

REVIEW

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## Saprotrophic cord systems: dispersal mechanisms in space and time

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**Abstract** In natural terrestrial environments, nutrients are often patchily and sparsely distributed, and the microclimate is constantly changing both temporally and spatially. To survive, fungi must be able to transfer to a new resource before the nutrient supplies in their current food base are exhausted. While the majority of fungi propagate as spores, some basidiomycetes can grow out of a resource as mycelium in search of new resources. The mycelium of these fungi typically aggregates to form linear organs, termed cords or rhizomorphs, that ramify at the soil–litter interface in forests, interconnecting disparate litter components to form extensive (many square meters or even hectares), long-lived (many years) systems. These mycelial systems form effective dispersal mechanisms in space and time. This article reviews the two main, but not mutually exclusive, mycelial dispersal (resource capture) strategies: (1) a “sit and wait” strategy, whereby a large mycelial network waits for resources to land on it and then actively colonises those resources; and (2) growing and searching actively for new resources. The way in which mycelia balance exploration and nutrient transport, and robustness to damage, against “cost” of production and speed with which an area can be colonised, is explored using techniques borrowed from graph theory and statistical mechanics.

**Key words** Basidiomycetes · Exploration · Fractal geometry · Networks

### Introduction

In natural terrestrial environments, nutrients are often patchily and sparsely distributed, and the microclimate is

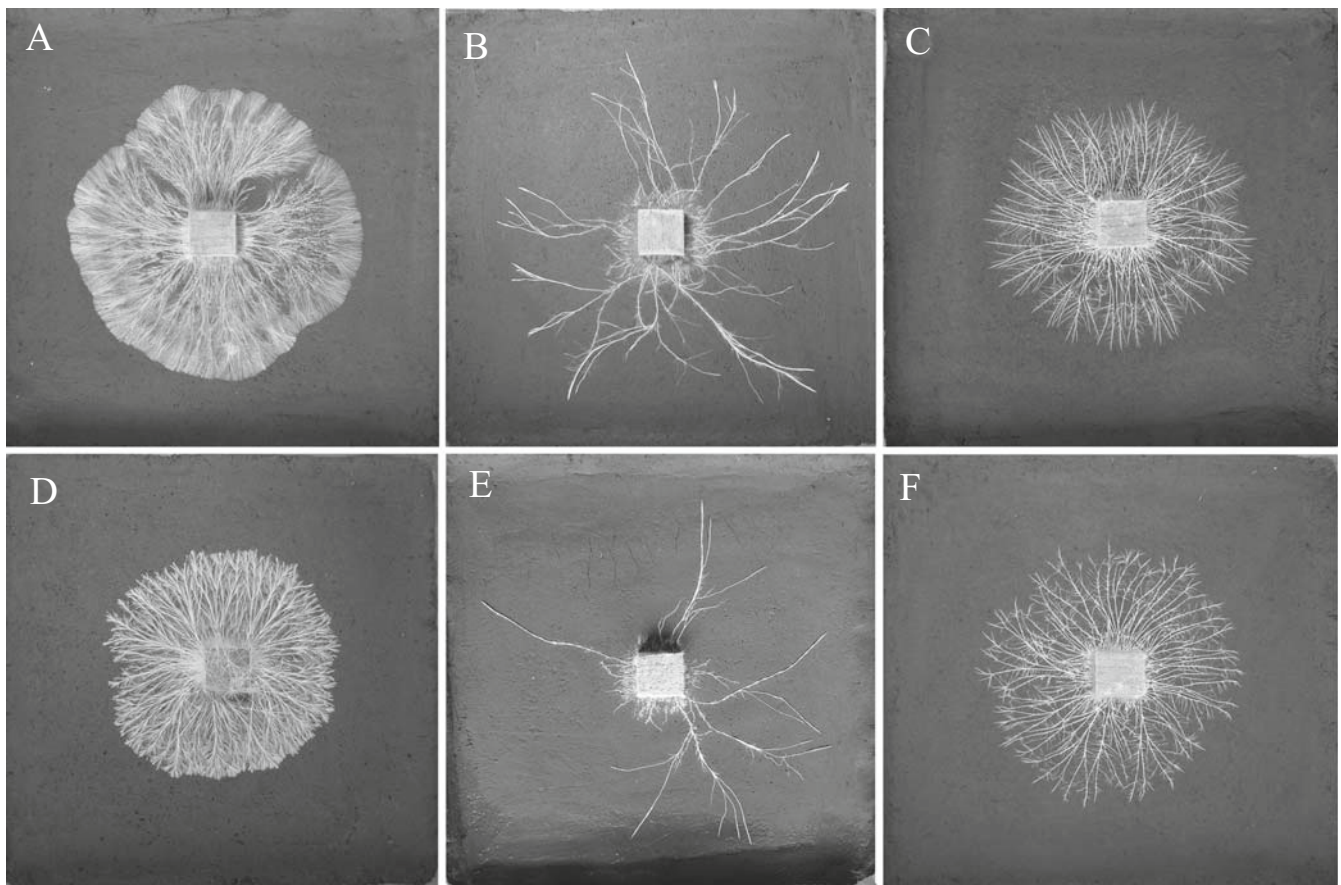
constantly changing, both temporally and spatially. To survive, fungi must be able to transfer to a new resource before the nutrient supplies in their current food base are exhausted. The majority of saprotrophs that decompose solid organic resources are confined to those resources until they produce sexual or asexual spores, and they have accordingly been termed resource unit restricted. These spores are usually relatively small, having the potential to travel thousands of metres, although spore catches are usually minimal at more than 20 km from a source, and the majority of spores settle within a few metres of the fruit body (Stenlid 2008). In this way they are dispersed in space and to some extent in time, but hyaline spores subject to UV radiation can lose more than 95% vitality within a few days (Kallio 1973), although pigmented spores survive longer (Burnett 2003). The probability of arrival on a suitable new resource under suitable environmental conditions is obviously extremely low, and a large amount of fungal biomass is lost in the form of unsuccessful spores. Some species disperse themselves in time, although usually not in space, by producing survival structures such as thick-walled conidia or sclerotia that remain in situ until the microclimate improves and/or new resources arrive.

