Section 1:
Basidiomycete Life-Style

CHAPTER 1

Mycelial Networks: Structure and Dynamics

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Contents

Abstract

For continuing survival saprotrophic fungi must be able to capture organic resources discontinuously dispersed in space and time. Some Basidiomycota can only achieve this by production of sexual and asexual spores or sclerotia — categorized as 'resource-unit-restricted', whereas 'non-resource-unit-restricted' Basidiomycota can also spread between organic resources as mycelium. Mycelial distribution and foraging within organic resources and among relatively homogeneously and heterogeneously distributed resources is reviewed. 'Non-resource-unit-restricted' Basidiomycota have evolved different patterns of mycelial spread appropriate to discovery of resources of different sizes and distributions. They show remarkable patterns of re-allocation of biomass and mineral nutrients on discovery and colonization of new resources. Network architecture is a significant factor in the acquisition and distribution of nutrients, and in survival when parts of the network are destroyed. The costs and benefits of different architectures to large mycelial networks are considered.

British Mycological Society Symposia Series
Published by Elsevier Ltd.

1. INTRODUCTION

For most Basidiomycota in terrestrial ecosystems the predominant body form is the mycelium, comprising an interconnecting series of apically extending tubes — hyphae. Hyphae provide a large surface:volume, ideal for secreting enzymes for extracellular digestion of resources (Chapter 2), and for subsequent uptake of small molecules. Mineral nutrients, carbon and energy sources are presumed to be taken up largely at hyphal tips, be they embedded within an organic resource or foraging externally for new resources, and translocated from these sources to sites of demand (sinks; Chapter 3). Nutrient acquisition and other aspects of physiology are affected by the local environment (Chapter 2), and mycelia exhibit remarkable physiological and morphological plasticity. Moreover, since mycelial activity in one region can be supported by supply of water and nutritional resources from elsewhere, growth can sometimes occur in inhospitable places and adverse conditions. The interconnectedness of mycelia is of crucial significance to the organization and ecological roles of fungi (Rayner *et al*., 1995).

In terrestrial ecosystems, the organic resources on which saprotrophic Basidiomycota depend are usually discrete, varying in size from small to large plant fragments, e.g. bud scales, leaves and large woody components. These resources are distributed heterogeneously in both space and time, for example, the relatively homogeneous carpet of forest floor leaf litter comprises spatially discrete leaves, input largely over a 6–8 week period in autumn by broadleaf deciduous trees, or more evenly during the year by many conifers. Branches are patchily distributed on the forest floor, falling throughout the year, though often with larger inputs following high winds. For continuing survival saprotrophic fungi must be able to capture these discontinuously dispersed resources. Some Basidiomycota can only achieve this by production of sexual and asexual spores or sclerotia, and have been categorized as 'resource-unit-restricted', whereas 'non-resource-unit-restricted' Basidiomycota can also spread between organic resources as mycelium. Spores, although allowing rapid spread, sometimes over long distances, contain only relatively small food reserves from which to produce a mycelium for invasion of the organic resource upon which it has landed. Sclerotia often provide larger resources and also allow survival in time. Growth as mycelium, in contrast, allows the fungus to draw upon a much larger supply of nutrients.

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This chapter considers mycelia growing within organic resources, and the ways in which they search and colonize them when discontinuous. It also examines the significance of network architecture, and the costs and benefits of large mycelial networks.

2. MYCELIA WITHIN ORGANIC SUBSTRATA

There is little information on mycelia within organic resources. Exceptions are maps of the extent of mycelia, inferred from interaction zone lines (see Chapters 7 and 11), and location of hyphae in relation to type of rot (Rayner and Boddy, 1988). The size of mycelia ranges from a few millimetres to many metres, in the case of longitudinally extensive (30 m or more) primary colonizers of attached branches and standing trunks (Boddy, 2001). The three-dimensional shape of the mycelial boundary is largely governed by the anatomy of the resource and by surrounding antagonistic fungi. For example, in wood, decay columns tend to be larger longitudinally than in other directions, reflecting difficulty of radial and tangential spreads. The diamond shaped cankers on sycamore (*Acer pseudoplatanus*) caused by *Dichomera saubinetii* (Ascomycota) result from spread between nutrient rich ray cells (Bevercombe and Rayner, 1980). Crucially lacking, however, is knowledge of the interconnectedness of different parts of the mycelium, and even the amount of mycelial biomass at different locations within organic resources. That there is spatial heterogeneity of mycelial distribution within wood decay columns is suggested by the common observation that when wood is incubated in a humid environment mycelium often grows out rapidly and profusely from the edges, and more slowly and less densely from more central regions.

