the availability to another, is not clear for wood decay fungi (Keddy 1989; Boddy 2000). Their mycelia colonise solid organic resources and utilise the nutrients within, so competition for territory and nutrients cannot be divorced (Boddy & Hiscox 2017). Interactions can occur at a distance, following contact at the hyphal level (mycoparastism), or following contact at the mycelial level (Boddy 2000).

Antagonism at a distance

Antagonism at a distance, including both attack and defence, impedes invasion of colonised territory by a competitor mycelium without mycelia actually making contact. Mycelia may produce volatile or diffusible organic compounds (VOCs and DOCs), or alter the pH of the territory they inhabit, which inhibits competitor growth and acts as defensive and attacking mechanisms (Heilmann-Clausen & Boddy 2005; Hynes *et al*. 2007). Many fungi produce mono- and sesquiterpenes, and aromatic compounds, some of which possess antifungal activity (Viiri *et al*. 2001; Hynes *et al*. 2007; El Ariebi *et al*. 2016). Reactions to VOCs and DOCs vary depending on the combination of species involved, and include altered spore germination and changes in mycelial morphology and enzyme activity (Rayner *et al*. 1994; Heilmann-Clausen & Boddy 2005). In some cases mutual inhibition of both competitors may occur (Boddy 2000), yet in others mycelial growth may be stimulated (Evans *et al*. 2008). Defences include physical barriers, for example pseudosclerotial plates, comprising narrow bands of melanised tissue which surround the territory occupied by the fungus (Rayner & Boddy 1988).

Interactions at the hyphal level

Interactions at the hyphal level include mycoparasitism and hyphal interference. Mycoparasitic relationships occur when one mycelium gains nutrition directly from another (Jeffries 1995). Some mycoparasites are biotrophic, deriving nutrition from living mycelia in a complex and specialised association between mycoparasite and host. The host remains relatively healthy, but suffers a loss of fitness due to abstraction of nutrients by the mycoparasite (Jeffries 1995). In contrast, necrotrophic mycoparasites cause death of the host mycelium and utilize nutrients from the dead or dying hyphae. These necrotrophs tend to have a broad host range and utilise unspecialised parasitic mechanisms (Jeffries 1995). In some cases, mycoparasitism may function as a temporary strategy to gain the territory of a competitor, following which the mycoparasite will switch to obtaining nutrition through wood decomposition, for example *Lenzites betulina*, which is parasitic on *Trametes* species (Rayner *et al*. 1987). To a certain extent, all wood decay basidiomycete species behave as necrotrophs during antagonistic interactions, because they utilise the mycelium of a displaced competitor for nutrition when capturing its territory.