By contrast, some fungi are able both to produce spores and to grow out of organic substrata, as mycelia, in search of new resources. These fungi have been termed non-resource unit restricted. Some effectively colonise individual organic resources as if they are simply parts of a larger resource, in which they are effectively if individual components touch. Thus, for example, *Heterobasidion annosum* (Fr.) Bref. colonises adjacent trees or stumps by mycelial spread through root grafts or woody roots that are in intimate contact (Stenlid 1986). Some *Collybia* spp. and *Marasmius* spp. form large patches in the leaf litter layer of woodlands, with no particular pattern, while others, e.g., *Clitocybe nebularis* (Batsch) Quél., form fairy rings – an ever-increasing annulus of mycelium about 30–40 cm wide (Dowson et al. 1989; Fricker et al. 2008; Lodge et al. 2008).

The fungi that utilize spatially discrete resources, centimetres or even metres apart, typically produce mycelium

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**Fig. 1.** Differences in foraging mycelial morphology, depending on species and temperature. Mycelia are growing from 4 cm<sup>3</sup> beech wood inocula across trays (24 × 24 cm) of compressed nonsterile soil. **A** *Hypholoma fasciculare* at 20°C after 28 days. **B** *Resinicium bicolor* at 20°C after 32 days. **C** *Phallus impudicus* L. after 27 days at 20°C.

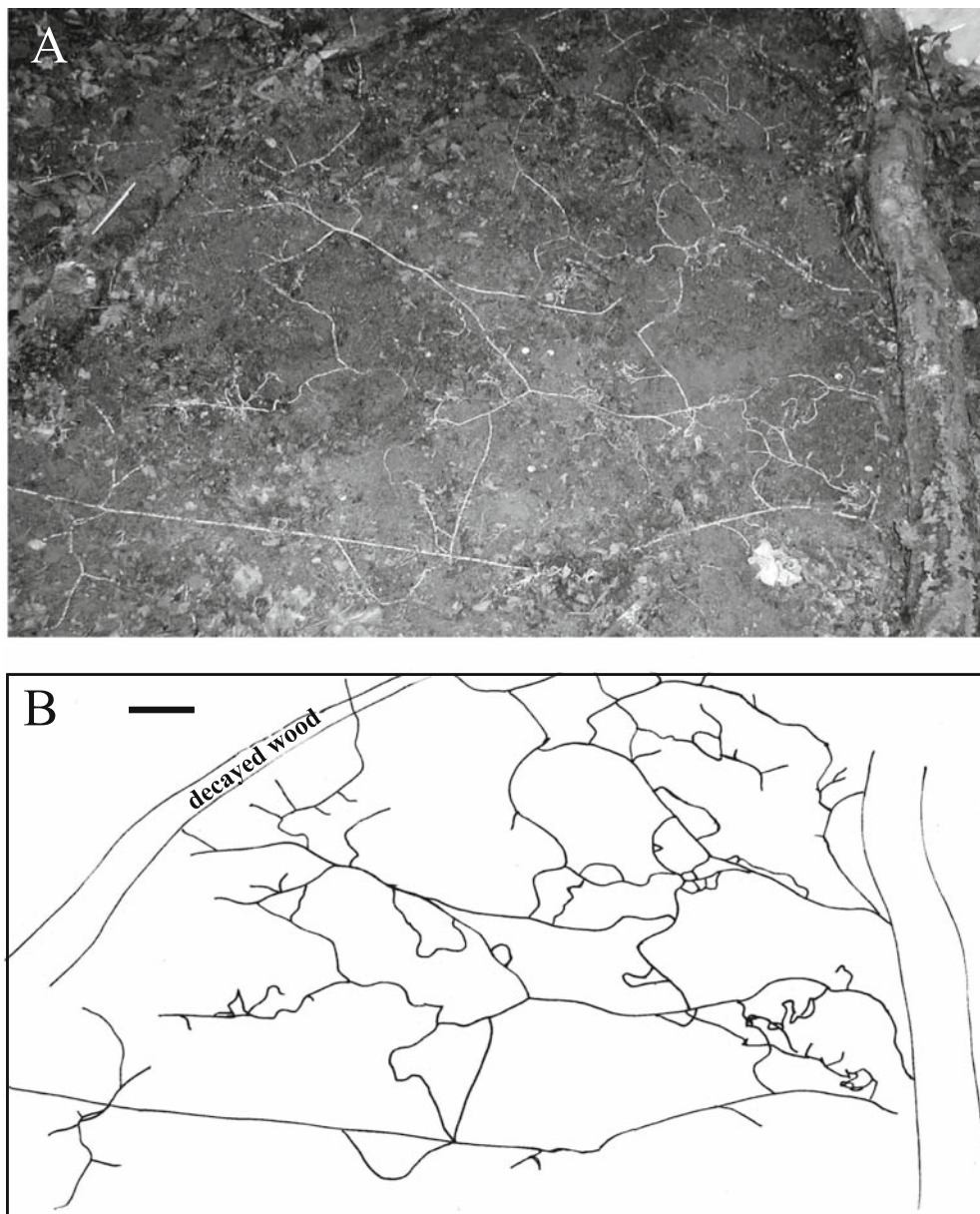
**D** *Coprinus picaceus* (Bull.) Gray after 28 days at 20°C. **E** *R. bicolor* initially at 5°C then changed to 20°C, after 70 days. **F** *P. impudicus* initially at 5°C then at 20°C, after 55 days. (Digital images courtesy of Alaa Alawi)

that aggregates to form linear organs, termed cords, e.g., *Hypholoma fasciculare* (Fr.) P. Kumm. and *Phanerochaete velutina* (DC.) Parmasto, or rhizomorphs, e.g., *Marasmius androsaceus* (L.) Fr. and *Armillaria* spp. (Boddy 1984, 1993, 1999; Hedger 1990; Cairney 1992, 2005; Rayner et al. 1995; Boddy and Jones 2007; Fricker et al. 2008). Rhizomorphs have a thick melanized rind, and the whole organ extends from the tip (Rayner et al. 1985). Mature mycelial cords are also insulated from the environment with a rind, but the whole organ does not extend apically; rather, it develops behind a mycelial margin of diffuse hyphae, each of which extends apically (Fig. 1). These mycelial systems, which form effective dispersal mechanisms in space and time, are the focus of this article. They extend from bulky organic resources at the soil–litter interface (Fig. 2) and have nutritional opportunities from encounters with both micro- and macro-organisms, but also are at risk of damage or destruction. Different species have evolved different mycelial configurations and responses, balancing between exploration, transport efficiency, and resilience to damage, with trade-offs against “cost” of production, speed with which a mycelium can colonise an area, and how complexity is controlled.

