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Fungal translocation - creating and responding to environmental heterogeneity

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It has been known for a long time that fungi may transport substances in their hyphae. Experiments using radioactive tracer isotopes have greatly expanded our knowledge about translocation and have revealed that many fungi may circulate resources throughout their mycelia. This article outlines a conceptual framework for when and where net-translocation of resources takes place. Effects of substrate qualities, mycelial growth and activity as well as interactions with living plant hosts and other microorganisms are discussed and exemplified with experimental data. It is concluded that translocation from more or less remote parts of the mycelium enables fungi to colonise substrates with a low initial resource availability and to actively increase the resource availability in the substrates, turning the colonising mycelium from a resource sink into a source. Thus, translocation not only occurs in response to environmental heterogeneity, but also allows fungi to create heterogeneity in their growth environment.

Keywords: translocation, environmental heterogeneity, mycelial activity

Translocation in fungal mycelia

Most fungi are built up from hyphae, and often a continuous hyphal network, i.e. the mycelium, of a fungal individual may extend over considerable distances (Thompson & Rayner, 1983; Olsson, 1999). Many, if not most, fungi may transport substances between their cells, and some, particularly basidiomycetes, translocate resources such as carbohydrates, nutrients and water freely throughout their whole mycelium (reviewed by: Jennings, 1987; Cairney, 1992; Boddy, 1999; Olsson, 1999). The ability to translocate resources implies that a mycelium is much more than a colony of physically connected, but otherwise independent, hyphae. The whole mycelium may be integrated into a single entity, where the local environment of one part of the mycelium may affect distant parts. Furthermore, the performance of a single hyphal tip may depend on the nutritional status of the whole mycelium. As resources can be removed from areas with a surplus to enable activity at other sites where resources are lacking, translocation makes fungi well adapted to colonise solid substrates with a high degree of spatial heterogeneity.

Many studies of mycelial translocation have used radioactive tracer isotopes. For example, Lindahl *et al*. (2001a) demonstrated transport of radioactive phosphorus between two wood blocks placed ~10 cm apart in soil and connected by mycelium of the wood-degrading fungus *Hypholoma fasciculare*. When the isotope ^{32}P was added to one of the wood blocks and ^{33}P to the other, phosphorus was found to be transported in both directions simultaneously (Fig 1). Similarly, Tlalka *et al*., (2002) showed bidirectional translocation of the ^{14}C-labelled amino acid analogue aminoisobutyric acid in mycelia of the wood-degrading fungus *Phanerochaete velutina*. These microcosm studies confirm the suggestion by Olsson & Gray (1998), that many fungi circulate substances throughout their mycelia. Circulation of resources would facilitate net translocation of resources from sites with high cytoplasmic availability to sites with low cytoplasmic availability, i.e. from sources to sinks.

This paper puts fungal translocation into an environmental perspective and discusses how translocation is affected by spatial heterogeneity in the abiotic and biotic environment. The paper also

