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Review

Basidiomycete mycelia in forest soils: dimensions, dynamics and roles in nutrient distribution

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Basidiomycete mycelia are ubiquitous in forest soils where they fulfil a range of key ecological functions. Population studies, based largely on basidiome collections, indicate that mycelia of many ectomycorrhizal and saprotrophic basidiomycetes can spread vegetatively for considerable distances through soil, but the extent to which these become physically or physiologically fragmented is unclear. This review considers aspects of the distribution, dynamics and translocatory activities of individual basidiomycete mycelia in forest soil, highlighting current gaps in our understanding and possible ways to address these.

INTRODUCTION

On the basis of basidiome collections, it is evident that forest soils in a broad range of habitats house diverse communities of basidiomycetes (e.g. Schmit, Murphy & Mueller 1999, de la Luz Fierros, Navarrete-Heredia & Guzmán-Davalos 2000, Ferris, Peace & Newton 2000, Packham *et al*. 2002). These include saprotrophic, mycorrhizal and pathogenic taxa which, collectively, play important roles in nutrient and carbon cycling processes (Dighton 2003). Studies of basidiome diversity and distribution, however, provide only a limited, and extremely selective, view of basidiomycete occurrence in forest soils. There is ample evidence, for example, that basidiome collections are poor indicators of below-ground ectomycorrhizal (ECM) fungal diversity and that below-ground diversity is much greater than implied by basidiome studies (Erland & Taylor 2002). Observations of this nature emphasise the need for more direct analysis of basidiomycete mycelia in soil.

While methods for estimating fungal biomass in soil, such as ergosterol or phospholipid fatty acid analysis (Zelles 1999, Montgomery *et al*. 2000), have provided useful information regarding the importance of fungi in soil microbial communities, they tell us little about the different functional or taxonomic groups of fungi. Investigations of mycelia of specific fungal groups in soil have been constrained by a lack of suitable techniques for discrimination between them, but some progress is now being made. A useful method for estimating ECM mycelial biomass in forest soils has, for example, recently been developed (Wallander *et al*. 2001). This involves burying mesh bags containing sand in forest plots and comparing mycelial biomass in bags from trenched plots (designed to sever ECM roots from their tree hosts, and so exclude ECM mycelia from the plots) with those from untrenched plots. Such comparisons, along with supporting $\delta^{13}C$ values, suggest that in Swedish conifer forest soils, 85–90 % of mycelium that colonises the sand-filled bags is ECM (Wallander *et al*. 2001, Hagerberg & Wallander 2002). The sand-filled mesh bag approach has thus been useful in demonstrating that ECM mycelial biomass varies seasonally (Wallander *et al*. 2001) and with soil depth (Wallander, Göransson & Rosengren 2004), along with determining the effect of differing forest management regimes on ECM mycelial biomass (Hagerberg & Wallander 2002, Nilsson & Wallander 2003). A less direct method that involved tree girdling, soil fumigation and measurements of dissolved organic carbon, has also been used to estimate that ECM mycelium may contribute >32 % to the soil microbial biomass in a Swedish conifer forest (Högberg & Högberg 2002). Important as these data are, however, they provide no information regarding mycelia of individual taxa.

Their indeterminate filamentous nature creates obvious problems for investigation of mycelia of individual basidiomycete taxa in the heterogeneous soil environment. When considering individual mycelia of a single taxon, the task becomes considerably more complex. Knowledge of the distribution, dynamics and activities of individual mycelia in soil is, however, crucial to understanding how different taxa influence and modify the soil environment, along with the spatial and temporal scales over which they operate. In this review I summarise current understanding of the distribution and activities of individual basidiomycete mycelia in forest soils, and highlight some fundamental gaps in our knowledge.

MYCELIAL GROWTH AND DYNAMICS IN MICROCOSMS

Because of the difficulties in identifying mycelia in the field, investigations of the development and dynamics of mycelia of individual basidiomycetes have largely been conducted in the laboratory. A variety of methods has been utilised (e.g. Jennings 1991), however those based on a non-sterile soil (or similar) substrate provide the most useful information regarding likely behaviour of mycelia in the field, thus only these are considered here.

Development of mycelial systems of various saprotrophic and ECM basidiomycetes has been investigated extensively in soil-based microcosms. This approach has been important in demonstrating patterns of development and temporal change with respect to diffuse versus rhizomorphic components of mycelia growing from colonised wood (e.g. Dowson, Rayner & Boddy 1986, 1988a) or ECM roots (e.g. Duddridge, Malabari & Read 1980, Read 1984, Finlay & Read 1986a) along with interspecific differences in mycelial growth forms (e.g. Dowson, Rayner & Boddy 1986, 1988a, Dowson *et al*. 1989b, Donnelly, Boddy & Leake 2004). Mycelia of many taxa typically grow as diffuse fans, with progressive aggregation behind this growing front into aggregated rhizomorphic structures (Read 1992, Boddy 1993, 1999, Olssen, Jakobsen & Wallander 2002). It has also become evident that growth of basidiomycete mycelia is strongly influenced by soil heterogeneity, in particular the patchy distribution of organic substrates and mineral nutrients. Thus, when a mycelium of a wood decomposer encounters and colonises a new woody resource, the pattern of mycelial growth has been shown to change, with invasive mycelia growing in a diffuse fashion (e.g. Dowson *et al*. 1986, Donnelly & Boddy 2001). Similarly, hitherto undetermined signals between fungus and plant trigger a series of morphogenetic events following contact between an ECM mycelium and a host root that leads to formation of the fungal sheath and Hartig net (Martin *et al*. 2001).

