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Grazing alters network architecture during interspecific mycelial interactions

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ABSTRACT

The changes that occur in mycelial architecture of *Phanerochaete velutina* interacting with *Hypholoma fasciculare* mycelium in soil microcosms in the presence and absence of the collembola *Folsomia candida* are investigated employing tools developed in graph theory and statistical mechanics. There was substantially greater overgrowth of *H. fasciculare* by *P. velutina* mycelium when grazed than when un-grazed. There was a marked disappearance of hyphal links in all un-grazed systems between 8 d and 34 d, predominantly in areas distant from the interaction, but this was much less evident in grazed systems. Further, new tangential cross-links connecting radial cords distant from the inoculum formed in grazed systems. The thickness of cords increased with time, and more so in grazed systems. There was no significant difference in transport efficiency between the grazed and un-grazed systems. The ability of the mycelial network to modify dynamically link strengths is crucial to achieving a balance between transport capacity/robustness to damage and overall cost of production.

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Introduction

In the natural environment fungal mycelia have to compete with other fungi and microorganisms for space and resources, and suffer predation from grazing invertebrates. Interspecific interactions between basidiomycete mycelia trigger dramatic changes in mycelial morphology, both in the vicinity of the antagonist and often elsewhere in the mycelium (Dowson et al. 1988; Holmer & Stenlid 1997; Boddy 2000; Woodward & Boddy 2008). A range of responses are observed depending on individual species and species combinations, including production of stationary 'barrages' that are resistant to invasion by opposing mycelium, mycelial fans, linear organs and pigments. For example, non-destructive image analysis of *Stropharia caerulea* growing in soil revealed a reduction in

extra-resource mycelial biomass and mass fractal dimension when grown in combination with *Phanerochaete velutina*, and reduction in number of major mycelial cords when grown in combination with *Phallus impudicus* (Donnelly & Boddy 2001).

Substantial morphological and physiological changes also occur in response to predation by invertebrates. For example, grazing of *P. velutina* by the collembola *Folsomia candida* resulted in changes to mycelial extension rate, hyphal coverage, fractal dimension and other qualitative aspects of morphology (Bretherton et al. 2006; Wood et al. 2006; Boddy & Jones 2008; Tordoff et al. 2008). Moreover, grazing altered the progression and outcome of interspecific mycelial interactions (TD Rotheray et al., unpub.). It appears that different species have evolved different strategies to balance their ability to explore new territory, defend space already occupied

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and maintain an effective transport network in the face of continuous attack. These are manifest in a range of network architectures and adaptive dynamics (Boddy 1999; Fricker *et al.* 2008a).

Recent work has begun to analyse mycelial network architecture (Bebber *et al.* 2007a, b; Fricker *et al.* 2007, 2008a, b; Lamour *et al.* 2007; Boddy *et al.*, in press) using tools developed in graph theory and statistical mechanics (Albert & Barabási 2001; Strogatz 2001; Dorogovtsev & Mendes 2002; Newman 2003; Amaral & Ottino 2004). This involves creating a digitised representation of the mycelial network as a graph, by plotting a series of connected nodes, representing branching points or anastomoses, and interconnecting links in the mycelium (Fricker *et al.* 2007). By mapping the network over time it is possible to examine changes in architecture, such as the formation of preferential transport routes through thickening of cords, development of cross linkages which increase resilience to attack, or local regression of mycelia as the network recycles redundant material. The network graph can be readily analysed to give theoretical predictions of the transport efficiency, resilience and cost of the network (Fricker *et al.* 2007). This analytical approach has demonstrated that mycelia of *P. velutina* develop a robust network that is resistant to damage, yet maintains a high transport efficiency (Bebber *et al.* 2007a). Moreover, this was achieved with a relative decrease in cost through preferential reinforcement of certain pathways and removal of intervening mycelium.