## Mycelial outgrowth and network development

Mycelia growing out from organic resources extend at different rates, cover the ground to different extents, and exhibit different branching and tangential connectivity patterns depending on species and isolates (Donnelly et al. 1995; Boddy 1999) (see Fig. 1), microclimate (Donnelly and Boddy 1997a; Owen 1997; Wells et al. 2001), nutrient status of the mycelial system to which they are connected and of the resource from which they are growing (Bolton and Boddy 1993; Donnelly and Boddy 1997b; Boddy et al. 1999; Zakaria and Boddy 2002), nutrient status and structure of the environment through which they are growing (Donnelly and Boddy 1998; Boddy et al. 1999; Zakaria and Boddy 2002), interaction with other mycelia (Donnelly and Boddy 2001), invertebrate grazing (Kampichler et al. 2004; Harold et al. 2005; Bretherton et al. 2006; Tordoff et al. 2006; Wood et al. 2006), and time, size, and age of the system (Donnelly et al. 1995; Boddy et al. 1999). Outgrowth patterns range between mycelia characterized by diffuse, slowly extending search fronts, with a high mass fractal dimension ( $D_M$  close to 2 in two dimensions),

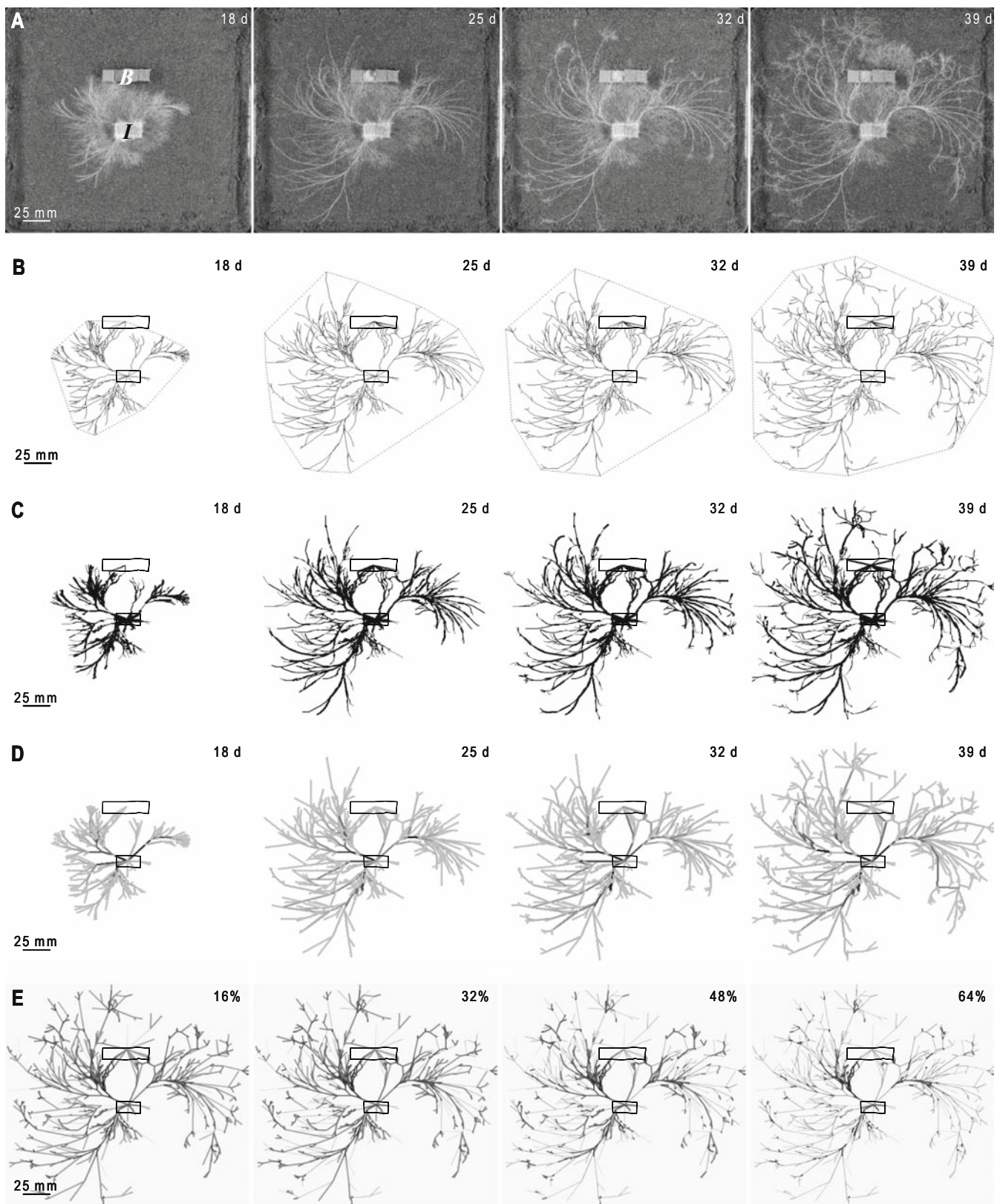
**Fig. 2.** Mycelial cord network of *Megacollybia platyphylla* (Pers.) Kotl. & Pouzar. **A** On the floor of a temperate, mixed deciduous woodland, revealed by careful removal of the leaf litter layer. **B** The same network redrawn to show connections clearly. Note the large number of loops. Bar **B** 25 cm



and open systems characterized by well-defined, rapidly extending cords throughout the system, with a lower  $D_M$  (between 1 and about 1.8). Fungi that exhibit the former patterns under optimal conditions, e.g., *H. fasciculare* (see Fig. 1A) and *Stropharia* spp., can be considered to be short-range foragers that are likely to be successful in discovering and exploiting abundant, relatively homogeneously distributed resources, since they search areas intensively. By contrast, fungi typically exhibiting the latter type of pattern, e.g., *Resinicium bicolor* (Alb. & Schwein.) Parmasto (see Fig. 1B,E) and *P. velutina* (Fig. 3), are adapted to long-range foraging because they are likely to be less successful at capitalizing on relatively homogeneously supplied nutrients, but would successfully discover large, more sparsely distributed resources.