Soil microcosm studies have also shown that, although for saprotrophic basidiomycetes it appears to depend on the relative size and quality of the woody resources, mycelium that interconnects old and new woody resources, or in the case of ECM fungi individual root tips, may regress and become more rhizomorphic, while extensive outgrowth of exploratory fan-shaped mycelium may follow (Dowson *et al*. 1986, 1989b, Read 1992, Boddy 1993, Wells, Donnelly & Boddy 1997, Donnelly *et al*. 2004). Discrete patches of organic matter or mineral nutrients in soil microcosms can also influence mycelial growth, with several ECM and saprotrophic taxa having been shown to grow reactively to form dense mycelial growth in such patches (e.g. Finlay & Read 1986a, b, Bending & Read 1995, Donnelly & Boddy 1997b, Wells *et al*. 1997, Perez-Moreno & Read 2000, Mahmood *et al*. 2001, Tibbett & Sanders 2002, Lilleskov & Bruns 2003, Donnelly *et al*. 2004, Rosling, Lindahl & Finlay 2004). More general soil characters, such as physical structure, carbon or mineral nutrient status, temperature, water potential, pH and litter type have also been shown to influence mycelial growth and development in soil microcosms (Morrison 1982, Erland, Söderström & Andersson 1990, Arnebrant 1994, Abdalla & Boddy 1996, Donnelly & Boddy 1997a, b, 1998, Boddy 1999, Wells, Thomas & Boddy 2001, Zakaria & Boddy 2002, Aquino & Plassard 2004). The ability of soil-borne mycelia to grow reactively in the heterogeneous soil environment is regarded as important to their functioning in soil and has been discussed in the context of foraging strategies elsewhere (e.g. Rayner 1991, Read 1992, Boddy 1993, 1999, Olssen *et al*. 2002, Donnelly *et al*. 2004).

The presence of other soil organisms, such as fungivores, can further influence the growth and development of basidiomycete mycelia in soil. Growth of ECM mycelia can be reduced by the presence of grazing collembolans, although this may depend on the population density of the fungivore (Ek *et al*. 1994, Setälä 1995). Extensive invertebrate grazing can eliminate rhizomorphic mycelia of certain saprotrophs from soil, while lower grazing intensity can significantly alter mycelial morphology (Boddy 1999). In the case of the wood decomposer *Hypholoma fasciculare*, certain collembolan taxa were shown to reduce diffuse mycelial growth, with the fungus adopting a more fast-growing rhizomorphic growth pattern (Kampichler *et al*. 2004).

INTERSPECIFIC MYCELIAL INTERACTIONS IN MICROCOSMS

Interactions between mycelia of different saprotrophic fungi have been observed in soil microcosms in a number of investigations, and can significantly alter patterns of mycelial growth. These interspecific encounters result either in a 'deadlock' situation where there appears to be a mutual interference between the different taxa, or a 'replacement', where mycelium of one taxon will out-compete another in soil and/or

previously-colonised substrate (Dowson, Rayner & Boddy 1988d, Holmer & Stenlid 1996, Boddy, 2000, Donnelly & Boddy 2001, Wells & Boddy 2002). Interactions between two saprotrophic fungi may result in the acquisition of carbon and (or) phosphorus from the mycelium of one by that of the other (Wells & Boddy 2002; see p. 14). The outcomes of interspecific mycelial interactions appear be influenced by the size and quality of the carbon substrata from which the fungi grow (Dowson *et al.* 1988d, Boddy & Abdalla 1998, Wells & Boddy 2002) and may influence growth of the mycelium at a distance from the zone of encounter (Boddy & Abdalla 1998, Boddy 2000).

Communities of ECM fungi in root systems of forest trees are extremely diverse and multiple taxa occur in roots sampled from soil volumes of a few cm^2 (Horton & Bruns 2001). The potential for encounters between mycelia of different taxa is thus immense, yet there have been few attempts to study their interactions in soil microcosm systems. Most investigations have focused on competitive interactions between ECM fungi on the basis of root system colonisation. These indicate that certain ECM fungi can negatively affect the growth of other ECM fungi, and that the outcomes of these interactions may vary with the edaphic environment (e.g. Erland & Finlay 1992, Mahmood 2003). These observations are suggestive of some level of mycelial interaction between the competing taxa. In what appears to be the only attempt to investigate mycelial interactions between ECM fungi directly, Wu, Nara & Hogetsu (1999) observed interactions that appear equivalent to the 'deadlock' and 'replacement' phenomena reported for saprotrophic basidiomycete mycelia. The nature and outcomes of interactions between ECM fungal mycelia thus appear likely to be broadly similar to those of saprotophs.

Donnelly & Boddy (2001) reported that mycelia of some saprotrophic taxa may avoid confrontation by growing over the mycelium of other taxa in soil microcosms. This raises an important issue regarding the use of soil microcosms to investigate mycelial interactions, or other aspects of mycelial growth and dynamics. The microcosms used to investigate saprotrophs contain only a thin layer of compacted soil and lack the litter layer below which, and within which, these fungi would grow in field soil (Boddy 1999). The microcosms used to study ECM fungi generally contain only a *ca* 2 mm layer of non-sterile peat (e.g. Leake, Donnelly & Boddy 2002). The possibility for mycelia of different taxa to avoid conflict, to some extent at least, by growing at slightly different depths in soil is thus excluded making it difficult extrapolate the microcosm observations to the field situation. Indeed, mycelia of some saprotrophic taxa are known to grow beneath the soil/litter interface in the field (Boddy 1999), and it is possible to demonstrate such three-dimensional growth in a soil microcosm system (Andersson *et al.* 2001). Other taxa may grow at different depths according to soil type (Dowson, Rayner & Boddy 1988b), further emphasising the artificial nature of the soil microcosm system. This caveat also applies to ECM fungi, for which there is strong evidence for vertical stratification of different taxa in forest soils (Dickie, Xu & Koide 2002, Landeweert *et al.* 2003a, Rosling *et al.* 2003; p. 12).

