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Opinion Article

Armed and dangerous – Chemical warfare in wood decay communities



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ABSTRACT

Fungal community structure and development in decaying woody resources are largely dependent on interspecific antagonistic interactions that determine the distribution of territory – and hence the nutrients within – between different individuals occupying that resource. Interactions are mediated by antagonistic mechanisms, which determine the combative outcome: either deadlock, where neither mycelium loses any territory, or replacement, where one mycelium displaces the other. These mechanisms function aggressively and/or defensively, and include changes in primary metabolism and growth, as well as secondary metabolite production and stress mitigation responses. This chemical warfare may occur as a constitutive defence through modification of the territory occupied by an individual, and the deposition of antimicrobial compounds within. Following detection of a competitor, the metabolite and enzymic profile of a mycelium alters both qualitatively and quantitatively, and different mechanisms may be stimulated when confronted with different competitors. Biotic and abiotic factors, even small alterations, can affect the deployment of these antagonistic mechanisms, altering the general hierarchy of combative ability between species and making it impossible to predict outcomes with certainty. Here we explore recent advances in our understanding of combative interactions between wood decayers, and explain why future research priorities involving the application of emerging biochemical and molecular technologies must focus on interactions in more ecologically realistic and meaningful scenarios.

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1. Introduction

Understanding the dynamics of decomposer community development is essential for modelling carbon cycling and other ecosystem functions, and the resilience of these processes to environmental change (e.g. McGuire and Treseder 2010). Fungal competition in decaying woody resources is

effectively competition for territory and the nutrients within, and encompasses both interference and exploitation competition; fungi exhibit the former by inhibiting other organisms and limiting their access to resources, and the latter by sequestering nutrients within the territory they occupy, hence preventing other organisms from using them (Boddy and Hiscox 2016). In general, fungal competition can be divided

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into primary resource capture, where a fungus colonises previously unoccupied territory, and secondary resource capture, where a fungus captures territory from fungi that have already colonised a resource (Boddy 2000). Success in primary resource capture is determined by efficient dispersal mechanisms, rapid growth rate, and the ability to use easily accessible nutrients (R-selected characteristics; Boddy 2000). Success in secondary resource capture depends on aggressive and/or defensive antagonistic mechanisms (C-selected), or at very late stages of decomposition, the ability to tolerate abiotic/biotic stress and disturbance (S-selected and R-selected; Boddy 2000).

The ultimate outcome of combative interactions can either be deadlock, where neither fungus loses any territory, or replacement, where one fungus displaces the other. Between these extremes lies a spectrum of outcomes, including partial replacement of one fungus by another, or mutual replacement, where both fungi capture territory from each other (Boddy 2000). These combative interactions can be mediated at a distance, following contact at the level of individual hyphae (e.g. hyphal interference and mycoparasitism, see Boddy and Hiscox 2016), or following contact at the mycelial level. The establishment of physical contact between two competing mycelia, often called 'gross mycelial contact', results in the induction of antagonistic mechanisms in one or both competitors. Competing mycelia undergo changes in morphology, secondary metabolite production, pigment deposition, accumulation of reactive oxygen species, and alterations in enzyme activity (see Section 2). These changes may function aggressively and/or defensively against a competitor, and different mechanisms may be stimulated when confronted with different competitors (Eyre et al. 2010). The majority of this review will concentrate on mycelial interactions, as they are the most frequently observed interaction type within wood decay communities.

2. Antagonistic mechanisms

Constitutive defence and antagonism at a distance

Constitutive defences function to impede the invasion of colonised territory by a competitor mycelium. Certain species modify the territory they occupy to make it less hospitable for invaders, for example lowering water potential or pH (Boddy et al. 1985; Tudor et al. 2013). Some fungi produce pseudo-sclerotial plates, thin shells of melanised tissue completely surrounding the territory they occupy, which maintain the conditions within, and can also act as a physical barrier against invasion (Rayner and Boddy 1988; Fig. 1A). Further, fungi produce, and perhaps accumulate, inhibitory secondary metabolites, which can slow or halt the extension of competitors (Heilmann-Clausen and Boddy 2005; Fig. 1B and C). These secondary metabolites span a variety of chemical classes; different species tend to produce a characteristic metabolite profile, although this is partly dependent on their growth conditions (Lemfack et al. 2013; Fig. 1D and E). Inhibitory effects of both diffusible and volatile organic compounds (DOCs and VOCs, respectively) have been demonstrated for fungi growing in wood blocks, across soil, and in artificial agar

media (Heilmann-Clausen and Boddy 2005; El Ariebi et al. 2016). DOCs have local antagonistic potential (e.g. in scenarios where they can accumulate or diffuse through substrata), whereas VOCs can act over greater distances and in heterogeneous environments. Whilst these chemical defences may help protect against invasion by most competitors, adaptive relationships occur where certain species are attracted to the metabolite profile emitted by a competitor, with certain VOC/DOC profiles stimulating competitor growth (Evans et al. 2008). Similarly, territory modification may provide an advantage for invading fungi with analogous preferences.

Morphological changes

Changes in mycelial morphology are most dramatic in areas in direct contact with the competitor: the interaction zone. Hyphae may aggregate to form barrages which physically block invasion by competitors, or to form invasive replacement fronts or cords (linear aggregations of hyphae) to penetrate competitor defences (Fig. 2A–C). Morphological structures may differ between regions of the same interaction front, indicating that antagonistic mechanisms are deployed in response to local stimuli (Rayner et al. 1994). Morphological changes during interactions are associated with changes in gene expression compared to non-interacting mycelia (Table 1). For example, cytokinesis-related proteins and 1,3-beta glucan synthase were upregulated in *Trametes versicolor* during antagonism with *Stereum gausapatum*, indicating increases in cell division and cell wall formation or alteration (Eyre et al. 2010). This was concomitant with a downregulation of chitin synthase expression in *S. gausapatum*; the decrease in growth of this fungus may be associated with its eventual replacement by *T. versicolor* (Eyre et al. 2010).

Melanin deposition is often associated with morphological changes at interacting hyphal fronts, and may be wall-bound or extracellular, often visible as pigmentation (Rayner et al. 1994). Melanins are formed by the oxidative linkage of aromatic metabolites into complex heteropolymers which alter hyphal hydrophobicity, and confer structural strength by strengthening cell-to-cell adhesion (Bell and Wheeler 1986). Similarly, hydrophobin proteins, which are involved in forming attachments in aggregating cells and have been linked to the formation of aerial hyphae and cell wall assembly, increase in expression in both competitors during interactions between *Phlebiopsis gigantea* and *Heterobasidion parviporum* (Adomas et al. 2006). Hydrophobins may also have a role in sealing off hyphae damaged by antagonistic processes, preventing loss of cytoplasm from surrounding compartments. A similar role has been suggested for the protein HEX-1 (hexagonal protein 1) which is upregulated in *Schizophyllum commune* during interactions with *Trichoderma viride* (Ujor et al. 2012). HEX-1 is a major component of the Woronin body, which functions to plug septa (the junctions between different hyphal compartments) and seal off damaged hyphae (Collinge and Markham 1987).

Changes in metabolism

The processes involved in antagonism are energetically expensive. Increases in respiration and nutrient acquisition

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