

# **Mycelial Foraging Strategies of Saprotrophic Cord-Forming Basidiomycetes**

**L. Boddy<sup>1</sup>, G.M. Tordoff<sup>1</sup>, J. Wood<sup>1</sup>, J. Hynes<sup>1</sup>, D. Bebber<sup>2</sup>,  
T.H. Jones<sup>1</sup> and M.D. Fricker<sup>2</sup>**

<sup>1</sup>*Cardiff School of Biosciences, Cardiff University, Cardiff, U.K.*

<sup>2</sup>*Department of Plant Sciences, University of Oxford, Oxford, U.K.*

## **Summary**

The mycelia of some saprotrophic wood decay basidiomycetes form extensive, long-lived systems, ramifying through forest floor soil and litter. Mycelia are effective dispersal structures, enabling capture of resources patchily and sparsely distributed in space and time. They operate two main resource capture strategies: (1) a ‘sit and wait’, whereby a large mycelial network waits for resources to land on it; and (2) to grow and search actively for new resources. Mycelial networks respond dramatically to encounter with new resources, and are remodelled continuously. Their success lies in this ability to remodel, and in their network architecture, both of which vary between species. This paper considers foraging strategies, mycelial architecture, remodelling, and nutrient uptake and translocation by saprotrophic cord-forming basidiomycetes in soil.

## **Introduction**

In terrestrial ecosystems, the organic resources upon which saprotrophic fungi depend are usually discrete, and vary considerably in size from small plant fragments, through leaves, twigs, branches and stumps, to whole trees. These resources are heterogeneously distributed in space and time, though the degree of heterogeneity varies depending upon the type of resource and scale of observation. For example, the leaf litter on the forest floor comprises spatially discrete leaves forming a relatively homogeneous layer by comparison with discrete, patchily distributed fallen branches. Temporally, arrival at the forest floor is also patchy, and while some resources may persist for many

years (e.g. wood), others are more ephemeral remaining for only a few months or years (e.g. flowers, fruits and leaf tissues of many angiosperms).

For continuing survival fungi must be able to spread between these spatially and temporally dispersed resources. This can be achieved by production of sexual and asexual spores, sclerotia or mycelium. Spores allow rapid spread, sometimes over long distances, but contain relatively small resources from which they produce mycelia to invade potential food sources. Sclerotia, often provide larger resources and allow survival in time. Mycelia grow within and sometimes between resources, and they can draw upon a larger supply of nutrients than spores when colonizing new territory. Though some remain small occupying only a few cm<sup>3</sup> others can cover several hectares of forest floor, and though some are relatively ephemeral others are potentially immortal (e.g. Boddy, 1993, 1999; Boddy & Jones, 2006). Fungi can be broadly classified as 'resource-unit-restricted' or 'non-resource-unit-restricted', depending on how they spread between food resources in space and time. The former are disseminated as spores or sclerotia, while the latter can also extend from a resource as mycelium. Non-resource-unit-restricted fungi are largely Basidiomycota and include: those that colonize large patches of leaf litter on the forest floor (e.g. *Collybia* spp. and *Marasmius* spp.); fairy-ring-formers that extend through the leaf litter layer as an ever increasing annulus of mycelium about 30 cm wide (e.g. *Clitocybe nebularis*); small and large rhizomorph formers (e.g. *Marasmius androsaceus* and *Armillaria* spp., respectively); cord-forming fungi (e.g. *Hypholoma fasciculare* and *Phanerochaete velutina* (e.g. Boddy 1984, 1993, 1999; Rayner *et al.*, 1995; Hedger, 1990; Boddy & Jones, 2006)). Those fungi that form large patches or fairy rings effectively colonize leaf litter as if it were a continuous substratum. By contrast, the cord- and rhizomorph-formers typically extend between spatially discrete woody resources separated by many cms or even meters (Boddy, 1993; Cairney, 2005). They can all draw on resources held within the mycelium to sustain growth and, apart from rhizomorph formers, can also absorb soluble nutrients from soil. Though mycelial cords (linear organs of predominantly parallel hyphae formed by aggregation behind a fanned growing front), like rhizomorphs (linear organs, in which the whole organ extends from the tip), are insulated from the environment they have an absorptive mycelial margin of diffuse hyphae and may colonize other litter components *en route* (Boddy, 1999; Watkinson *et al.*, 2006). This paper considers the ways in which cord-forming fungi colonize spatially and temporally discontinuous woody resources, their response to encounter with new resources, the significance of network architecture, and the costs and benefits of maintaining large mycelial networks.