The apparent juxtaposition of ECM and saprotrophic fungi in soil means that direct interactions between their mycelia will be commonplace and may have significant implications for decomposition processes (Cairney & Meharg 2002). Leake *et al.* (2002) have, for example, reported sequential colonisation of litter patches by ECM and saprotrophic fungi. Gadgil & Gadgil (1975) reported that presence of ECM fungi in nature reduced decomposition in forest soil, a phenomenon (now referred to as the 'Gadgil effect') attributed to competitive or antagonistic interactions between ECM and saprotrophic mycelia. Although it has not been observed universally, Koide & Wu (2003) have provided further evidence for the effect and suggested that it might arise from competition for water between ECM and saprotrophic mycelia. While the caveat regarding the depth of soil and lack of soil profile applies equally to the following discussion, thin layer soil microcosms have demonstrated a potential for direct interactions between mycelia of the two fungal groups. The outcomes of such interactions appear variable, and along with varying for different fungi, will depend on relative carbon availability from the plant host for the ECM fungus and the decaying wood from which the saprotroph mycelium has developed (Lindahl 2000, Lindahl, Stenlid & Finlay 2001b). Thus either fungus may grow over the other as a dense mycelium (Lindahl *et al.* 1999, 2001b) or there may be initial 'deadlock' between the mycelia, followed by eventual replacement of one fungus (Leake *et al.* 2001, 2002; p. 14). As was the case for interactions between saprotrophic mycelia, radiotracer studies suggest that either fungus may obtain some carbon and (or) phosphorus from mycelium of the other during these encounters (Lindahl *et al.* 2001b, Leake *et al.* 2002). For certain combinations of fungi, the influence of an interacting mycelium may be confined largely to the zone of interaction, however for others the effect on growth may be more widespread within the mycelium (Leake *et al.* 2002). Although, providing only indirect evidence, the presence of certain saprotrophs can reduce root infection by ECM fungi (Shaw, Dighton & Sanders 1995, Murphy & Mitchell 2001), further suggesting interaction between their respective mycelia.

MYCELIAL GROWTH AND DYNAMICS IN THE FIELD

Direct observations

For saprotrophic basidiomycetes that form robust linear mycelial organs (i.e. rhizomorphs *sensu* Cairney, Jennings & Agerer 1991) in litter and surface soil,

useful information on the dimensions of individual mycelia and their dynamics has been obtained at a scale of several metres by careful excavation and observation *in situ* (Thompson & Rayner 1982, 1983). In some instances the same genotype, as inferred by somatic incompatibility testing (see below), has been shown to be present in tree stumps >100 m apart (Thompson & Boddy 1983), suggesting that mycelia of some taxa may be larger than so far demonstrated by excavations. Field observations on rhizomorph-forming basidiomycetes have further confirmed the microcosm-based observations that edaphic conditions, disturbance, litter availability and interactions with other fungi can strongly influence mycelial growth and development (Dowson, Rayner & Boddy 1988c, Dowson *et al.* 1989b). Similar methods have also been used to investigate the distribution and development of mycelia of litter-decomposing saprotrophs, especially those that form 'fairy rings' and, in the case of *Clitocybe nebularius*, somatic incompatibility testing confirmed that a 'fairy ring' comprised a single mycelial genet (Ogawa 1985, Dowson, Rayner & Boddy 1989a). The below-ground distribution of dense mycelial patches ('shiro') of ECM fungi such as *Tricholoma* spp. has also been investigated by direct observation (e.g. Ogawa 1977, 1985), however the extent to which the latter represent single or multiple mycelia of the fungi remains unclear.

Genotyping basidiome and (or) rhizomorphic tissue

Although the absence of basidiomes of a taxon cannot be interpreted as indicating absence of the corresponding mycelium in soil, basidiome presence clearly signals the existence of a soil-borne mycelium. For this reason, basidiome distribution, coupled with genetic analysis of vegetative mycelium from basidiomes, has been widely used as an indirect method to infer distribution patterns of soil-borne mycelia of certain species in the field. For some pathogenic and saprotrophic species, a similar approach has been taken using isolates of the fungi obtained from infected trees or logs. Initially this was achieved largely by somatic incompatibility testing (e.g. Korhonen 1978, Dahlberg & Stenlid 1990, Kirby, Stenlid & Holdenrieder 1990), sometimes accompanied by isozyme analysis (e.g. Sen 1990, Rizzo & Harrington 1993), of isolated mycelia. The requirement that the fungi be grown in axenic culture, together with concerns regarding genetic resolution of the method for certain taxa and a lack of understanding of its genetic basis (Sen 1990, Jacobson, Miller & Turner 1993, Guillaumin *et al.* 1996), has limited the application of this method in the context of most soil-dwelling basidiomycetes. The technique, however, remains popular for certain taxa, notably *Armillaria* spp., for which multiple studies have demonstrated broad congruence between data obtained by somatic incompatibility testing and molecular methods (see p. 11) (e.g. Guillaumin *et al.* 1996, Dettman & van der Kamp 2001, Ferguson *et al.* 2003).

The limitations of somatic incompatibility testing, combined with the relatively rapid nature of molecular techniques that can be performed on DNA extracted directly from vegetative basidiome tissue, has resulted in a move towards DNA-based techniques in recent years. A range of DNA-based methods that includes random amplified polymorphic DNA (RAPD), inter-simple sequence repeat (ISSR), single-strand conformational polymorphism (SSCP), amplified fragment length polymorphism (AFLP) and simple sequence repeat marker (SSR) analyses have been variously utilised in this context (Kretzer *et al.* 2003). As is the case for somatic incompatibility testing, the molecular methods are not absolute and in some instances can fail to distinguish between closely-related genotypes, or may be confounded by the presence of somatic variation (Gryta, Debaud & Marmeisse 2000). Nonetheless, they provide a very useful means for estimating genotype distribution in the field. For both somatic incompatibility testing and the molecular typing methods, genotype information has generally been cross-matched with maps that indicate the locations from which basidiomes were collected in the field, allowing the spatial distribution of the genotypes to be estimated. Where basidiomes are identified as being of the same genotype they are assumed to have arisen from a common (genetically identical) below-ground parent mycelium and the distribution of a mycelium inferred from basidiome distribution (Dahlberg & Stenlid 1995). For those taxa, such as *Armillaria* spp. and *Marasmius androsaceus*, that produce robust rhizomorphs, isolates from these structures (and in the case of *Armillaria* spp., isolates from infected tree tissue) have also been used to infer genotype distribution (e.g. Holmer & Stenlid 1991; Smith, Bruhn & Anderson 1992, Ferguson *et al.* 2003).