As mycelial networks develop they are continuously remodelled through a complex combination of growth, branching, hyphal fusion, and regression of different mycelial regions. As already mentioned, at growing fronts hyphae tend not to be aggregated, and immediately behind the front cords are often thin, resulting in high resistance to transport and long path lengths to the inoculum. As the network develops, some hyphae aggregate to form cords that strengthen links between locations within the system, while other hyphae regress, i.e. links are removed, resulting in much more open/less dense systems over time ( $D_M$  decreases; Donnelly et al. 1995; Boddy et al. 1999; Bebber et al. 2007b) (Fig. 3). The effects that these morphological changes have on cost of production, nutrient movement, and resilience to damage can be assessed by mathematical analysis of mycelial network architecture.





**Fig. 3.** Changes in *Phanerochaete velutina* mycelial network architecture over time, growing across compressed, nonsterile soil from a 2-cm<sup>3</sup> beech wood inoculum (*I*) to an additional resource (*B*), at the time points (*d*, days) indicated (**A**). Branch points and anastomoses were manually coded as nodes connected by links, to give a network representation of the colony (**B**). The area covered by the foraging mycelium was determined from the convex hull (*dotted line*). The relative diameter of each link was determined by image analysis, with appropriate calibration, to give a weighted network illustrated by varied link thick-

ness (**C**). The normalised betweenness centrality of each link represents the number of shortest paths between pairs of nodes that pass through each link and gives a measure of the relative importance of each link to the predicted transport performance of the network (**D**). The resilience of the network at 39 days was tested by repeated removal of a proportion of the weakest links (**E**). After removal of 64% of the links, the only component remaining connected to the original inoculum is the additional resource, reflecting the reinforcement of the interconnecting cords

## Analysis of mycelial outgrowth and network development

Mycelial network architecture can be analysed using techniques borrowed from graph theory and statistical mechanics (Bebber et al. 2007a,b; Fricker et al. 2007, 2008; Lamour et al. 2007). Network topology is extracted from digital images by classifying junctions (branch-points and anastomoses) as nodes or vertices ( $V$ ), and the cords between nodes as links or edges ( $E$ ). For example, *P. velutina*, growing from a wood inoculum over soil in microcosms, forms a sparsely connected network over a 5- to 6-week period (Fig. 3A). The major cords present can be manually digitised to give a network representation (Fig. 3B), although it is not possible to capture all the very fine hyphae in the early stages of diffuse growth using this approach. In general, the number of nodes and links increases as the colony grows. However, as the network develops behind the foraging margin, there is consolidation of certain links to form well-connected routes and regression of the remainder, thinning out the network. The extent and timing of these changes depends on the overall level of nutrient availability in the system. Thus, the example shown here has access to substantial resources in the initial inoculum and the discovered resource and is only just beginning to thin out the initial network at the end of the experiment (Fig. 3A,B). In microcosms with less resource, consolidation and recycling takes place earlier as the system has to make more efficient use of limited resources to drive further exploration (Bebber et al. 2007a). The number of closed loops (cycles) in the network formed during network remodelling can be determined as  $E - V$ . This value (the cyclomatic number) indicates the number of alternate pathways among points in the network and is particularly important as it determines both the robustness to damage and the capability of parallel flow for nutrients. To allow comparison of networks with differing numbers of nodes, the cyclomatic number can be normalised to the maximum number possible for a planar network of a specified size by dividing by  $(2V - 5)$  to give the alpha coefficient. The alpha coefficient, measured over the whole colony, increased over time from near 0, as expected for a branching tree, to  $0.11 \pm 0.04$  in control systems and to  $0.20 \pm 0.05$  in systems with an additional wood block resource (Bebber et al. 2007a). Thus, these fungal networks progress from a branching tree to a weakly connected lattice-like network behind the growing margin, through a process of fusion and reinforcement to form loops, and selective removal and recycling of excess redundant material.

The changes in thickness of the cords during growth and network remodelling can be captured by image analysis of the reflected intensity of each cord, with appropriate calibration, to give each link a weight that depends on its length ( $l$ ) and cross-sectional area ( $a$ ) (Fig. 3C). The mass of material in each link is estimated as  $la$ , as long, thick cords are obviously more costly to produce than short thin cords. The material cost of the network can then be calculated as the total cost summed across all links ( $C = \Sigma la$ ). The area ( $A$ )

explored by the network during foraging can be estimated from the area of the smallest convex polygon that would circumscribe the whole network, termed the convex hull (Fig. 3B), provided the network is reasonably space filling. The cost per unit area covered by the network (i.e., the cost density) is then given by  $CA^{-1}$ . As the network thins out, the link density and material cost density decline, particularly in the central region behind the foraging margin (Bebber et al. 2007a).