3. MYCELIA FORAGING BETWEEN RELATIVELY HOMOGENEOUSLY DISTRIBUTED RESOURCES

Fungi have evolved a variety of foraging and behavioural responses to encounters with new resources. Fungi that utilize individual, relatively homogeneous resources, e.g. a leaf litter layer, effectively colonize as if individual components are simply parts of a larger resource. Mycelia form large patches with no particular pattern, e.g. *Collybia* spp. and *Marasmius* spp., or form fairy rings, e.g. *Clitocybe nebularis* (Dowson *et al.*, 1989). Nothing is known of the network architecture of mycelial patches, but fairy rings of *C. nebularis* extend through the leaf litter layer as an ever increasing annulus of mycelium ~30–40 cm wide (Dowson *et al.*, 1989; Figure 1a–d). The band is differentiated into three distinct zones: (1) the leading edge comprises mycelial cords (linear organs of predominantly parallel hyphae) spreading across the leaf litter layer and up to 6 cm into soil beneath; (2) a central region of dense mycelium which ramifies throughout, and presumably causes, intensely bleached leaf litter but does not extend into the mineral soil; (3) mycelium at the trailing edge which becomes progressively fragmented before completely disappearing. (Fruit bodies are produced from the middle of zone 2.) This outwardly extending annulus does not form as a result of lack of nutrients in central areas, as these are replenished every autumn, nor are toxic metabolites likely to be the cause, since when part of the annulus was transplanted into this region it grew well (Dowson *et al.*, 1989). Rather, these mycelia exhibit highly polarized growth, such that when a turf containing all zones of the annulus was relocated elsewhere, growth continued in the original direction of travel with limited lateral growth (Dowson *et al.*, 1989). Young mycelia of *C. nebularis* form patches, but what triggers annulus formation is