Studies of this nature have yielded important information regarding the distribution of basidiomycetes in forest soil. Genotypes of the facultatively pathogenic *Armillaria bulbosa* and pathogen *A. ostoyae* have famously been reported to be spread over many hectares (Smith *et al.* 1992, Ferguson *et al.* 2003) and clearly reflect persistent soil-borne mycelia. Although, considerably smaller, individual genotypes of certain ECM taxa are estimated to span tens of m in some forests, suggesting that their mycelia may grow vegetatively for considerable distances through soil, presumably by progressively infecting host root tips (e.g. Dahlberg & Stenlid 1990, Bonello, Bruns & Gardes 1998, Sawyer, Chambers & Cairney 1999). For other ECM taxa, individual genotypes appear to be largely restricted to small areas, with multiple genotypes co-occurring in areas of a few m^2 and being assumed to reflect mycelial growth from recently germinated basidiospores (e.g. Gryta *et al.* 1997, Gherbi *et al.* 1999, Fiore-Donno & Martin 2001, Redecker *et al.* 2001, Dunham, Kretzer & Pfrender 2003). Mixtures of widespread and more spatially-restricted genotypes have also been reported for some ECM species (e.g. Anderson, Chambers &

Cairney 1998, Fiore-Donno & Martin 2001, Bergemann & Miller 2002) and for the saprotroph *Marasmius androsaceous*, albeit on a much smaller spatial scale (Holmer & Stenlid 1991). Using these methods, mycelia of certain ECM genotypes have been shown to persist for up to 11 years (e.g. Selosse *et al.* 1998; Anderson, Chambers & Cairney 2001, Bergemann & Miller 2002, Selosse 2003), and estimates based on genotype distribution patterns coupled with rough estimates of mycelial growth rates suggest that some may persist for significantly longer (e.g. Dahlberg & Stenlid 1990, Baar, Ozinga & Kuyper 1994, Bonello *et al.* 1998). In contrast, genotypes of other species, such as *Hebeloma cylindrosporum*, do not appear to persist from year to year, in some sites at least, suggesting that their soil-borne mycelia may be more ephemeral (Gryta *et al.* 1997, Guidot, Debaud & Marmeisse 2001).

In many of the above studies, widespread genotype distribution in nature has been suggested to reflect the presence of large below-ground genets (i.e. continuous mycelial individuals; Dahlberg & Stenlid 1995). As acknowledged by many of the authors of the work and discussed elsewhere (e.g. Brasier 1992, Anderson & Kohn 1995), while this may be the case, it is impossible to ascertain with any certainty whether or not these mycelia are actually continuous or have fragmented as ramets (i.e. spatially discontinuous mycelial units of the same genotype). The extent of fragmentation will be important functionally as, in part at least, it will define the spatial limits within which the mycelia can effect movements of carbon and minerals through soil (see p. 14). It is further important in the context of carbon and nutrient transfer between trees *via* below-ground ECM mycelial networks in forests. There is convincing evidence that such transfers can occur (Simard *et al.* 1997, Simard, Jones & Durall 2002), and the widespread potential for ECM mycelial networks to interlink different tree species has been highlighted by the observation that the same fungal species infect multiple neighbouring trees in the field (Horton & Bruns 1998, Kennedy, Izzo & Bruns 2003). Understanding the significance of the networks in processes such as nutrient cycling and plant community dynamics at the ecosystem scale will demand more detailed understanding of physical and physiological continuity in below-ground mycelia.

With greater sampling intensity in a given area, more confidence may be ascribed to the likely interconnectedness of single genotype basidiomes as a genet. Basidiome sampling, along with isolation from trees and large pieces of woody litter, are, however, constrained by patterns of availability in the field. Furthermore, since no information can be ascertained regarding vertical distribution of the fungi in the soil profile, data derived by these means can provide only the roughest estimates of two-dimensional mycelial distribution in the field. For taxa that produce robust rhizomorphic mycelia in soil, such as *Armillaria* spp., it is feasible to isolate the fungi from mycelia in soil cores. For those *Armillaria* spp. that produce abundant rhizomorphic growth in soil (Rizzo & Harrington 1993) it is thus possible to increase sampling intensity in the absence of, or in addition to, basidiomes or infected plant material and obtain more detailed estimates of genet distribution below-ground. Some workers have, for example, used stratified protocols to sample rhizomorphs at several spatial scales to investigate below-ground genet distribution (Legrand, Ghahari & Guillaumin 1996, Prospero, Rigling & Holdenrieder 2003). This approach provided a more convincing view of genet distribution than would be possible from sampling at a single spatial scale. Moreover, it allowed the authors to conclude that, while genets of the pathogenic *A. ostoyae* may be spatially co-located with those of the saprotrophs *A. gallica* or *A. cepistipes*, genets of the two saprotrophic taxa rarely co-occur.