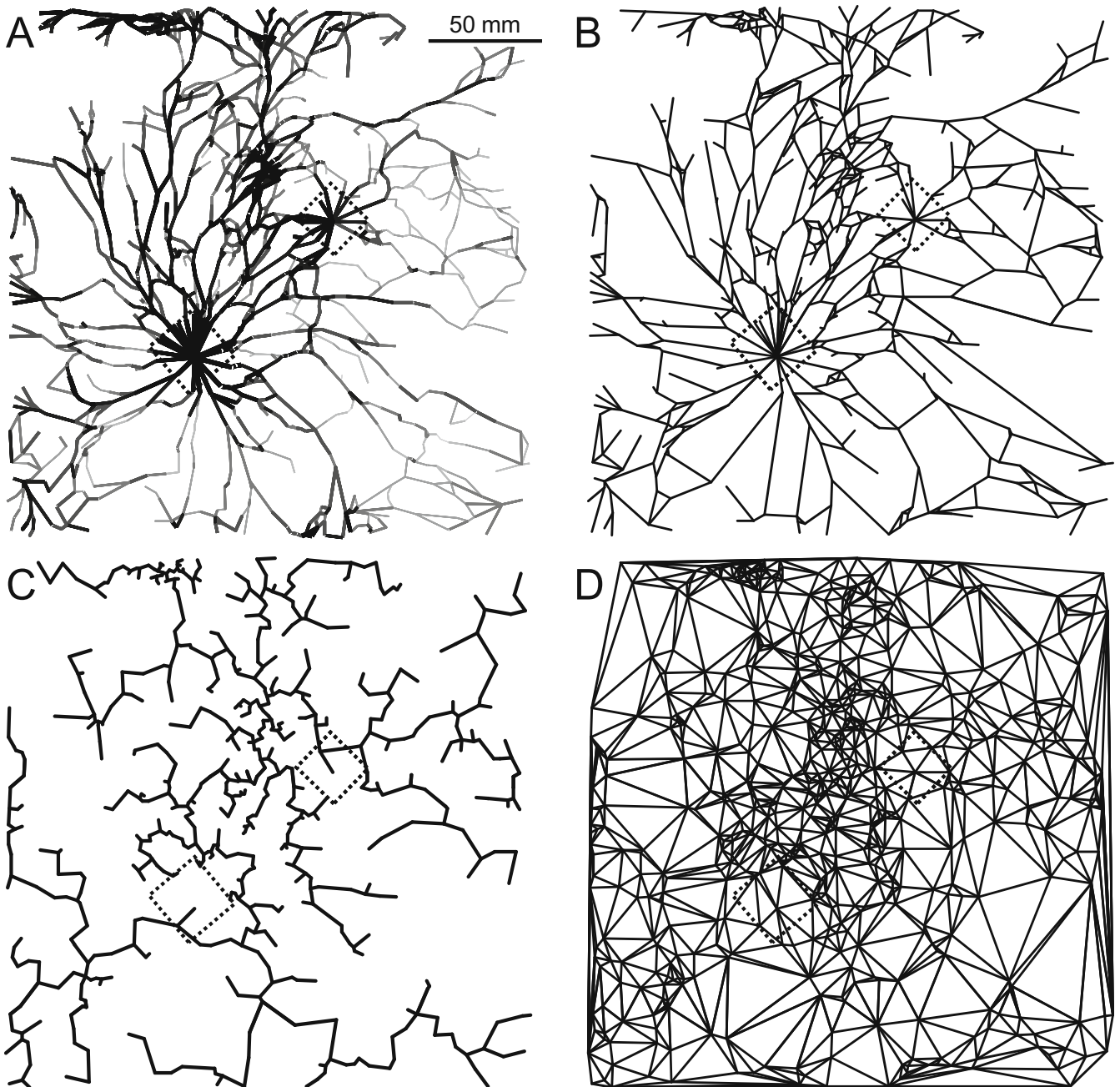
The weighted network also allows prediction of the physiological resistance to transport of nutrients and water through the colony. Each cord is modelled as a cylinder packed with identical hyphae, rather than a single tube that increases in diameter, although the internal structure of cords can be much more complex (Thompson and Rayner 1982). Thus, the number of hyphae present in each cord, and therefore the presumed transport capacity, scales with the cross-sectional area. By analogy with electrical resistance, the resistance of each link can be estimated as  $r = l/a$ , i.e., longer, thinner cords have greater resistance to flow. As a first approximation, it might be expected that transport will follow the path of lowest resistance between any two nodes in the network. This shortest path is not necessarily the shortest Euclidean distance between them, as it reflects the increased flow through cords of larger diameter. Taking road systems as an analogy, motorways may be the quickest way to get from one place to another, even though smaller roads go by a shorter distance. The shortest path is calculated by the smallest sum of  $r$  for all possible routes between two points. The relative importance of any particular node or link can be estimated by the number of shortest paths that go through that node or link, termed the betweenness centrality (Fig. 3D). The importance of the inoculum as a transport hub, as revealed by its betweenness centrality, declined from ~90% to ~70%, indicating that the mycelial network becomes more decentralized as it grows, forming cross-links that bypass the inoculum (Bebber et al. 2007a).

In general, colonies showed two separate zones: (1) a peripheral exploratory zone at the growing margin of each cord dominated by many thin, low-capacity links; and (2) an inner zone with fewer, thicker, high-capacity links. As the inner zone expanded, the increase in cross-sectional area of key links resulted in shorter physiological path lengths, leading to higher transport capacity. Increased transport capacity could be obtained simply by increasing the thickness of all cords, but this would make the network more costly to construct, in terms of the material used. In fact, the cost density actually decreased as the networks grew. Thus, network remodelling achieved greater transport capacity with a relative decrease in the amount of material used through more efficient allocation of material.

It is not straightforward to generate suitable reference models to test the extent that differential cord weighting improves the performance of the network. At present there are no suitable algorithms available to generate weighted planar networks with defined properties. In other areas of network theory, comparisons are typically made with a ref-

erence network produced by random rewiring of the links. However, this does not make sense biologically. Similarly, randomly reassigning the weights to different links does not give an intuitively satisfying model against which to test performance, as it also has no biological basis. We have therefore developed test networks in two steps (Fig. 4). The first test network used has an identical network topology

but with uniform link thickness, such that the total amount of material in the whole network is the same (Fig. 4B). This step tests the extent that differential weighting affects the predicted transport performance of the network but does not directly test how well the topology performs. Thus, in the second step, uniform networks with the same total amount of material and node positions are generated using



**Fig. 4.** Comparison between weighted fungal networks and neighbourhood graphs. *Phanerochaete velutina* was grown from a wood block inoculum over compressed soil in the presence of an additional resource, and the weighted network was digitised using a MatLab software interface. **A** The weighted fungal network in which line thickness and intensity indicate the relative area of each cord. **B** A simplified version of the network that retains nodes arising from branching or fusion, but not nodes simply required to trace the outline of each cord