## **Mycelial dispersal**

Whether fungi are dispersed as spores, sclerotia or mycelium they risk loss of a large amount of biomass (as a result of invertebrate grazing, antagonistic microorganisms and death due to unfavourable microenvironment) in the quest for new resources. Non-resource-unit-restricted fungi have minimized this by adopting a variety of different strategies for encountering and then responding

to new resources. These include: (1) growing and searching actively for new resources, with an array of responses to finding them; (2) operating a 'sit and wait' strategy, whereby a large mycelial network waits for resources to land on it and then actively colonizes those resources, often with responses occurring elsewhere in the system; and, most commonly (3) a combination of both. With all of these strategies the mycelial networks are continuously remodelled in response to abiotic (e.g. nutrient sources, microclimate or destructive events) and biotic (e.g. interaction with other fungi or grazing by invertebrates) cues. This occurs through a complex combination of growth, branching, hyphal fusion and regression of different regions of the mycelial system. Morphology changes as does a complex set of physiological processes associated with uptake, storage and redistribution of nutrients throughout the network. These morphological and physiological changes are highly coordinated such that locally perceived environmental changes are responded to both locally and over a larger scale. Different fungi respond differently in space and time leading to different long-term behaviour/foraging strategies.

### Foraging in space

The pattern of mycelial outgrowth from resources into soil and litter, in search of new resources, varies between species (Fig. 1; Boddy, 1999; Boddy & Jones, 2006). Some, for example, *Resinicium bicolor*, have open systems characterized by well-defined, rapidly extending cords throughout the system. These can be considered to be long-range foragers that would be unsuccessful at capitalizing on homogeneously supplied nutrients, but would successfully discover large, sparsely distributed resources. Mycelia of other species (e.g. *H. fasciculare* and *Stropharia* spp.), are characterized by diffuse, slowly extending search fronts, and can be considered to be short-range foragers: they search areas intensively and are likely to be successful in discovering abundant, relatively homogeneously distributed resources (Fig. 1c,d). These patterns are modified by the quantity and quality of the initial resource, soil structure and nutrient status, the microclimate, and invertebrate grazing (Fig. 1f; Boddy, 1999; Boddy & Jones 2006). When new resources are encountered mycelial morphology often alters dramatically with considerable reallocation of biomass: when new resources are substantially larger than those from which the mycelium was growing changes typically include thickening of resource-connected cords, regression of non-resource-connected mycelium, and cessation or slowing of radial extension (but subsequently with outgrowth from the newly colonized resource) (Boddy, 1993, 1999; Donnelly & Boddy, 1997). With short-range foragers (e.g. *H. fasciculare*) similar, though less dramatic, visible changes even occur when newly encountered resources are similar in size to the original resource (Fig. 1g-i).

Superimposed upon these morphological responses are a complex set of physiological responses that contribute to a highly co-ordinated uptake, storage and redistribution of nutrients throughout the network (Watkinson *et al.*, 2006). Nutrients (e.g. nitrogen and phosphorous) can be transported from wood resources to growing fronts, and nutrients scavenged as mycelia grow