Here we investigate the changes that occur in mycelial network structure of *P. velutina* interacting with *Hypholoma fasciculare* in soil microcosms in the presence and absence of the collembola *F. candida*. In this three-way interaction, we hypothesise that: (1) *P. velutina* will reinforce the mycelial network in the vicinity of the interaction; (2) collembola grazing will reduce transport efficiency due to severance of cords; and (3) the biomass of the network in proportion to the area covered will be greater in un-grazed systems, as the collembola remove mycelia in grazed systems.

Methods

Soil microcosm systems

Details of the experimental set up are given by TD Rotheray (2008). Briefly, beech wood blocks ($2 \times 2 \times 2$ cm) were pre-colonised with *P. velutina* and *H. fasciculare* for 3 months and then positioned 9 cm away from diagonally opposite corners of trays (24×24 cm) of compressed, non-sterile soil at different times, such that the mycelia met at the centre. Trays were incubated at 20 °C in the dark. Two days after mycelia had contacted each other, *F. candida* (20 at each corner of the tray) were added. Changes in the mycelial networks were recorded at 2–4 d intervals by digital photography (Nikon® Coolpix™ 5700) at a height of 47 cm with artificial illumination provided by two 1000 W spot flood lamps.

Network digitisation

Three replicates each of grazed and un-grazed systems were selected using randomly generated numbers from 10

available. Six images for each replicate were selected at $t = 0$ d, 4 d, 8 d, 12 d, 20 d and 34 d after collembola addition. Each image was cropped to remove background, resized to 1773×1773 pixels, and saved as an 8-bit greyscale .tif image. Image series were imported into a custom MatLab (The Mathworks Inc., Natick, USA) program (available from MDF on request) and aligned with respect to one another. Alignment was achieved by selecting consistent landmarks on successive images, and calculating a linear spatial transformation to correct for translation, rotation and scaling. The network was extracted as a series of N nodes, each representing a branch or anastomosis, joined by a set of K links representing the intervening cords. Node positions were stored as a list of their Cartesian (x, y) coordinates, whilst links were stored as a weighted $N \times N$ adjacency matrix, where each entry represents the diameter of the link between node i and node j (D_{ij}). As the structure of the network within the wood blocks cannot be characterised, the inoculum was represented as a single central node with multiple links leading to the cords emanating from the edge of the block (Figs 1 and 2). At each time point new growth was added as new nodes (with associated links), and complete regression was identified by disconnecting the relevant nodes. At this stage it is not possible to discriminate a genuine cord-fusion event from cords that are growing over each other. This will cause an over-estimate of anastomoses, particularly early in development before proper junctions have had time to become established. Nevertheless, manual dissection of fully networked systems shows that more established overlying cords are almost invariably linked in *P. velutina*. Nodes connected to only two other nodes (termed k_2 nodes), representing a bend in a cord, were removed from the adjacency matrix during analysis and the weight of the resultant link between the junctions at either end adjusted to take into account the length and thickness of the intervening links.

Estimation of link weights

As cords differ in thickness, the links in the adjacency matrix were weighted by an estimate of the cord diameter between node i and node j (D_{ij}). The pixel resolution of the images was not sufficient to obtain direct measurements of diameter, so an average value of the local reflectance intensity was used as a proxy for cord thickness. Samples were taken 12 pixels away from each node along each cord to ensure that only intensities of the cord of interest were included. The local neighbourhood was averaged using a Gaussian smoothing filter with a radius of 5 pixels and the maximum intensity recorded. The values from both ends of each cord were averaged to give the intensity for that cord. Intensities were converted to diameter using a calibration based on the measured relationship between the reflected intensity of *P. velutina* cords with actual diameter (Bebber *et al.* 2007a). The cost of each link was estimated from its length (l_{ij}) times the cross-sectional area ($a_{ij} = \pi(D_{ij}/2)^2$), whilst the predicted resistance to transport was calculated as $l_{ij}a_{ij}^{-1}$, making the simplistic assumption that a cord comprises a circular bundle of equally sized hyphae. The link weight was colour-coded across the network according to a rainbow scale, with red representing thick cords. Development or regression of links was measured as

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