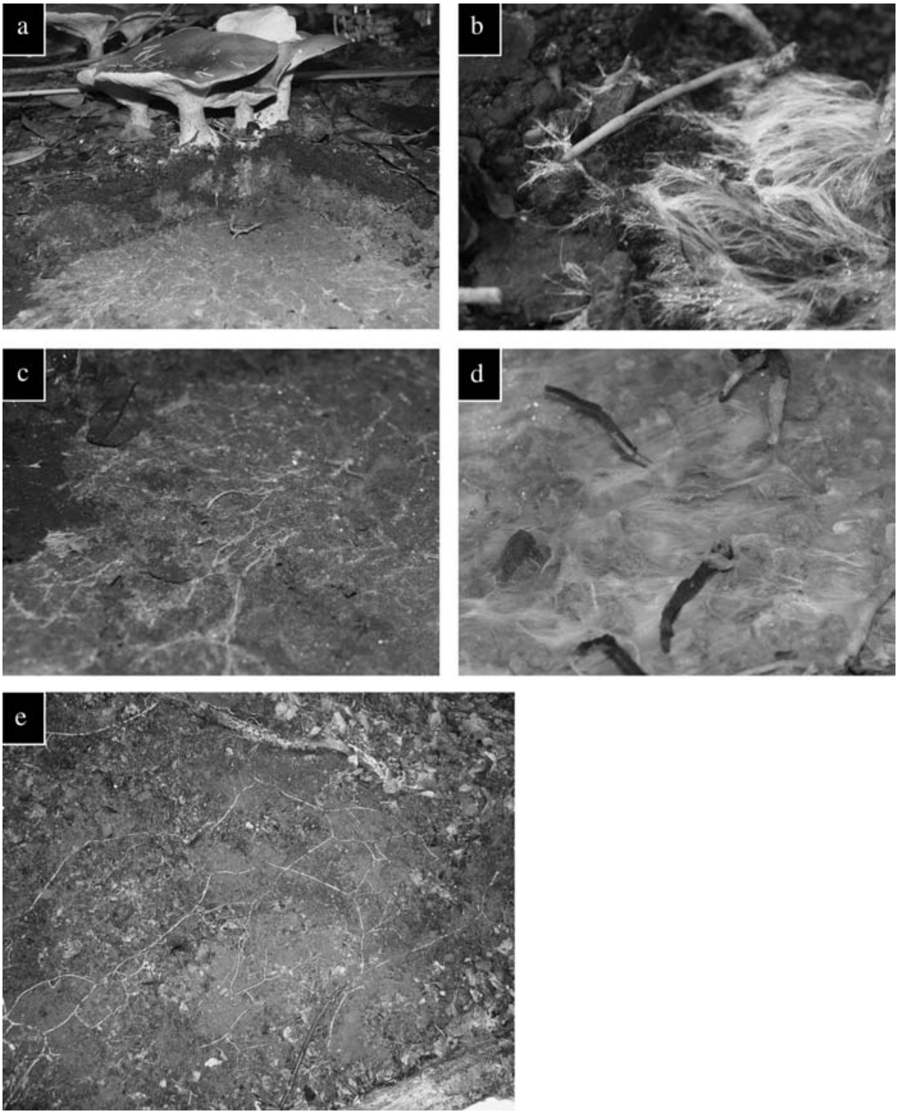

Figure 1 (a–d) Mycelium of a *Clitocybe nebularis* Fairy Ring which had Developed under a Paving Slab in a Garden. (a) Location of Fruit Bodies in Relation to Mycelium. Note Aggregation into Cords, but still with Diffuse Mycelium, towards the Leading Edge (Left). (b) Mycelium Aggregating into Fine Cords at Leading Edge. (c) Thicker Cords amidst Dense Fine Mycelium. (d) Very Dense, Fine Mycelium in Central Zone of Annulus. (e) Mycelial Network of *Megacollybia platyphylla* in a Mixed Deciduous Woodland, Revealed by Removal of Surface Litter. Digital Images (a)–(d) Courtesy of David Moore.

unknown. Presumably ring formation is related to size and might be expected to start when a patch is over 80 cm diameter (i.e. double the width of the mycelial band).

4. MYCELIA FORAGING BETWEEN RESOURCES DISTRIBUTED HETEROGENEOUSLY IN SPACE AND TIME

Fungi that utilize spatially discrete resources, with centimetre- or even metre-scale separations, have developed a variety of foraging strategies. They commonly form linear mycelial aggregates termed rhizomorphs, e.g. *Marasmius androsaceus* and *Armillaria* spp., or cords, e.g. *Hypholoma fasciculare* and *Phanerochaete velutina* (e.g. Boddy, 1984, 1993, 1999; Hedger, 1990; Cairney, 1992, 2005; Rayner *et al*., 1995; Boddy and Jones, 2006). Rhizomorphs are linear organs, with a thick melanized rind, the whole organ extending from the tip (Rayner *et al*., 1985). Mycelial cords are also insulated from the environment with a thick rind, but they develop from a mycelial margin of diffuse hyphae, each of which extends apically. They can all draw on water, nutrients and energy held within other parts of the mycelium to sustain growth outside the organic resource(s) to which they are connected. In addition, although mycelial cords are insulated from the environment, they are able to absorb water and soluble nutrients via individual hyphae at the mycelial margin or that sometimes develop elsewhere, and they may colonize small litter components *en route* to large organic resources (Boddy, 1999; Watkinson *et al*., 2006).

Fungi producing extra-resource mycelium risk loss of a large amount of biomass, as a result of invertebrate grazing, antagonistic microorganisms and death due to an unfavourable microenvironment, but this is minimized by a variety of different strategies. These include: (1) active growth and search for new resources; (2) a ‘sit and wait’ strategy, in which a mycelial network awaits arrival of resources, e.g. by branch fall, and then active colonization, often responding elsewhere in the system; and (3) most commonly, a combination of both. With all these strategies the mycelial networks are continuously remodelled in response to environmental cues, which can be abiotic (e.g. nutrient sources, microclimate or destructive events) and biotic (e.g. interaction with other fungi or grazing by invertebrates). Remodelling occurs through a complex combination of growth, branching, hyphal fusion and regression of different mycelial regions. Throughout the network, not only does morphology but also a complex set of physiological processes associated with uptake, storage and redistribution of nutrients change (Bebber *et al*., 2006; Watkinson *et al*., 2006). Both morphological and physiological changes are highly coordinated so that responses to local environmental changes can propagate through the mycelial network.

4.1 Search and Response Behaviour

Fungi have evolved a wide variety of patterns of mycelial outgrowth from resources into soil and litter (Figure 2; Boddy, 1999; Boddy and Jones, 2006). These have been quantified in terms of radial extension rate, hyphal coverage, and surface and mass fractal dimension (D_S and D_M, respectively) (Boddy, 1999; Boddy *et al*., 1999; Boddy and Donnelly, 2007). These range between mycelia characterized by diffuse, slowly extending search fronts, with a high D_M (close to 2 in two dimensions), e.g. *H. fasciculare* (Figure 2b) and *Stropharia* spp., and open AU :2