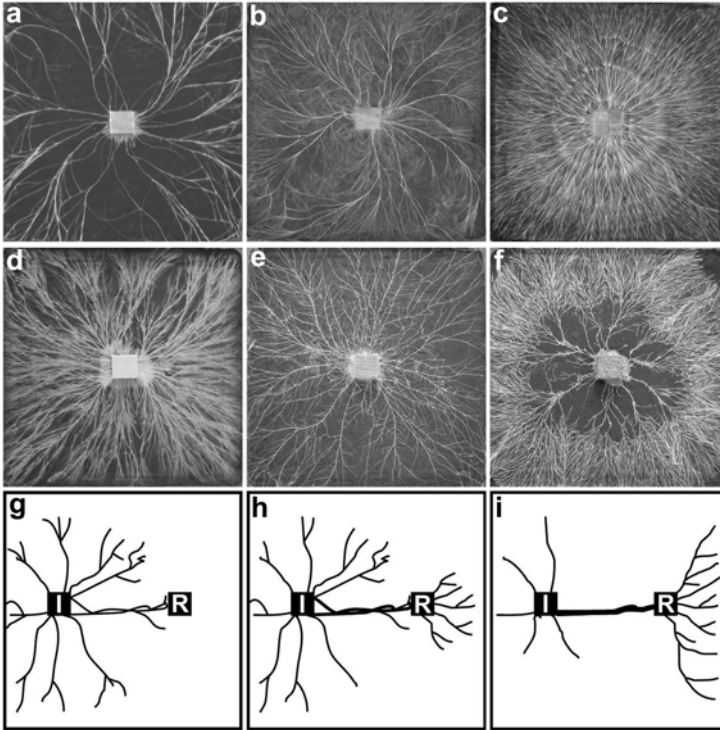


Figure 1. Foraging patterns of the cord-forming basidiomycetes *Resinicium bicolor* (a), *Phanerochaete velutina* (b), *Coprinus picaceus* (c), *Hypholoma fasciculare* (d) and *Phallus impudicus* (e,f) growing in 24 x 24 cm soil microcosms. Mycelia are extending from 4 cm<sup>3</sup> *Fagus sylvatica* wood inocula. In (f) *P. impudicus* has been grazed for 60 days by the collembola *Folsomia candida*, whereas (e) is an ungrazed control. (g-i) illustrate the typical pattern of mycelial biomass reallocation following contact (g) and colonization of a new wood resource. As colonization proceeds there is gradual thickening of connective cords and regression of mycelium not connecting the inoculum with the new resource (h). After several months non-connective mycelium has almost completely regressed (i). I, inoculum; R, new wood resource.

through soil can be translocated away from the growing front, and commonly accumulate in wood resources connected within the mycelial system (Cairney, 1992; Boddy, 1993; Wells, Donnelly & Boddy, 1997; Wells, Harris & Boddy, 1998). Rates of translocation can be rapid (sometimes  $> 25 \text{ cm h}^{-1}$ ), the largest fluxes being through cords interconnecting one resource with another (Boddy, 1993). Many factors, including distribution and quantity of organic resources, affect the balance between, and the main sites of, uptake, storage and demand for carbon and mineral nutrients (Boddy & Jones, 2006).

### Foraging in time

The large, persistent networks formed by saprotrophic basidiomycetes al-

low these fungi to capture resources arriving, by litter fall or root death, at any time. Though most commonly found on the forest floor, networks are even found in the canopy of tropical forests where they effectively form a net (Hedger, 1990). Established systems, though persistent, are dynamic: carbon and mineral nutrients are continually rerouted to site of need (Wells *et al.* 1998), and renewed mycelial growth enables colonization of the newly arrived resources. Moreover, sometimes renewed growth occurs elsewhere to supplement nutrient supplies (Wells *et al.*, 1997; Wood *et al.*, 2006). In a microcosm (24 x 24 cm) experiment in which a new wood resource was