Genotyping using DNA extracted directly from soil

It is clear that the spatial dimensions of basidiomycete mycelia if forest soil can probably vary considerably and that mycelia appear to be distributed in a more-or-less patchy manner. Production of extensive mycelia is generally thought to be limited to soil-borne basidiomycetes in mature, relatively undisturbed forests (e.g. Dahlberg & Stenlid 1990, 1994, Bonello *et al.* 1998, Sawyer *et al.* 1999), although relatively large genets of *Leccinum duriusculum* have been reported under trees <20 yr old in a garden situation (Selosse 2003). Taxa that grow vegetatively to produce extensive genets in mature forests may also exist as multiple small genets in younger forests (Dahlberg & Stenlid 1990, 1994), and there is evidence that disturbance or different edaphic conditions can promote the existence of multiple spatially-restricted genets (Dahlberg & Stenlid 1994, Gryta *et al.* 1997, Ferguson *et al.* 2003, Guidot *et al.* 2004). Not all basidiomycetes in mature forest situations, however, produce extensive genets and it is becoming increasingly clear that generalisations regarding mycelial systems in soil may be misleading. There are, for example, increasing reports that some ECM taxa (e.g. some species of *Amanita*, *Laccaria*, *Lactarius* and *Russula*) form only small genets in mature, undisturbed forests (Gherbi *et al.* 1999, Fiore-Donno & Martin 2001, Redecker *et al.* 2001). As these authors have suggested, this may reflect the relative inability of these taxa to form rhizomorphic mycelia in soil.

For most soil-borne basidiomycetes, isolation of mycelium from soil cores is not an option. For these fungi, direct investigation of below-ground mycelial distribution has required development of molecular probes that can discriminate the target mycelium in a mixed DNA sample extracted directly from soil. Simple sequence repeat (SSR) markers appear to hold excellent promise in this regard, and SSR markers have been developed for a range of ECM taxa that includes: *Cantharellus formosus* (Dunham *et al.* 2003), *Hebeloma*

spp. (Jany, Bousquet & Khasa 2003), *Pisolithus* spp. (Kanchanaprayudh *et al*. 2002, Hitchcock *et al*. 2003), *Rhizopogon* spp. (Kretzer, Molina & Spatafora 2000, Kretzer *et al*. 2003), *Russula brevipes* (Bergemann & Miller 2002), *Suillus grevillei* (Zhou, Miwa & Hogetsu 2001a) and *Tricholoma matsutake* (Lian *et al*. 2003), along with *Armillaria* spp. (Langrell, Lung-Escarmant & Decroocq 2001, Lefrancois, Lung-Escarmant & Langrell 2002). For some species, these have been used to infer genet distribution using DNA from basidiomes (Zhou *et al*. 2001a, Bergemann & Miller 2002, Dunham *et al*. 2003, Kretzer *et al*. 2003). However, to date there is only a single published study of the use of SSR markers to directly assess below-ground mycelial distribution. Zhou *et al*. (2001b) used SSR markers to compare the fine-scale distribution of ECM root tips and soil-borne mycelia of *S. grevillei* in the vicinity of basidiomes and at positions where basidiomes had been present during the preceding year. They found that some below-ground genets were present in the absence of basidiomes, demonstrating the utility of SSR marker-based investigations of mycelial distribution below-ground.

Guidot *et al*. (2001) also compared the distribution of mycelia of *Hebeloma cylindrosporum* using DNA extracted from basidiomes and ECM root tips, analysing of a region of the ribosomal IGS. ECM genotypes were found to be located no more than 20 cm from the corresponding basidiomes, suggesting that genets of this taxon had a restricted patchy distribution at the site. Although Guidot *et al*. (2001) reported a reasonable correspondence between estimates of genet distribution of *H. cylindrosporum* based on DNA derived from basidiomes and ECM root tips, the results of Zhou *et al*. (2001b) show that emphasis on these structures does not necessarily reflect the extent of below-ground genets and highlights the need for direct analysis of DNA extracted directly from soil cores. Several recent studies have shown the efficacy of direct soil DNA extraction, coupled with ITS PCR, cloning or DGGE and sequencing (Landeweert *et al*. 2003a, 2004, Smit, Veenman and Baar 2003), or terminal restriction fragment length polymorphism (TRFLP) analysis (Dickie *et al*. 2002, Edwards *et al*. 2004), for analysis of below-ground communities of ECM and saprotrophic fungi. Two of these investigations found evidence for vertical stratification in the distribution of mycelia of some ECM taxa in the soil profile, suggesting that a degree of niche differentiation may exist within this group (Dickie *et al*. 2002, Landeweert *et al*. 2003a). The direct soil DNA extraction approaches have also been effective in demonstrating the patchy nature of the distribution of basidiomycete mycelia in soil and have provided evidence that forest soil characteristics can influence mycelial growth (Smit *et al*. 2003, Edwards *et al*. 2004). Quantitative PCR methods have recently also been applied to DNA extracted directly from soil to quantify mycelia of individual ECM basidiomycetes (Guidot, Debaud & Marmeisse 2002, Landeweert *et al*. 2003b, Guidot *et al*. 2004). While none of the direct DNA extraction work has so far been targeted to investigate the distribution of individual mycelial genotypes in soil, the ability of SSR markers to discriminate genotypes in mixed DNA samples, should facilitate considerable progress in this context in the near future.

MOVEMENTS OF CARBON AND MINERALS IN SOIL-BORNE MYCELIA

Regardless of their individual dimensions or longevity in soil, mycelia are dynamic and will grow reactively according to nutrient and carbon substrate availability, edaphic conditions and the activities of other mycelia and soil organisms. The net result is a structurally and physiologically heterogeneous entity wherein different regions simultaneously fulfill varied functions (Rayner 1991, Cairney & Burke 1996). The interconnectedness of these regions as part of an integrated mycelial collective is viewed as the key to the success of the mycelial life-style (Rayner 1991). There is ample evidence that saprotrophic and ECM basidiomycete mycelia can acquire mineral nutrients and carbon at certain locations and effect their translocation to sites of demand elsewhere within the mycelial system (Jennings 1987, Cairney 1992, Finlay 1993, Olsson 1999). Much of what is known about translocation in these mycelia relates to fungi that form more-or-less rhizomorphic mycelia. The following discussion thus focuses largely on these fungi, however, information from non-rhizomorphic mycelia is included where appropriate.