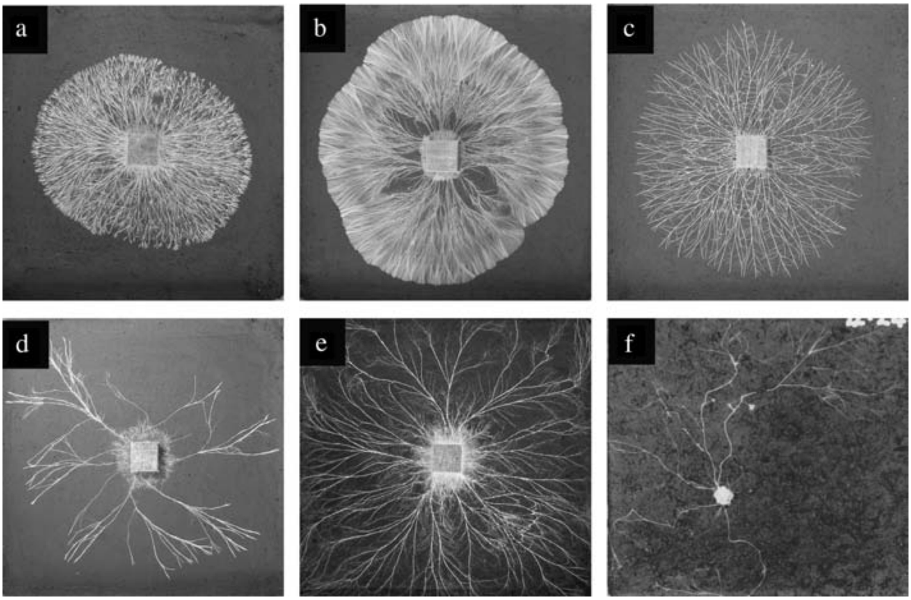

Figure 2 Patterns of Mycelial Outgrowth of Four Cord-Forming Basidiomycota across Compacted Soil in 24 × 24 cm Trays from *x* cm (a–e) and *y* cm (f) Beech (*Fagus sylvatica*) Wood Inocula. (a) *Coprinus picaceus*, (b) *Hypholoma fasciculare*, (c) *Phallus impudicus*, (d) *Resinicium bicolor* and (e and f) *Phanerochaete velutina*. Digital Images (a)–(d) Courtesy Alaa Alawi, and Digital Images (e) and (f) from Photographs taken by Rory Bolton.

systems characterized by well-defined, rapidly extending cords throughout the system, with a lower D_M (between 1 and ~1.8), e.g. *Agrocybe gibberosa*, *Coprinus picaceus*, *Phallus impudicus*, *P. velutina* and *Resinicium bicolor*. The former can be considered to be short-range foragers that are likely to be successful in discovering and exploiting abundant, relatively homogeneously distributed resources as they search areas intensively (Figure 2b), and the latter long-range foragers that would be less successful at capitalizing on relatively homogeneously supplied nutrients, but would successfully discover large, more sparsely distributed resources. Mycelial systems tend to become more open with time as they become larger (D_M decreases; Donnelly *et al.*, 1995; Boddy *et al.*, 1999; Figure 2a, c and d); patterns are modified by the quantity and quality of the resource from which the mycelium is extending (Bolton and Boddy, 1993; Donnelly and Boddy, 1997a; Boddy *et al.*, 1999; Zakaria and Boddy, 2002; Figure 2e and f), soil structure and nutrient status (Donnelly and Boddy, 1998; Boddy *et al.*, 1999; Zakaria and Boddy, 2002), microclimate (Donnelly and Boddy, 1997b; Owen, 1997; Wells *et al.*, 2001), interaction with mycelia of other species (Donnelly and Boddy, 2001) and invertebrate grazing (Kampichler *et al.*, 2004; Harold *et al.*, 2005; Bretherton *et al.*, 2006; Tordoff *et al.*, 2006; Wood *et al.*, 2006; Chapter 9).

When new resources are encountered the mycelium responds with dramatic changes in morphology (system architecture) and often with considerable reallocation of biomass. When the new resources are substantially larger than those from which the mycelium emanated, mycelium connecting the new resource with the original resource usually aggregates to form thick cords, while radial extension slows or ceases, and non-resource-connected mycelium regresses (Dowson *et al.*, 1986, 1988; Bolton *et al.*, 1991; Boddy, 1993, 1999; Bolton, 1993; Donnelly and Boddy, 1997a; Figure 3a–c). Subsequently mycelium grows out from the newly colonized resource, and foraging continues, though the amount of time before foraging continues depends on the sizes of the original and new resource (Bolton, 1993; Boddy and Jones, 2006). With short-range foragers (e.g. *H. fasciculare*), there are similar, although less dramatic, changes to system architecture even when newly encountered resources are similar in size to the original resource.

Not only does the mycelium respond by changes to system architecture but also with physiological responses: there is highly coordinated uptake, storage and redistribution of nutrients throughout the network (Watkinson *et al.*, 2006; Chapter 3). Mineral nutrients (e.g. nitrogen and phosphorous) can be transported from wood resources to support growth at the mycelial margin, and nutrients scavenged as mycelia extend through soil can be translocated away from sites of uptake to sites of demand or storage, and commonly accumulate in wood resources connected within the mycelial system (Wells and Boddy, 1990; Wells *et al.*, 1990, 1997, 1998, 1999; Cairney, 1992). Rates of translocation can be rapid (sometimes $>25\,\mathrm{cm\,h^{-1}}$), the largest fluxes being through cords interconnecting resources (e.g. Wells and Boddy, 1990). Many factors, including the overall nutritional status of the mycelial system, and the distribution and quantity of colonized and newly encountered organic resources, affect the balance between, and the main sites of, uptake, storage and demand for carbon and mineral nutrients (Abdalla and Boddy, 1996; Hughes and Boddy, 1996; Wells *et al.*, 1998, 1999; Boddy and Jones, 2006).