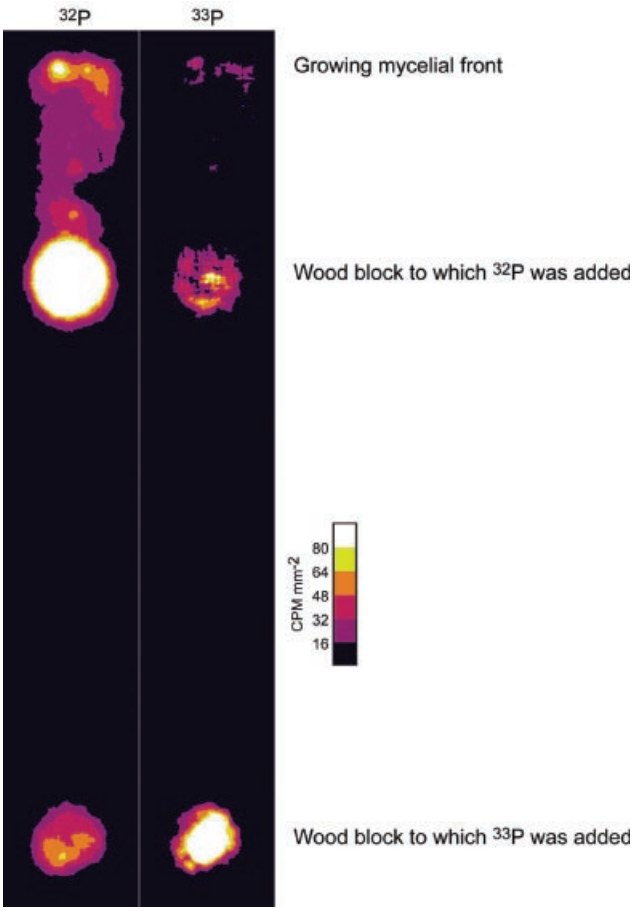

Fig 1 Autoradiographic images of the distribution of radioactivity in two wood blocks connected by mycelium of *Hypholoma fasciculare* in a soil microcosm. The fungus was inoculated onto the lower wood block and grew out into the soil where it colonised the upper wood block. The mycelium on the lower wood block was supplied with ^{33}P-phosphate and the mycelium on the upper wood block was supplied with ^{32}P-phosphate. The two autoradiograms were acquired from the microcosm 29 days after addition of the tracer isotopes. The left image shows the distribution of ^{32}P, which has been translocated from the addition point at the upper wood block to the lower wood block and to the growing mycelial front. The right image shows the distribution of ^{33}P, which has been translocated from the addition point at the lower wood block to the upper wood block and further to the growing mycelial front (from Lindahl *et al*., 2001a, with permission).

discusses how fungi themselves may use translocated resources to modify their environment. Although some of the experiments referred to in this article focus on translocation of phosphorus, most of the theoretical discussion refers to carbohydrate translocation. However, the ideas most likely apply to all translocated substances that accumulate in fungal biomass, including amino acids and phosphates.

Sources and sinks in heterogeneous environments - a conceptual framework

Fungi often live in heterogeneous environments, and in most cases resources are unevenly distributed over a fungal mycelium. Plant litter, such as straw, foliage and woody debris enters the soil environment as discrete units. Carbohydrates have to be translocated out of these resource units, in order to enable the fungi to grow in the soil outside the units and colonise new litter units (Wells *et al*., 1995; Frey *et al*., 2003).

Davidson & Olsson (2000) modelled the outgrowth into soil of a nematophagous fungus, *Arthrobotrus superba*, from woody food bases. Good fit with experimental results (Persson *et al*., 2000) was found, when it was assumed that active translocation took place from the wood block to the advancing mycelial front and that the fungus was totally dependent on the wood block as a source of carbohydrates (Fig 2a,b,c). The model predicted that the mycelium could reach a maximum distance out in the soil from the piece of wood and that this distance depended on the amount of colonised wood as well as the assumed maintenance energy needed for growth through the soil (Fig 2d).

Living roots, acting as sources of carbohydrates for mycorrhizal fungi, are also discrete sources and the fungi have to translocate carbohydrates to support growth outside the roots (Finlay & Read, 1986). The same situation occurs for many soil pathogens, where carbohydrates have to be translocated from already colonised hosts or from dead organic matter, to enable infection of new host plants (Shaw & Kile, 1991). Only rarely are the available resources evenly distributed throughout a mycelium. This may happen when the resource units are large compared to the size of the fungal mycelia, as in the case of some wood-rotting fungi in logs (large substrates) or some endophytic fungi (small mycelia).

The cytoplasmic availability of compounds is determined by the rates of uptake and release out of hyphae as well as by chemical conversions. High cytoplasmic availability of a specific compound may occur at sites of rapid uptake or at sites of rapid conversion from another compound in storage. Low cytoplasmic availability may occur as a consequence of rapid metabolism or exudation. Different sub-units of a mycelium experience different environmental conditions and may be functionally differentiated from each other. The cytoplasmic availability of various compounds may therefore vary considerably between different parts of the mycelium, creating a potential for net-translocation between mycelial sub-units. The source strength of a mycelial sub-unit can be defined as the added rate of all processes that contribute to an increased cytoplasmic availability of a compound - uptake as well as chemical conversions. The source strength with respect to a particular compound

