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# Antagonistic fungal interactions influence carbon dioxide evolution from decomposing wood



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## ABSTRACT

Fungal species vary in the rate and way in which they decay wood. Thus, understanding fungal community dynamics within dead wood is crucial to understanding decomposition and carbon cycling. Mycelia compete for wood territory, by employing antagonistic mechanisms involving changes in morphology, and production of volatile and diffusible chemicals. This is metabolically costly, and may affect the rate of use of the resource. The metabolic rate during pairwise interactions between wood decay ascomycetes and basidiomycetes was determined by measuring CO<sub>2</sub> production. CO<sub>2</sub> evolution altered over time, but changes were combination-specific. In only two combinations – when the dominant competitor overgrew the opponent's territory as mycelia cords – did CO<sub>2</sub> evolution increase over the course of the whole interaction. In most interactions, CO<sub>2</sub> evolution increased only after complete replacement of one competitor, suggesting utilisation of the predecessor mycelium or differences in decay ability due to alteration of the resource by the predecessor. There was no relationship between rate of CO<sub>2</sub> evolution and combative ability nor outcome of interaction.

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## Introduction

Fungal community structure and development within wood is largely determined by interspecific interactions (Boddy and Heilmann-Clausen, 2008). Wood is a solid substratum, so competition for resources is effectively competition for space/territory, since when a fungus holds territory it potentially has access to all of the resources within that territory, provided that it has the enzymatic capacity to decompose lignocellulose (Boddy, 2000). Competition for territory, and hence changes in fungal community structure, is brought about by

combative, antagonistic interactions whose ultimate outcome can be: (1) deadlock, where neither species gains headway; (2) replacement, where one species wrests territory from the other; (3) partial replacement, where one species captures some but not all of the antagonist's territory; or (4) mutual replacement, where one species takes some of the territory formerly occupied by the other and *vice versa* (Boddy, 2000).

Antagonistic interactions can be mediated at a distance and following contact (Boddy, 2000; Woodward and Boddy, 2008). Complex and varied morphological, physiological and biochemical changes occur during interactions, influenced by

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the species present and environmental conditions, including rapid cell division, branching, hyphal aggregation, aerial growth, autolysis, pigment production, release of volatile organic compounds (which also act as info-chemicals), diffusible enzymes, toxins and antifungal metabolites (Griffith et al., 1994; Boddy, 2000; Baldrian, 2004; Hynes et al., 2007; Evans et al., 2008; Woodward and Boddy, 2008). These physiological and biochemical changes determine the outcome of the interaction. Inevitably they have a metabolic cost, so it might be anticipated that interactions result in an increase in decay rate to provide the necessary carbon and energy.

Wood decay fungi can be broadly categorised into primary, secondary, late secondary and end stage colonisers depending on their position within the successional community. Primary colonisers generally arrive at the resources as spores; many of which will have been latently present in standing trees and attached branches as endophytes (Parfitt et al., 2010). Mycelia proliferate through the uncolonised wood, first rapidly utilising easily accessible nutrient sources and then more recalcitrant compounds (Boddy and Heilmann-Clausen, 2008). Early secondary colonisers subsequently arrive at the resource as spores, as do many later secondary and end stage colonisers, though some arrive as mycelium which has grown out of colonised resources in search of new ones, often forming linear aggregates of hyphae called cords (Boddy and Heilmann-Clausen, 2008). In general, there is a hierarchy of combative ability where late secondary colonisers > early secondary colonisers > primary colonisers, although these relationships are not always transitive (Boddy, 2000). End stage fungi and some secondary colonisers are not combative but succeed in some situations because they are tolerant of certain environmental stresses (Boddy and Heilmann-Clausen, 2008).

The aim of the present study was to investigate the time course of interspecific fungal interactions in wood and how these interactions might alter fungal metabolic rate, with potential implications for wood decay rate. We set out to determine the effects of interspecific antagonistic interactions on metabolic rate, using CO<sub>2</sub> as a surrogate, by testing the

hypotheses that: (1) when fungal individuals interact in wood there is an increase in respiration, because these aggressive encounters are energetically expensive; (2) different interaction outcomes, e.g. deadlock and replacement, result in different costs which might occur if different mechanisms are employed; and (3) some predecessors will affect respiration by a succeeding fungus.

## Methods

### Preparation of inocula

Inocula of eight native, beech (*Fagus sylvatica*)-inhabiting fungi (Table 1) from different stages of decay were prepared by incubating 2 × 2 × 2 cm beech wood blocks on colonised 0.5 % malt agar (MA: 5 g l<sup>-1</sup> malt extract, 15 g l<sup>-1</sup> agar; Lab M, Lancs, UK) at 20 °C in the dark (following A'Bear et al., 2012). Species were chosen to cover the main stages of fungal succession, as determined in previous studies (Rayner and Boddy, 1988; Boddy and Heilmann-Clausen, 2008). Blocks were left to colonise for 12 weeks, by which time growth had proliferated through the blocks, as determined by reisolating from diverse regions within the block onto agar. The initial decay state of colonised blocks was determined through measurement of wet volume/dry weight (15 replicates, destructively sampled). There were no significant differences between the density of blocks colonised with different species (0.54 g cm<sup>-3</sup>), with the exception of *Trametes versicolor* (0.49 g cm<sup>-3</sup>; df = 89, F = 8.374, P < 0.001).

### Outcome of interspecific interactions

Pre-colonised blocks, scraped free of adhering mycelium using a scalpel, were paired with cut vessels touching and held together with a sterile rubber band which was removed after 5 d. Paired blocks were placed directly onto perlite (30 ml; a siliceous rock that does not absorb CO<sub>2</sub>) moistened with sterile distilled water to achieve a water potential of

**Table 1 – Details of fungal species used**

Ecological role	Species <sup>a</sup>	Strain	Source	Division	Class	Order	Family
Primary coloniser	<i>Hypoxylon fragiforme</i>	HpfFF1	Beech wood isolation	Ascomycota	Sordariomycetes	Xylariales	Xylariaceae
	<i>Biscogniauxia</i> sp.	BxnFF1	Beech wood isolation	Ascomycota	Sordariomycetes	Xylariales	Xylariaceae
	<i>Vuilleminia comedens</i>	VcWVJH1	Beech wood isolation	Basidiomycota	Agaricomycetes	Corticales	Corticariaceae
Early secondary coloniser	<i>Trametes versicolor</i>	TvCCJH1	Fruit body isolation	Basidiomycota	Agaricomycetes	Polyporales	Polyporaceae
	<i>Stereum hirsutum</i>	ShSS1	Fruit body isolation	Basidiomycota	Agaricomycetes	Russulales	Stereaceae
	<i>Bjerkandera adusta</i>	BaSS1	Fruit body isolation	Basidiomycota	Agaricomycetes	Polyporales	Meruliaceae
Late secondary/tertiary coloniser	<i>Hypholoma fasciculare</i>	HfDD3	Fruit body isolation	Basidiomycota	Agaricomycetes	Agaricales	Strophariaceae
	<i>Phanerochaete velutina</i>	Pv29	Beech wood isolation	Basidiomycota	Agaricomycetes	Polyporales	Phanerochaetaceae

a Species identities previously confirmed by ITS sequencing.

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