4.2 Persistent Mycelial Networks: ‘Sit and Wait’ Strategy

Saprotrophic cord- and rhizomorph-forming Basidiomycota produce extensive long-lived mycelial networks on the forest floor, eventually covering several square metres to many hectares (Thompson and Rayner, 1982; Thompson and Boddy, 1988; Smith *et al.*, 1992; Ferguson *et al.*, 2003; Cairney, 2005; Figure 1e). The largest recorded to date is a genet of *Armillaria ostoyae* spanning 965 ha, with a maximum separation of 3,810 m and estimated as 1,900–8,650 years old (Ferguson *et al.*, 2003). The true extent and degree of connectivity within a genet is not known, however, since parts of mycelia can be separated from each other during development, and can also rejoin if parts of the same genet meet again. Similar systems are also found in the canopy of tropical forests where they effectively form a net (Hedger, 1990). Whether on the forest floor or in the canopy, these large, persistent networks allow capture of resources arriving by litter fall or root death at any time.

Although persistent, established systems are dynamic both as continued extension at growing fronts (Thompson and Rayner, 1983) and as renewed mycelial growth from mature cords. Arrival of new resources can result in reallocation of

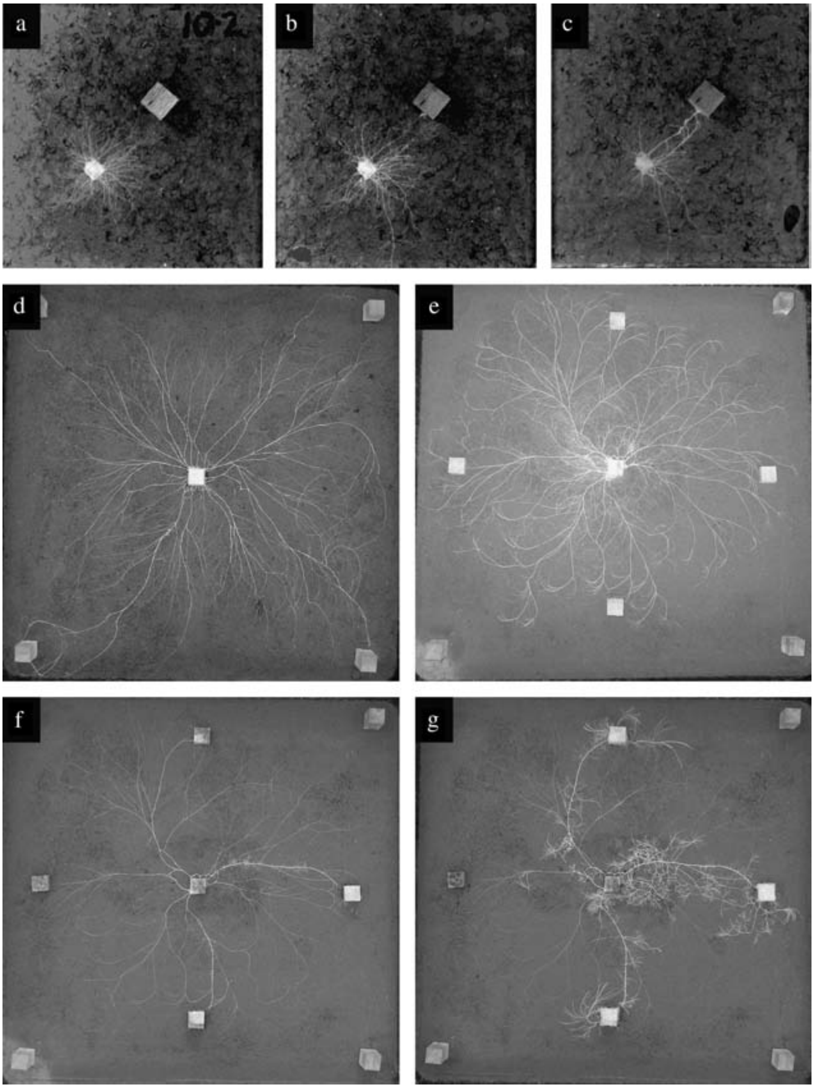

Figure 3 Reallocation of Mycelial Biomass of *Phanerochaete velutina* following Colonization of New Wood Resources. (a–c) Extending from a 0.5 cm^3 Beech (*Fagus sylvatica*) Wood Inoculum to an 8 cm^3 Wood Resource, in 24 × 24 cm Trays of Non-Sterile Soil, after, respectively, 11, 15 and 20 Days. Note Regression of much of the Mycelium not Connected to a New Resource, and Thickening of Connected Cords (c). (d–g) Growth in 57 × 57 cm Soil Trays, with Four New Wood Resources (Located Half Way along each Microcosm Side) added after 36 Days in (e)–(g). (d) Control with No Additional Wood Resources. Images were Captured 78–85 Days after adding the Central Wood Inoculum. Note Thickening of Cords Connecting Inoculum with New Resources (f and g), and Thinning of Other Areas compared with 78 Days Control having No Additional Resources (e). Outgrowth from the Newly Colonized Lower Resource is Evident from 78 Days (Perspex Blocks in the Corners of Trays were for Support of Other Replicates in Stacks). Proliferation of Mycelium occurred along Cords linking the Central Wood Inoculum with New Resources between 78 Days (f) and 85 Days (g). Digital Images (a)–(c) from Photographs taken by Rory Bolton. Digital Images (d)–(g) Courtesy of Jon Wood.