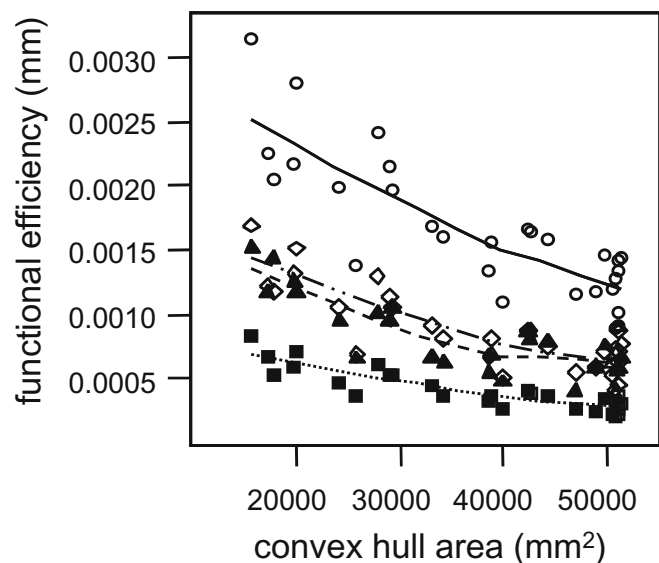
correctly. The amount of material present in the network is distributed evenly across all links to give a uniform network. **C, D** The nodes present in the simplified graph were then connected according to well-defined rules to give the minimum spanning tree (**C**) or the fully connected Delaunay triangulation (**D**). In each case the relative thickness of the lines gives an indication of how thick cords might be using the same total amount of biomass

defined connection rules to give a Delaunay triangulation (DT; Fig. 4D), as a maximally connected network, and a minimal spanning tree (MST; Fig. 4C), as the shortest network path connecting all nodes. Effectively, we asked what the consequences for transport would be if the fungus had chosen to allocate the same amount of resource evenly over the existing network or over the MST and DT networks.

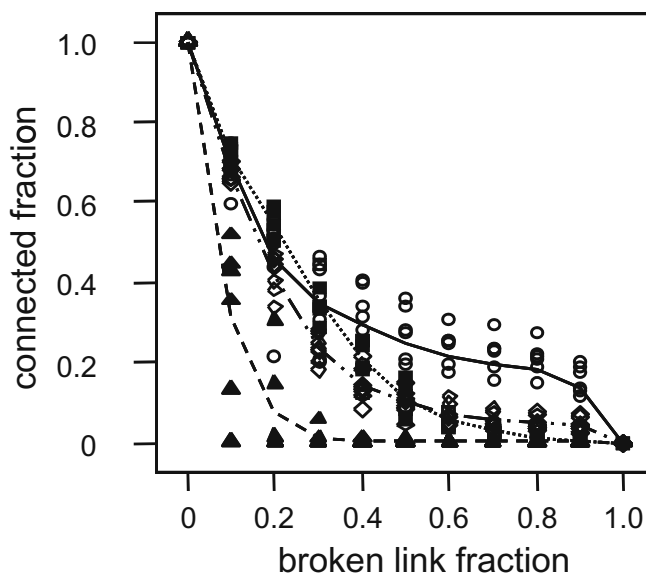
Perhaps unsurprisingly, the real weighted fungal networks had much shorter physiological paths, especially in the central region, than their paired uniform networks (Bebber et al. 2007a,b). More surprising was the observation that the weighted fungal network outperformed both the uniform DT and the uniform MST when the predicted transport from the inoculum to all other nodes was considered. Although very well connected, the DT performed poorly, as distributing material across the large number of links present gave each one low  $a$  and consequent high resistance. Conversely, the MST performed better than the DT as it was populated with few, but extremely thick, links. The uniform fungal network was similar in performance to the MST, although it clearly has a different architecture, but the real weighted fungal network showed the best predicted transport behaviour (Fig. 5). By normalising to the DT, the local efficiency ( $E_{loc}$ ) of the real network, uniform network, and MST were calculated as  $4.40 \pm 0.11$ ,  $2.22 \pm 0.07$ , and  $2.08 \pm 0.12$ , respectively (Bebber et al. 2007a). Thus, differential weighting of links in the real network gave a greater than fourfold improvement in local efficiency, in comparison to a fully connected uniform network constructed with the same total cost. The ability of fungal net-

works to modify link strengths in a dynamic way is, therefore, crucial for achieving high transport capacity.

High transport capacity and low construction cost could have come at the expense of other network properties, such as robustness to damage, as there is no *a priori* reason why link weight allocation for one feature necessarily enhances another. This concept is clearly seen in the improved global transport efficiency of the uniform MST, even though the MST would be expected to be very vulnerable to disconnection during attack. Robustness to damage, e.g., by physical breakage or grazing by invertebrates (Kampichler et al. 2004; Bretherton et al. 2006; Tordoff et al. 2006; Wood et al. 2006; Boddy and Jones 2007, 2008), is of major significance to long-lived mycelial systems. Having a large number of alternate pathways is important in this context, and the differential strengthening of links not only imparts high transport capacity but also robustness to damage, which can be seen by examining the effects of breaking links in models of the fungal networks compared with corresponding uniform networks. Links were broken in an order assuming that the probability of breakage increased with length and decreased with the thickness of the link; i.e., long, thin links were broken before short, thick ones (see Fig. 3E). Robustness was quantified as the proportion of the total material cost of the network that remained connected to the inoculum. The fungal networks maintained a much greater system connected with the inoculum than did the uniform fungal, DT, or MST networks (Fig. 6); i.e., the fungal networks were much more robust to damage. This result represents a minimum estimate of the real network resilience in nature, as the network is also able to respond to local damage by