For many basidiomycete mycelia, absorption of carbon occurs within decomposing organic material or at the symbiotic interface in an ECM root, while absorption of mineral nutrients from soil is likely to be confined largely to the relatively diffuse hydrophilic hyphae at the leading edge of exploratory fans (Unestam & Sun 1995). That ^{32}P added to mature rhizomorphic mycelium of the saprotroph *Mutinus caninus* was not translocated to other parts of the mycelium in a field labelling experiment (Clipson, Cairney & Jennings 1987) has been interpreted as an indication that little absorption of the ion occurred in this part of the mycelium (Wells & Boddy 1995b). Other investigations have, however, found evidence for absorption of ^{32}P-labelled phosphate by cut rhizomorphs, albeit reduced compared to growing front hyphae (Timonen *et al*. 1996). Slow absorption of ^{134}Cs by intact rhizomorphs of *Armillaria* spp. (Gray, Dighton & Jennings 1996) and rapid immobilisation of ^{32}P at the point of application to fungal mycelium (Olsson & Gray 1998, Lindahl, Finlay & Olsson 2001) have also been reported, indicating that absorption by rhizomorphic mycelium cannot be entirely ruled out. Some absorption may thus occur in regions of mycelia away from the growing front (Clipson *et al*. 1987, Gray *et al*. 1995, Olsson & Gray 1998, Sun *et al*. 1999), but the

Table 1. Estimated velocities of translocation of various radioisotopes within basidiomycete mycelia.

Fungus	Isotope translocated	Velocity (cm h^{-1})	Reference
Saprotrophic			
Armillaria mellea (R)[a]	[^{14}C]glucose	<3.5 (a)[b]	Granlund *et al.* (1985)
A. mellea (R)	[^{3}H]glucose	<1.2 (b)	Granlund *et al.* (1985)
A. mellea (R)	^{32}P	<2.5 (a)	Granlund *et al.* (1985)
Armillaria spp. (R)	^{134}Cs	<14.2 (a)	Gray *et al.* (1996)
Armillaria spp. (R)	^{134}Cs	<17.9 (b)	Gray *et al.* (1996)
A. gallica (R/D)	^{137}Cs	<0.6 (a)	Gray *et al.* (1996)
A. ostoyae (R/D)	^{137}Cs	<0.8 (a)	Gray *et al.* (1996)
Serpula lacrimans (R)	[^{14}C]glucose	<24.8 (a)	Brownlee & Jennings (1982)
Phanerochaete velutina (R)	[^{14}C]glucose	<336 (a)	Wells *et al.* (1995)
P. velutina (R/D)	^{14}C-aminoisobutyric acid	$<5.0\times10^{-2}$ (a)	Tlalka *et al.* (2002)
Schizophyllum commune (D)	^{137}Cs	$<2.1\times10^{-4}$ (a)	Gray *et al.* (1995)
S. commune (D)	^{14}C-AIB/^{32}P	$>1.8\times10^{-3}$ (a)	Olsson & Gray (1998)
Pleurotus ostreatus (D)	^{14}C-aminoisobutyric acid/^{32}P	$>1.8\times10^{-3}$ (a)	Olsson & Gray (1998)
Ectomycorrhizal			
Paxillus involutus (R)	^{32}P	$>7.7\times10^{-3}$ (b)	Timonen *et al.* (1996)
Suillus bovinus (R)	^{14}C-photosynthate	>20.0 (a)	Finlay & Read (1986a)

[a] Type of mycelium (R, rhizomorphic; D, diffuse).
[b] Direction of translocation (a, acropetal; b, basipetal).

hydrophobic nature of the hyphae, or in the case of *Armillaria* spp. rhizomorphs and a melanized rind, will clearly hinder this process (Gray *et al.* 1995, 1996).

MECHANISM(S) OF TRANSLOCATION

Bi-directional translocation of carbon and minerals is known to occur within mycelia, and current evidence indicates that it occurs from sources to sinks in mycelial systems that are independent of mycelial growth (Lindahl *et al.* 2001a). The physiological mechanisms underlying translocation remain the topic of debate, with diffusion, mass flow, and cytoplasmic streaming processes having been variously canvassed (Jennings 1987, Cairney 1992, Finlay 1993, Olsson 1999). As highlighted by others, these mechanisms might operate simultaneously, and translocation might be driven by different mechanisms in different fungi or under different edaphic conditions (Olsson 1999, Jacobs *et al.* 2004). Velocities of translocation of radio-labelled solutes along basidiomycete mycelia have been estimated and found to vary by several orders of magnitude (Table 1). In most instances these estimates are more rapid than would be anticipated as a result of simple diffusion alone, and where estimated velocities were of a similar order to diffusional movement, patterns of movement did not fit predicted models for diffusion (Gray *et al.* 1996).