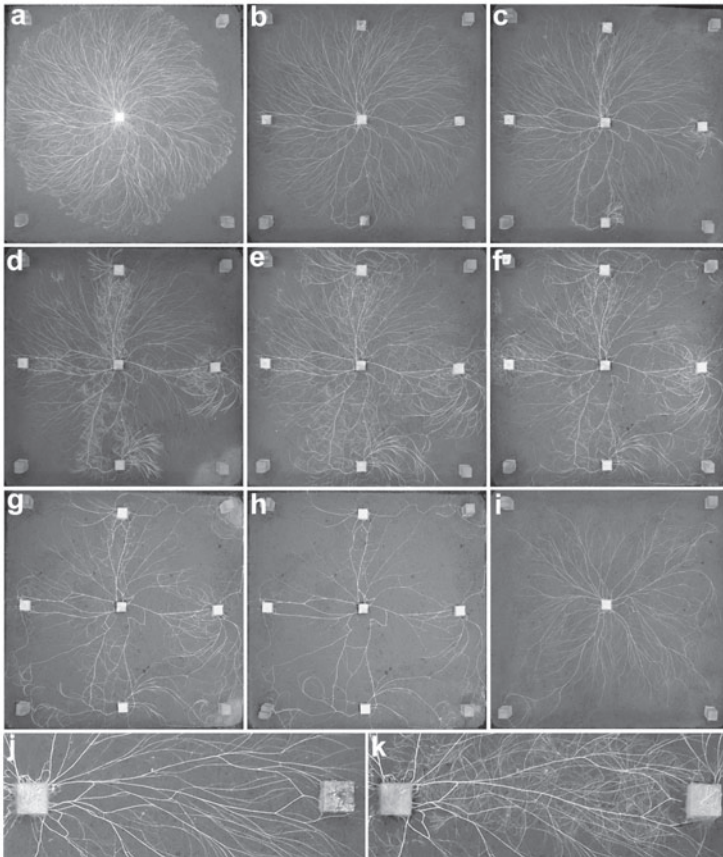


Figure 2. Time series of *Phanerochaete velutina* growth in 57 x 57 cm soil microcosms, with four new wood resources (located half way along each microcosm side) added after 36 days. Images were captured 31 (a), 64 (b), 78 (c), 85 (d), 99 (e), 127 (f), 155 (g) and 186 (h) d after adding the central wood inoculum. Note thickening of cords connecting inoculum with new resources, and thinning of other areas compared with 99 d control having no additional resources (i). Outgrowth from the newly colonized lower resource is evident from 78 d. (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 64 (j) and 85 days (k).

added behind the margin of a *P. velutina* system, growing on a nutrient poor soil, ephemeral patches of much branched fine hyphae developed that were sites of nutrient uptake (Wells *et al.*, 1977). When new resources were added to larger systems (57 x 57 cm), upon colonization mycelium began to proliferate along cords connecting them with the inoculum wood resource (Fig. 2; Wood *et al.* 2006). Subsequently, fine mycelium proliferated throughout the system, also developing from minor non-connective cords, and leading to an increase in hyphal coverage. Such proliferation may again be a response to satisfy the increased mineral nutrient requirements of the system.

### Analysis of network architecture and function

Within the extensive mycelial networks formed by saprotrophic, and indeed some ectomycorrhizal, basidiomycetes there is considerable scope for communication, since hyphae maintain continuity with their immediate ancestors and also become connected with neighbouring regions via *de novo* formation of cross-links (anastomoses). Thus there is both radial and tangential connectivity, resulting in systems with many connected loops (Fig. 3). Understanding network architecture is important because different architectures will impart different ecological characteristics and affect functioning. For example: tangential connections make communication pathways between peripheral regions shorter and provide alternative transport pathways; highly connected networks are more resilient to disturbance, including invertebrate grazing, since even though some connections will be severed others will remain. Routes between different regions, shortest path lengths, and effect of loss of connections can be investigated mathematically by graph/network theory (Bebber *et al.*, 2006). These analyses reveal that mycelial networks of the saprotroph *Phanerochaete velutina* strengthen some connections (particularly



Figure 3. Mycelial network of *Megacollybia platyphylla* in a mixed deciduous woodland, revealed by removal of surface litter.

those between captured resources) thereby enhancing transport capacity among them. Meanwhile, construction costs decline as unwanted connections are resorbed and recycled. Simulations of cord breakage show that the non-random distribution of cords of different strengths in the network increases its resilience to fragmentation (Bebber *et al.*, submitted). Resilience does not, however, only depend on the network architecture, but also on the ease and efficiency with which networks can reconnect, by regrowth following damage. Fungi provide one of the few real, and experimentally tractable, examples of networks that rebuild themselves following damage. Analyses of cord-forming fungi are likely to reveal a range of evolutionary solutions to network design that may inform the development of other types of transport network.

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