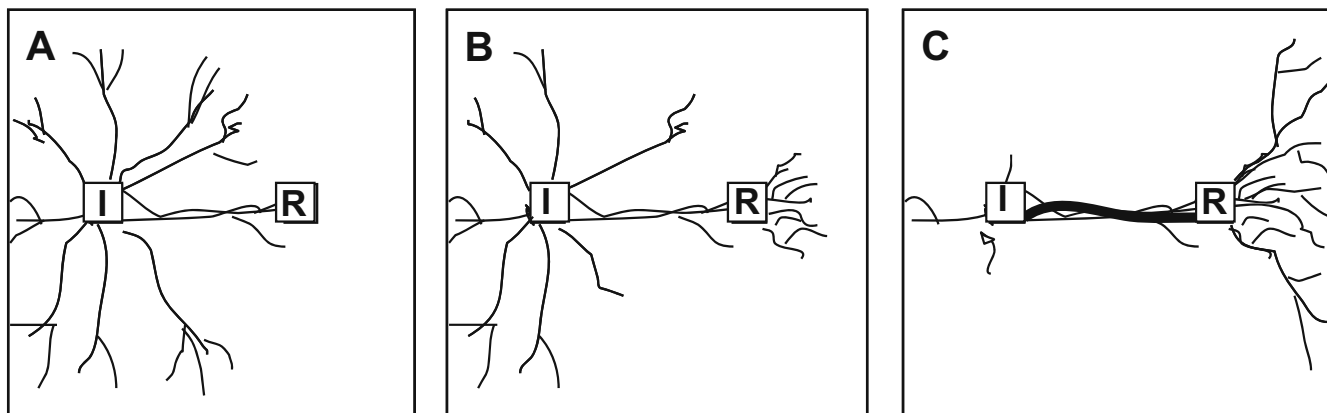


**Fig. 5.** Comparison of transport efficiency between weighted fungal and uniform model networks. The predicted functional efficiency of the fungal network was calculated as the inverse of the sum of the shortest paths from the inoculum to every node as the colony increased in area. Weighted fungal networks ( $\circ$ , —) have the highest functional efficiency, in comparison to uniform networks constructed with the same topology ( $\diamond$ , ---), or connected using a Delaunay triangulation ( $\blacksquare$ , .....), or minimum spanning tree ( $\blacktriangle$ , ---)



**Fig. 6.** Comparison of network resilience between weighted fungal and uniform model networks. The amount of mycelium remaining connected to the inoculum was measured as an increasing fraction of links were broken. When more than ~30% of the total fraction of the link area was broken, the weighted fungal networks ( $\circ$ , —) maintained a greater connected core than the uniform fungal network ( $\diamond$ , ---), or networks connected using a Delaunay triangulation ( $\blacksquare$ , .....), or minimum spanning tree ( $\blacktriangle$ , ---)





**Fig. 7.** Redistribution of mycelial biomass when a short-range forager encounters a new resource (*R*) in model soil systems. **A** Mycelium growing from an inoculum (*I*) makes contact with a new resource. **B** The new resource is colonised; mycelium grows out from the new

resource. Meanwhile, there is regression of some of the mycelium attached to the inoculum and thickening of the cord connecting the inoculum with the new resource. **C** Further regression of mycelium not interconnecting the inoculum with the new resource has occurred

modification of adjacent link strength, and hyphae can also regrow and reconnect.

### Incorporation of newly discovered resources into the system

Mycelial system architecture and physiology change dramatically when new resources are discovered. When these new resources are relatively large compared with those from which the mycelium is growing, mycelium connecting the new resource and the original resource commonly aggregates to form thick cords (Dowson et al. 1986, 1988; Boddy 1993, 1999; Bolton 1993; Donnelly and Boddy 1997a; Fricker et al. 2008) (Fig. 7). Meanwhile, radial extension slows or even stops, and mycelium that is not connected to the new resource regresses. When the new resource has been colonised, mycelium grows out from it in search of further resources; the amount of time before foraging recommences depends on the sizes of the original and new resources (Bolton 1993; Boddy and Jones 2007). When newly encountered resources are smaller, similar changes to network architecture occur with short-range foragers (e.g., *H. fasciculare*) but not with long-range foragers. These changes are, however, less dramatic.

Analysis of *P. velutina* networks growing from wood inocula over soil and encountering new resources in microcosms (Bebber et al. 2007a) emphasises these points. Connections between the inoculum and new resource were strengthened such that the inoculum–resource path was shorter than to all other nodes near the margin. Decentralization, as indicated by a declining betweenness centrality of the inoculum with time, accelerated as the new resource formed a new hub (see Fig. 6).

In nature, following outgrowth from a newly encountered resource, further new resources will be discovered with further mycelial responses. Size and nutrient status of resources already within the mycelial system relative to newly encountered resource(s) affect mycelial responses;

large resources have an overriding influence (Hughes and Boddy 1996; Boddy and Jones 2007). Foraging continues during favourable microclimatic regimes, but when conditions become less favourable, e.g., in cold winters, outgrowing mycelium tends to regress, although thick cords interconnecting resources remain (Bolton 1993). Renewed foraging occurs when conditions improve in spring.

Clearly, global, coordinated reorganization of the whole mycelial system is triggered when new resources are encountered. Exactly how this local sensing occurs and what is the signal(s) that elicits site-specific developmental responses are unknown. Several suggestions have been made, including changes in intracellular hydrostatic pressure, intracellular amino acid concentration, and electrical potentials (Olsson and Hansson 1995; Rayner et al. 1995; Watkinson 1999).