biomass, with thickening of cords connecting resources, and regression of non-connective fine mycelium (Wood *et al.*, 2006; Figure 3d–g). Moreover, sometimes renewed growth occurs elsewhere as ephemeral patches of much branched fine hyphae or along cords interconnecting new and original resources (Wells *et al.*, 1997; Wood *et al.*, 2006; Figure 3g). The patches have been shown, using ^{32}P orthophosphate, to be sites of nutrient uptake (Wells *et al.*, 1977), and presumably developed to satisfy the increased demand for nutrients to produce mycelial biomass and enzymes during early stages of colonization and decomposition. Carbon and mineral nutrients are continually rerouted to sites of need in mycelial systems interconnecting a variety of resources in different states of decay (Wells *et al.*, 1998).

5. ANALYSIS OF NETWORK ARCHITECTURE AND FUNCTION

Within the mycelial networks of saprotrophic Basidiomycota there is considerable scope for communication, since hyphae maintain continuity with their immediate 'ancestors' and if contact is made with neighbouring regions can become connected via *de novo* formation of cross-links (anastomoses). This results both radially and tangentially in systems with many connected loops (Figure 4).

The mycelium has evolved differently in different species resulting in a range of network architectures, adapted differently for differing balances of exploration, transport efficiency and resilience to damage. Highly interconnected mycelia are costly to construct but offer alternate transport routes and thus resilience to damage. Sparse networks with fewer interconnections can extend further for a

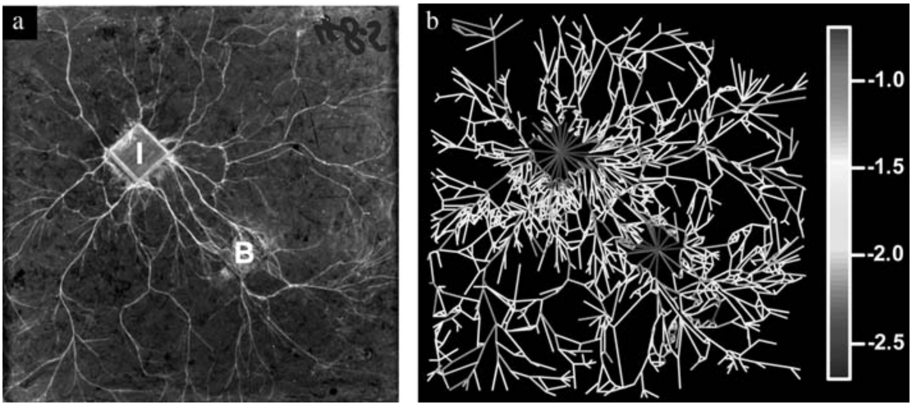

Figure 4 (a) Mycelium of *Phanerochaete velutina* after 25 Days Growth from a 4 cm^3 Beech Wood Inoculum (I) across a Tray (24 × 24 cm) of Compressed Non-Sterile Woodland Soil. The Fungus has Met and Colonized a Second Wood Block (B). Digital Image Courtesy of Rory Bolton. (b) The Digitized Network of the Same Mycelium Coloured by $\log_{10}$ of Link Cross-Sectional Area. The Number of Nodes $V = 1{,}738$, Links $E = 2{,}617$ and the Number of Separate Parts $G = 1$. The Number of Closed Loops (Cycles) in the Illustrated System is $E - V + G = 880$, and the Fraction of All Possible Cycles Present $\alpha = 0.25$.

given construction cost, but risk the loss of pathways should one part of the network become damaged. Networks can vary not only in their connectedness but also in the strength of their connections. Thick cords confer greater transport capacity and resistance to breakage, but are more costly to produce. While these concepts have been implicit in discussions of fungal foraging strategies and fractal descriptions of mycelia, the architecture of mycelial networks has been little explored until recently (Bebber *et al.*, 2006; Fricker and Bebber, in press; AU :3 Fricker *et al.*, 2007).