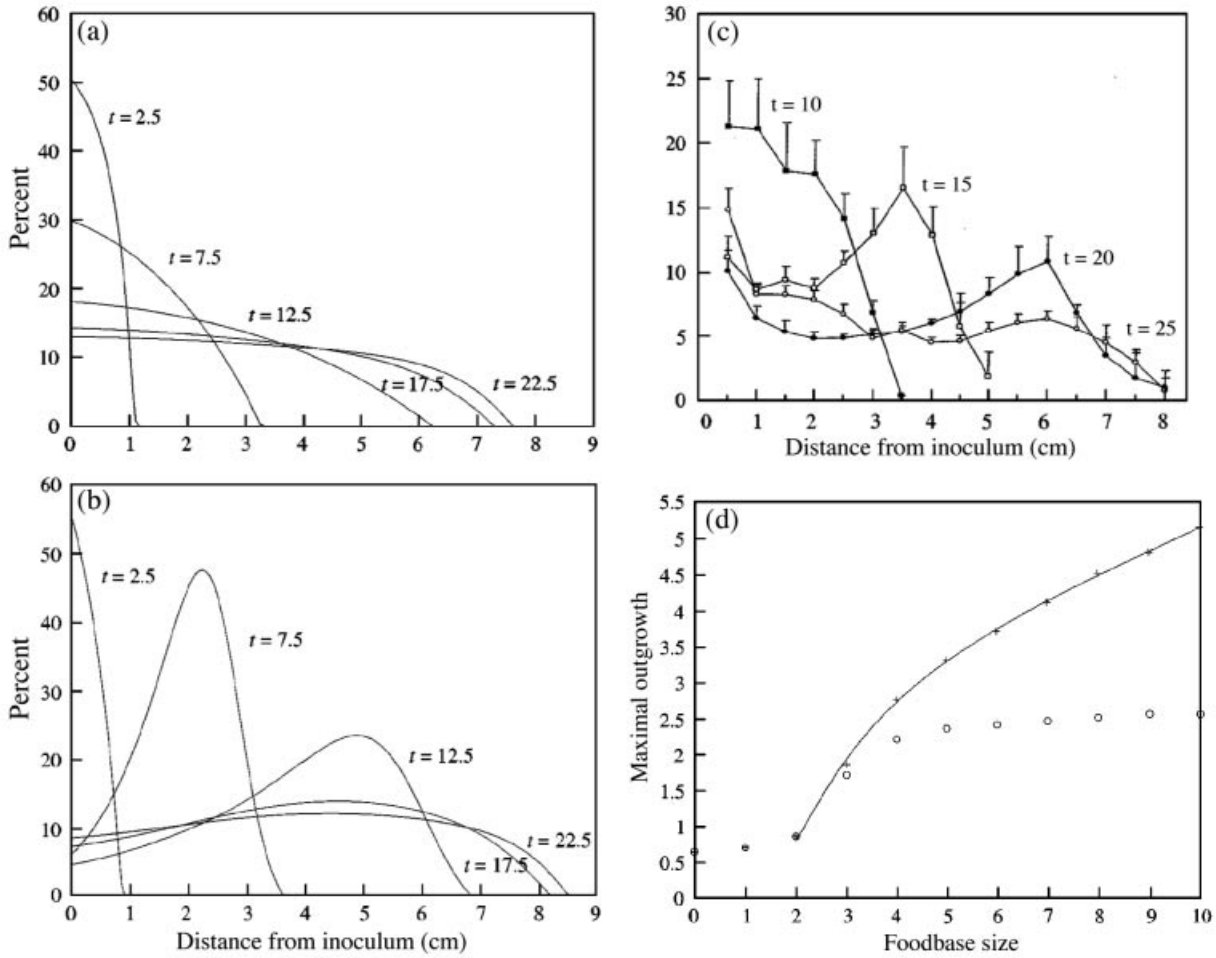

Fig 2 Model estimates and observed distribution patterns of a labelled substrate in a fungal mycelium growing out from a food base into an inert environment. The label was added to the food base (inoculum) at the time of inoculation (t = 0 where t is days after inoculation). (a) Predicted label distribution with passive diffusion as the only translocation mechanism. (b) Predicted label distribution with active translocation of the labelled substrate throughout the mycelium (Davidson & Olsson, 2000, with permission). (c) Observed distribution of radioactivity when ^{14}C-methylglucose was added to mycelia of *Arthrobotrys superba*, growing into soil from wooden discs (Person *et al*., 2000 with permission). (d) Model prediction of the maximal extension of a mycelium from a food base into an inert environment. Open symbols represent a model using passive diffusion as the only translocation mechanism. Closed symbols represent a model of active translocation. An actively translocating mycelium may use the increased resource availability to extend further into the inert substrate (Davidson & Olsson, 2000).

represents the potential of a sub-unit to supply this compound to the entire mycelium. The sink strength of a mycelial sub-unit can be defined as the added rate of all processes that contribute to a decreased cytoplasmic availability of a compound and represents the potential of a sub-unit to withdraw this compound from the common mobile pool.