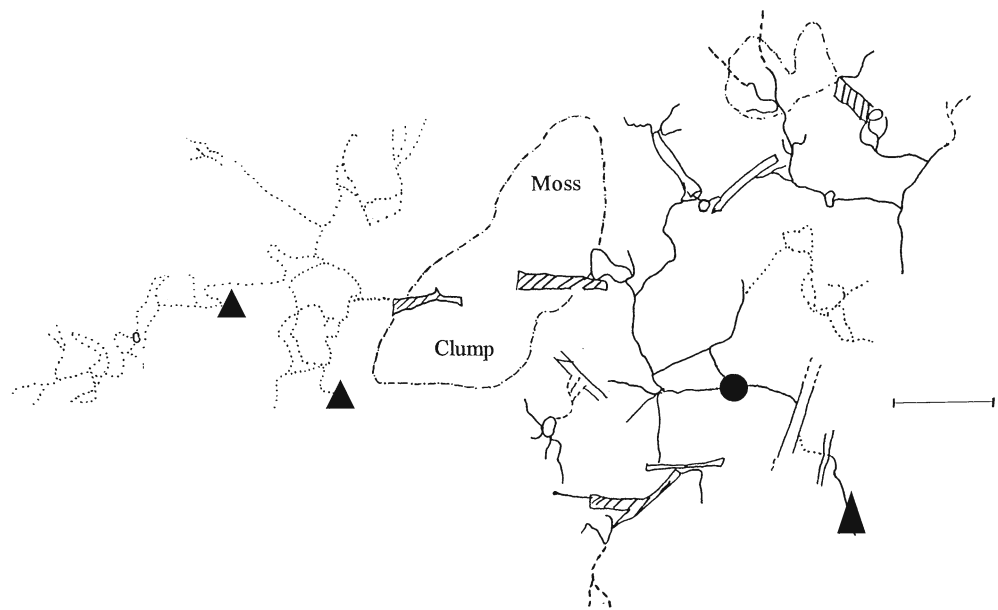
### Established mycelial networks

In forest and woodland, genets of saprotrophic basidiomycetes can cover several square metres to many hectares (Thompson and Rayner 1982, 1983; Thompson and Boddy 1988; Smith et al. 1992; Ferguson et al. 2003; Cairney 2005) (see Fig. 2). The largest organisms on the planet may be *Armillaria* species. To date, the most extensive found is a genet of the pathogenic *Armillaria ostoyae* spanning 965 hectares, with a maximum separation of 3810 m and estimated to be 1900–8650 years old (Ferguson et al. 2003). However, because parts of large mycelia can become separated from each other when rhizomorphs are destroyed, and rejoin again if parts of the same genet meet subsequently, the extent of interconnectivity is unknown.

Although little detailed network analysis has been performed on field systems of cords and rhizomorphs, an evidently important feature is the numerous loops that they contain (see Fig. 2), conferring robustness to damage. In a study of a 25-m<sup>2</sup> part of an *Armillaria gallica* Marxm. & Romagn. rhizomorph system, disruption of two critical links



**Fig. 8.** Mycelial cord network of *Stropharia aeruginosa* (Curtis) Quél. *Continuous line*, present at first (November 1992) and second mapping 6 months later; *dotted line*, only present at first mapping; *dashed line*, only present at second mapping. *Dot and dashed line* indicates boundary of a clump of moss containing many fine hyphae of *S. aeruginosa*. *Circles*, fruit body; *triangles*, attachment to *Urtica dioica* L. rhizomes; *hatched areas*, colonised wood. *Bar* 10 cm. (After Donnelly 1995)



would have lead to loss of 13% and 11%, respectively, being disconnected from the rest of the mapped network (Lamour et al. 2007). However, in established networks interconnecting numerous organic resources, disconnection does not mean that that part of the system ceases to function, merely that it functions separately from the rest of the system. In time, renewed outgrowths from the two parts of the system may encounter one another and form de novo interconnections. Indeed, although persistent, established systems are dynamic, with some parts dying back and renewed mycelial growth occurring in other places (Fig. 8), enabling further foraging and colonisation of newly arrived resources.

These large networks of mycelial cords and rhizomorphs form a dispersal vehicle in space and time, being in a position to colonise new dead organic resources rapidly when they arrive on/in the system when litter falls or woody roots die. In tropical forests, mycelial networks form in the canopy as well as on the forest floor. These suspended networks operate in a similar manner to their terrestrial counterparts but preempt the latter by catching and colonising falling litter (Hedger 1990).

### Nutrient supply and demand in mycelial cord systems

As well as a highly responsive network architecture, mycelial cord systems exhibit highly coordinated uptake, storage, and redistribution of nutrients (Watkinson et al. 2006; Tlalka et al. 2008). Mineral nutrients (e.g., nitrogen and phosphorus) can be transported both from wood resources to the mycelial margin and from the margin to sites of demand or storage (Wells and Boddy 1990; Wells et al. 1990, 1997, 1998, 1999; Cairney 1992). Nutrients often accumulate in wood resources connected within the mycelial system, where they might be “safer” than in extra-resource mycelium that is more vulnerable to damage. The balance between the main sites of uptake, storage, and demand for

carbon and mineral nutrients is determined by many factors, including the distribution, quantity, and quality of colonised and newly encountered resources and the overall nutritional status of the mycelial system (Abdalla and Boddy 1996; Hughes and Boddy 1996; Wells et al. 1998, 1999; Boddy and Jones 2007).

When a new resource arrives on a saprotrophic mycelial system, the network responds by establishing mycelial growth to colonise the new resource, sometimes by growth elsewhere to supplement nutrient supplies, and by movement of carbon and mineral nutrients (Wood et al. 2006; Wells et al. 1997, 1998). The dynamic nature of nutrient partitioning within mycelial systems interconnected with several resources was demonstrated in 50-cm-diameter mycelia growing across soil in microcosms from a central wood inoculum (Wells et al. 1998). Twelve additional resources were added in pairs to each system at 10-day intervals over 60 days.  $^{32}\text{P}$  added to the central inoculum moved between resources over time: the most recently supplied resources were not the main sinks of supplied  $^{32}\text{P}$ ,  $^{32}\text{P}$  being initially greatest in colonised resources; acquisition by most recently added resources increased with time, supported by efflux from other resources that had earlier been the main sinks for  $^{32}\text{P}$ .

Rates of translocation can be rapid in cord systems, sometimes  $>25 \text{ cm h}^{-1}$ , although actual fluxes have not been determined because of difficulties in estimating the size of conduits. None the less it is evident that the largest fluxes are through cords interconnecting resources (Wells and Boddy 1990).

### Conclusions

Not only are the chances of encountering new resources greater for large extra-resource mycelia than for spores but also, because of the supplies of nutrients within large

mycelial networks, established mycelia have a much better chance of colonising newly encountered resources. Nonetheless, cord-forming fungi do sometimes colonise via basidiospores. For example, freshly felled beech (*Fagus sylvatica* L.) logs contained many small decay columns of *P. velutina* extending from the buried cut surface in woodland where extensive systems were already established, indicative of arrival as spores (Coates and Rayner 1985).

Different species have evolved different solutions to the problem of balancing mycelial configurations efficient in exploration and transporting nutrients, and robust to damage, against “cost” of production and speed with which an area can be colonised, resulting in a range of network architectures. Mycelial networks that are highly interconnected are costly to construct but are robust to damage because they offer alternate transport routes. Sparser networks can extend further for a given cost of construction, but the chance of losing transport pathways if part of the network is damaged is greater.

Several desirable network properties emerge, simply by differential allocation of resources to links in a network constructed by local iterative development without centralized control. During growth there is overproduction of links and nodes, followed by selective reinforcement of some links and loss of others. This mechanism could be considered somewhat analogous to Darwinian evolution, if the links that are removed are in some sense less fit, or less competitive, than those that remain and are strengthened (Bebber et al. 2007a).

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