5.1 Quantifying Network Characteristics

D_M is a useful metric for comparing space filling by mycelia (Boddy and Donnelly, 2007), but it only expresses a small fraction of the complex architecture of mycelial systems. Tools for analysing networks are, however, emerging from graph theory and statistical mechanics (Albert and Barabási, 2001; Strogatz, 2001; Dorogovtsev and Mendes, 2002; Newman, 2003; Ottino, 2004; Amaral, in press), AU :4 that are applicable to mycelial networks (Bebber *et al.*, 2006, 2007; Fricker and Bebber, in press; Fricker *et al.*, 2007), and have already proved valuable for understanding the properties of many physical systems that can be described as sets of connected entities, including biological networks such as protein–protein interactions and food webs (Bork *et al.*, 2004; Dunne *et al.*, 2004).

A network is simply a set of nodes, or vertices, connected by a set of links, or edges. Weights, that define properties such as resistance to breakage or transport capacity, can be associated with either nodes or links, or both. The nodes of a fungal mycelium are the tips, branch points and fusions of hyphae or cords, while the links are the hyphae or cords themselves. Various weights can be assigned to the nodes and links. For example, the mass of a cord can be approximated by its volume, the length multiplied by the cross-sectional area. Similarly, assuming that cords are composed of bundles of hyphae rather than being hollow tubes, the resistance to flow could be a function of the length divided by the cross-sectional area, i.e. long thin tubes have a greater resistance to flow.

The properties of nodes are often defined by the links to which they are connected. In the case of networks without link weights (the majority of examples in the literature lack this information), the number of links per node (termed degree k) is often used to describe something about the connectedness of the network. This measure is unlikely to be of interest in describing mycelial networks, as the majority of nodes will be of degree $k = 3$ (the branches and fusions) or 1 (the cord tips). Instead, the sum of link weights per node, known as the node strength, is likely to be of greater interest. For example, calculating the node strength for link cross-sectional area could indicate which nodes are likely to be important in transport.

The number of nodes (V), links (E) and separate part G, known as disconnected components or subgraphs, $G = 1$ (for an unbroken network), form the network that can be used to calculate the number of closed loops (cycles) in the network via the simple relation $E - V + G$ (Figure 4). This cyclomatic number AU :5

is extremely important, for it indicates the number of alternate pathways among points in the network that determine both the resilience to damage and the capability of parallel flow. The cyclomatic number is typically normalized to the maximum number possible for a network of a given size, allowing networks with differing numbers of nodes to be compared.

5.2 Modelling Transport

The fungal mycelium is essentially a transport network for nutrients, water and metabolites (Chapter 3). Modelling of transport in the mycelium has been attempted using various approaches, including partial differential equations and autonomous agents (Edelstein and Segel, 1983; Deutsch *et al.*, 1993). Since these methods ignore the network structure of the mycelium, greater insights can be obtained by taking an explicitly network-based approach into the analysis of transport. One way to achieve this is to calculate shortest path distances from each node to every other. If the effective physiological distance, or transport resistance, from one end of a cord to the other is modelled as the cord length divided by its cross-sectional area, the shortest path from one node to another will be the route with the smallest sum of these distances. The shortest path is therefore effectively the path of least resistance. Analysis of shortest paths of *P. velutina*, growing from wood blocks over soil, shows that the shortest paths from the wood blocks to other nodes of the fungus are smaller than they would be in a network with identical topology (i.e. number and location of links and nodes) but with uniform cord transport capacity (Bebber *et al.*, submitted). The fungus has therefore allocated resources to cords in a way that increases its transport efficiency. The only nodes for which the fungus is less efficient than in the randomized system are those at the periphery of the mycelium, where very fine hyphae are located (Figure 4). Here the fungus has optimized mycelial distribution for searching for new resources rather than optimizing for transport.

The routes taken by shortest paths can reveal other aspects of network transport. For example, the importance of a node can be estimated by its betweenness centrality, which is the proportion of shortest paths that pass through that node (Freeman, 1977). The proportion of paths that pass through the node with the greatest betweenness centrality is the central point dominance. In fungal networks, resources such as wood blocks usually have the greatest betweenness centrality.

The shortest path is usually only one of the several routes that could be taken from one node to another. Transport through a real network will often make use of these alternate routes, in the same way that electricity will flow through each of a set of resistors in parallel. Use of shortest paths to characterize transport necessarily ignores the importance of these parallel pathways through the network. Methods for solving current flow (e.g. Wu, 2004) through networks of electrical resistors can in principle be used to model flow through mycelial networks, for example, by applying a voltage to the inoculum and grounding the hyphal tips. This may provide more realistic models of flow than simply using the shortest path.