Although the data are limited to only a few species, it appears that movements are generally more rapid along rhizomorphic than diffuse mycelia (Table 1). A characteristic feature of the rhizomorphic mycelium of many ECM and saprotrophic basidiomycetes is the presence of large diameter 'vessel' hyphae (Cairney *et al.* 1991). There are many reports that these hyphae lack cytoplasm and septal cross-walls (e.g. Duddridge *et al.* 1980, Agerer 1988, Cairney, Jennings & Veltkamp 1989, Cairney 1990), and they have frequently been implicated as specific conduits that may be a major route for water and solute translocation *via* a mass flow mechanism (e.g. Duddridge *et al.* 1980, Read 1984, Eamus *et al.* 1985, Jennings 1987). In *Serpula lacrymans* at least, there is evidence to suggest that large diameter 'armbone' hyphae in young mycelia are routes for translocation (Jennings 1987), suggesting that the cytoplasmic lengths of 'vessel' hyphae may be competent in translocation. As has been highlighted previously (Jennings 1987, Cairney 1992, Finlay 1993) and, to my knowledge, still currently applies, there is no direct evidence for involvement of empty 'vessel' hyphae in translocation. Indeed, not all 'vessel' hyphae in saprotrophic rhizomorphs lack cytoplasmic contents (Cairney *et al.* 1989) and a recent study of rhizomorphs of the ECM basidiomycete *Paxillus involutus* using laser scanning confocal microscopy found that septal cross-wall dissolution was extremely rare (Schweiger, Rouhier & Söderström 2002). Furthermore, rhizomorphs of *Armillaria luteobubilina* that grew from wood blocks in the laboratory, and so must have been competent in translocation, lacked any obvious 'vessel' hyphae (Pareek, Cole & Ashford 2001). Collectively these observations raise questions about the significance of empty portions of 'vessel' hyphae as a specific translocation pathway. Furthermore, while the tension created by transpiration from a tree host might logically provide the driving force for a mass flow along the rhizomorph apoplast, including the empty lengths of 'vessel' hyphae (Finlay 1993), Timonen *et al.* (1996) found that varying host transpiration had no effect on the velocity of ^{32}P translocation in ECM extramatrical mycelium. While this does not preclude a role for the empty lengths of 'vessel' hyphae in water transport, it strongly suggests that phosphorus movement to the

ECM roots occurs *via* an alternative route. Under certain laboratory conditions, it is possible that evaporative water loss may contribute to a mass flow of solution within the rhizomorph apoplast (Wells, Boddy & Evans 1995), but the extent to which this phenomenon would occur in soil is unclear. Under most circumstances, mass flow in the apoplast of a saprotrophic rhizomorph would require a mechanism for generation of turgor at the source (Jennings 1987, Cairney 1992). As outlined previously (Cairney 1992), there is currently no evidence for a mechanism that would allow for sufficient solute accumulation, and so generation of the necessary hydrostatic pressure, in the empty 'vessel' hyphal apoplast of saprotrophic hyphae.

Our perceptions of translocation in basidiomycete mycelia have altered significantly with the discovery of a motile tubular vacuole system in hyphae that appears to facilitate both intra- and intercellular transport via a peristalsis-like mechanism (Shepherd, Orlovich & Ashford 1993a, b). Although initially observed only in apical hyphal compartments, the vacuolar system has subsequently been found in extramatrical hyphae, including rhizomorphic mycelium, of an ECM *Pisolithus* sp., raising the possibility that it may play a role in long-distance translocation of nutrients (Allaway & Ashford 2001).

While direct evidence for a role in long-distance translocation is lacking at this stage, the vacuoles are known to contain significant quantities of phosphorus and potassium, and probably also nitrogen, and could act as a conduit for their movement along hyphae (Ashford & Allaway 2002). The observations that radial translocation *via* putative anastomoses can occur in basidiomycete colonies (Olsson & Gray 1998) and that simultaneous bi-directional translocation of carbon or phosphorus can occur (Granlund, Jennings & Thompson 1985, Lindahl *et al*. 2001a) have been taken as supporting the hypothesis that solutes may circulate within mycelia (Olsson 1999). Thus, absorbed substances may be added to the circulation stream in mobile forms, or chemically immobilised, with remobilisation effected according to demand and circulated via the motile vacuole system (Boddy 1999, Lindahl *et al*. 2001a). There is further circumstantial evidence to support bi-directional translocation of ions in non-rhizomorphic basidiomycete mycelium (Connolly & Jellison 1997). The observation that nitrogen, potassium and magnesium may be co-translocated with phosphorus in mycelium of the ECM basidiomycete *Paxillus involutus*, is also consistent with a intra-vacuolar translocation (Jentschke *et al*. 2001). There are reports of oscillatory transport of amino acids in mycelium of the saprotroph *Phanerochaete velutina*, a phenomenon that might be explained by a cycle of absorption, vacuolar compartmentalisation, vacuolar efflux and translocation (Tlalka *et al*. 2002, 2003). Such observations appear consistent with the circulation model.

SIGNIFICANCE AND SPATIAL SCALE OF MYCELIAL TRANSLOCATION

Irrespective of the mechanism(s) of translocation, it is clear that basidiomycete mycelia can effect significant movements of carbon and other elements in soil (e.g. Berg 1988, Perez-Moreno & Read 2000, Frey, Six & Elliot 2003). In ECM systems, significant carbon translocation can occur towards the growing mycelial front (e.g. Finlay & Read 1986a, Wu, Nara & Hogetsu 2001, 2002), may occur across multiple soil horizons (Heinonsalo, Hurme & Sen 2004), and is often more marked towards regions of mycelial proliferation associated with patches of organic matter or mineral enrichment (Bending & Read, 1995, Leake *et al*. 2001, Rosling *et al*. 2004). Carbon may also be translocated to interconnected ECM root tips (Finlay & Read 1986a, Wu *et al*. 2001). In addition, saprotrophic mycelia have been shown to translocate carbon from woody material to foraging mycelium, but more-so to mycelium in other woody material (Wells *et al*. 1995). ECM fungi translocate ^{32}P-phosphate both to infected root tips and to the growing mycelial front, in a particular to patches of mycelial proliferation (e.g. Skinner & Bowen 1974, Finlay & Read 1986b, Timonen *et al*. 1996, Lindahl *et al*. 1999). ^{15}N supplied as various compounds is also translocated to the ECM roots and the mycelial growing front (e.g. Melin & Nilsson 1952, Finlay *et al*. 1988, Arnebrant *et al*. 1993, Brandes *et al*. 1998). The situation appears similar for saprotrophic taxa, with ^{32}P-phosphate being translocated to the mycelial front in soil and to colonised woody substrates (e.g. Wells & Boddy 1990, 1995b, c, Wells, Hughes & Boddy 1990, Lindahl *et al*. 1999, 2001a). Where multiple pieces of woody substrate are interconnected by a mycelium, ^{32}P-phosphate translocation does not occur uniformly towards each, and may vary with the extent of decay and the length of time that each substrate has been colonised (Wells & Boddy 1995a, Wells, Harris & Boddy 1998, 1999). Nitrogen translocation in saprotrophs has been studied less frequently, but the amino acid analogue ^{14}C-aminoisobutyrate is translocated to the growing front by several taxa (Olsson & Gray 1998, Tlalka *et al*. 2002, 2003). Interactions between mycelia of different taxa can significantly influence patterns of carbon and mineral movements within mycelia and there is considerable potential for movement between mycelia of different taxa (Lindahl *et al*. 1999, 2001b, Leake *et al*. 2001, 2002, Wells & Boddy 2002).