5.3 Modelling Resilience

In nature, fungal mycelia are threatened by damage from physical disturbance and targeted attack by grazers such as Collembola (Chapter 9). Network architecture plays an important role in resilience to damage, through both route redundancy and the probability of link breakage. Assuming a spatially random mode of attack, the probability of a link being attacked is proportional to its length. If, when attacked, the probability of link breakage is inversely proportional to its cross-sectional area, then the joint probability of a link being attacked and broken is proportional to length divided by cross-sectional area. The effect of attack on transport can be followed by examining the global efficiency, the sum of the reciprocals of all shortest paths, as the network disintegrates (Latora and Marchiori, 2001). Paths that are no longer traversable due to the formation of multiple disconnected components are infinitely long, and thus contribute zero to the global efficiency. Global efficiency therefore declines with increasing proportions of broken links. Another way of characterizing resilience is through the reachability, or availability, of a network (Ross and Harary, 1959). Reachability is the proportion of shortest paths that still exist (i.e. are not infinitely long). Reachability is one for a network that has not been fragmented (i.e. consists of one subgraph), since all nodes are mutually available. Reachability does not depend on path length and is therefore independent of the link breakage probability function, whereas the efficiency will be greater if thick cords are less likely to break than thin ones.

Another way to measure resilience is to measure the proportion of the original network that remains connected to the wood block as increasing numbers of links are broken. In nature, disconnection from a food supply is likely to result in death of the disconnected part. When networks of *P. velutina* were tested against model networks with uniform link weights, more of the fungal network remained attached to the inoculum when a given proportion of links were broken (Bebber *et al.*, submitted). This demonstrated that the allocation of resources to cords not only increases transport efficiency, but also increases the resilience of the network to this kind of random attack. Inspection of network models that have been attacked in this way suggests that the secret to this increased resilience is the maintenance of a connected core structure as peripheral cords are broken. This pattern is intriguingly similar to that obtained in real networks after attack by certain species of Collembola (Chapter 9). Other mycophagous species may attack networks in other ways, depending, for example, on the size of their mouthparts.

5.4 Changes in Network Architecture over Time

As already mentioned, in peripheral regions cords are thin and at growing fronts hyphae are not aggregated, and therefore have high resistance to transport and long path lengths to the inoculum. As the network develops, some links become strengthened, such that the path lengths become dramatically shortened over time, while other links are removed, leading to an overall decrease in the material cost density over time (Bebber *et al.*, submitted). The expectation would be that such strengthening would be accompanied by an increase in the overall construction cost of the network. However, thinning and removal of extraneous cords actually results in a decrease in the volume of material per unit area covered by the network (Bebber *et al.*, submitted). The mechanism by which certain cords are selected for reinforcement while others are broken down remains unknown. A possible conceptual model is one of Darwinian evolution, in which multiple cords are produced but only the 'fittest', in some sense, survive and produce further growth.

5.5 Future Research Direction

One of the most important avenues for further research will be the comparison of network structures and dynamics among the many different cord-forming fungal species. Like any organism, a fungus must partition limited resources among competing requirements. For example, a very dense, highly connected network might have high transport capacity and resilience to damage or attack because of multiple transport pathways. However, it would incur a large material cost of construction per unit area of explored space, and would cover new ground slowly. Conversely, a sparse system could extend further for the same material cost, but would have fewer alternate routes and therefore lower resilience to disconnection. Variation in these tradeoffs among species could reveal important axes of niche differentiation in fungi.

Further, fungi provide one of the few real network systems that can be experimentally manipulated, and that can actually rebuild themselves following damage. Analyses of cord-forming Basidiomycota mycelial systems are therefore likely to reveal a range of evolutionary solutions to network design that may inform the development of other types of transport network, e.g. road, rail and telephone.

ACKNOWLEDGEMENTS

We thank N.E.R.C. for funding much of the research reported here. The research on fungal foraging patterns has been conducted over many years and with many collaborators to whom we extend our thanks: Saleh Abdalla, Alaa Alawi, Rory Bolton, Sam Bretherton, Clare Culshaw, Peter Darrah, Damian Donnelly, Chris Dowson, Simon Harold, Melanie Harris, Carolyn Hughes, Juliet Hynes, Hefin Jones, Christian Kampichler, Jonathan Leake, Louise Owen, Alan Rayner, Johann Rolschewski, Timothy Rotheray, Phillip Springham, Joanna Thomas, Wendy Thompson, Monica Tlalka, George Tordoff, Sarah Watkinson, John Wells, Jonathan Wood and Jamil Abd Zakaria.

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