Of necessity, most of our knowledge of the development and dynamics of mycelial systems, along with their abilities to translocate carbon and mineral nutrients has been derived from microcosm studies. Importantly, these systems have allowed development of theories and non-linear mathematical models that fit the characteristics of observed macroscopic patterns of mycelial growth and that have provided a novel view of the indeterminate interconnected mycelial lifestyle

(e.g. Davidson *et al*. 1996, Rayner 1996, Rayner, Watkins & Beeching 1999, Boswell *et al*. 2003). Microcosms within which ECM mycelia have been studied have been $<40\ cm^2$ (Finlay & Read 1986a), while the largest adopted for saprotrophs have been $50\ cm^2$ (Wells *et al*. 1998). The spatial dimensions of the mycelia in microcosms are thus several orders of magnitude smaller than the dimensions predicted for genets in the field (see p. 10) and numerous questions remain to be answered before the relevance of the models to the larger scale and greater heterogeneity of the forest soil environment can be ascertained. A basic tenet of indeterminate mycelial growth is that, although parts of a mycelium may act to some extent autonomously, they remain interconnected as the mycelium expands (Rayner, Griffith & Ainsworth 1995). With the exception of the easily-excavated rhizomorph systems of a few saprotrophs, we currently have insufficient knowledge of mycelia in forest soils to predict the extent to which large putative genets represent single interconnected mycelia, or have been physically fragmented by invertebrate grazing or other forms of disturbance.

As described by Carlile (1995) and recently emphasised by Klein & Paschke (2004), removal of protoplast from older (proximal) regions of a mycelium can, in effect, lead to physiological fragmentation of distal regions of the same genet. This idea was expanded by Olsson (1999), such that a genet may be viewed as comprising one or more 'functional mycelium units (FMUs)', i.e. network of interconnected hyphae that forms an individualistic organism. Within the genet, multiple FMUs may be separated from each other by regions of functionally inert mycelium, but may anastomose with each other to form larger FMUs (Olsson 1999). The extent to which such physiological fragmentation occurs in basidiomycete genets in forest soils is unclear. At the microcosm scale (<50 cm), the demonstrated translocation of solutes within ECM and saprotrophic mycelia clearly indicates physiological continuity, albeit that regression of certain parts of mycelia can occur (Boddy 1999). To my knowledge, however, the greatest distance over which translocation has been demonstrated in nature is <75 cm for a saprotroph (Wells & Boddy 1995b). Movement of carbon, presumably *via* ECM mycelium, between two trees that were separated by some 50 cm has also been demonstrated in nature (Simard *et al*. 1997), but because of root growth the distance of translocation in fungal mycelium is likely to have been significantly less. Mycelial systems in the field are more complex than those that develop in microcosms and generally interconnect many more resource units (Boddy 1999). In labelling central woody resource units with ^{32}P, Wells & Boddy (1995b) observed that, although many of the other resource units that were interconnected by the same mycelium were sinks for translocated ^{32}P, some interconnected resources received no label. This was not related to distance from the labelled resource, and the authors suggested that it might indicate that certain of the interconnected resources had no requirement for phosphorus. It might equally signal physiological fragmentation of parts of the mycelium. Indeed, the empty 'vessel' hyphae observed in rhizomorphic mycelia may reflect such physiological fragmentation. It is thus possible that our assumptions that empty lengths of these hyphae represent a discrete translocatory pathway in rhizomorphic mycelium may be misplaced. They may simply be a component of the general rhizomorph apoplastic space and so contribute no more to translocation than the inter-hyphal spaces.

CONCLUSIONS

Basidiomycete mycelia are abundant in forest soils, yet our understanding of their distribution, dynamics and functioning in the field remains relatively poor. While clearly able to effect movements of carbon and key minerals in forest soils, the spatial scales within which individual mycelia operate as physically and (or) physiologically integrated entities in nature is unknown. This currently constrains our abilities to predict their contributions to the cycling and redistribution of nutrients and carbon at the ecosystem scale. DNA-based methods for identifying individual mycelial genotypes, where coupled with direct DNA extraction from soil and an appropriate sampling strategy, have the potential to reveal much about the three-dimensional distribution of mycelia in soil. This, however, will require development of appropriate genetic markers for the fungi in question. Demonstration of the physical and physiological integrity of the mycelia can only be achieved by labelling experiments in the field. While the use of radiotracers will continue to be valuable, the efficacy of stable isotopes in this context has also been demonstrated in investigations of inter-plant carbon and nitrogen transfer via mycorrhizal fungi (Simard *et al*. 2002). Stable isotope probing is a technique that allows separation of nucleic acids that are labelled with a stable isotope from those that are not (e.g. Radajewski *et al*. 2000, Morris *et al*. 2002). Importantly, it has also recently been successfully used for analysis of fungal DNA and RNA extracted directly from soil (Lueders *et al*. 2004). While many technical problems will have to be overcome, labelling with a stable isotope, followed by RNA extraction and fractionation on the basis of isotopic labelling and analysis using genetic markers may ultimately prove to be a useful tool in understanding the scale of mycelial activities in forest soils.

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