Source strength of mycelial sub-units

The source strength of a mycelial sub-unit depends mainly on the rate with which resources may be taken up by the hyphae. The uptake rate in turn depends on the quality of the colonised substrate as well as on the biomass and activity of the fungal mycelium in the substrate. The substrate may be dead organic matter, in the case of saprotrophs, and living host plants in the case of necrotrophs and biotrophs. The source strength is also affected by the presence of other organisms and their interactions with the mycelium. In the following sections, the effects of substrate quality, mycelial activity and interacting organisms on the source strength of a mycelial sub-unit will be outlined and exemplified by experimental results.

Substrate quality

The quality of a substrate is determined by the chemical form, concentration and physical availability of the nutritionally valuable compounds in the substrates. For saprotrophic growth, a high concentration of low molecular weight (LMW) compounds, such as monosaccharides or amino acids,

increases the quality of a substrate. Predominance of polymeric compounds, such as cellulose or chitin, which require enzymatic degradation before uptake is possible, leads to a lower substrate quality. A high concentration of lignin that physically shields the cellulose fibres also decreases the quality of a substrate. As fungi degrade a substrate, it rapidly becomes depleted in LMW compounds, and subsequently also in non-lignified cellulose. Furthermore, reactive polyphenolic compounds, formed through fungus-mediated oxidation of lignin, form complexes with other compounds, rendering them less available for uptake. Thus, as decomposition progresses, the available resources within a substrate become depleted or immobilised in recalcitrant complexes and the quality of the substrate and thereby the source strength of the mycelium in the substrate decreases.

Wells & Boddy (1990) inoculated wood blocks with either of the wood decomposing fungi *Phanerochaete velutina* and *Phallus impudicus*, and introduced wood blocks in different stages of decomposition into soil microcosms. As the soil most likely was of limited value as a source of carbohydrates, the rate of mycelial production outside the wood would give an indication of the capacity of the mycelium within the wood to provide carbohydrates to the soil mycelium. The amount of mycelium that grew out into the soil was negatively correlated to the decay of the wood, illustrating how the carbohydrate source strength of mycelium in wood decreases, as decomposition progresses.

Plants respond to infections of necrotrophic fungi through defence mechanisms that aim at limiting the physical availability of plant tissues to the infecting fungus. A substrate of high quality for necrotrophic growth is a host plant that is more susceptible to infection. The susceptibility of a plant is influenced by stress factors, nutrition and climate (Agrios, 1997), but also on specificity patterns, with certain fungi better adapted to infect certain host plants.

The quality of a root as a substrate for mycorrhizal fungi may to a large extent be determined by the nutritional status of the plant. A plant with low availability and/or high demand of nitrogen and phosphorus may allocate more photosynthetically-derived carbohydrates to the roots and its mycorrhizal associates, in order to improve the capacity of the mycorrhizal fungi to provide nutrients. Wallander & Nylund (1992) grew mycorrhizal *Pinus sylvestris* seedlings in semi-hydroponic systems and measured the amounts of extraradical mycelium formed by three different ectomycorrhizal fungi. The amounts of extraradical mycelium decreased drastically in response to elevated NH_4^+ concentration in the growth medium, illustrating how the nutritional status of the host plant affects the carbohydrate source strength of the mycorrhizal roots. Even in systems with high NH_4^+ levels, mycelial growth could be restored by removing phosphorus from the medium. Rouhier & Read (1998) found a drastic increase in the production of extraradical mycelium by the ectomycorrhizal fungi *Suillus bovinus* and *Paxillus involutus*, when their pine seedling hosts were exposed to elevated CO_2 concentrations.

As in the case of necrotrophs, specificity in the interaction between mycorrhizal fungi and their host plants may influence the quality of a root viewed from the perspective of the fungus. Some non-photosynthetic plants are known to parasitize mycorrhizal fungi (Leake, 1994), in which case the quality of the plant root must be considered as particularly low.

Mycelial activity

The biomass and activity of a mycelial sub-unit influences its source strength. Here it may be useful to introduce the broad concept of 'mycelial impact', defined as the potential of a mycelial sub-unit to affect its environment. Conditioning of the substrate creates a physical environment that fits the demands of the mycelium. The chemical environment may be modified through uptake and exudation of compounds, and the biological environment may be altered through interactions with other organisms, ranging from antagonism to mutualism.

The environmental impact of a mycelium has got two components; one quantitative - the amounts of mycelial biomass, and one qualitative - the activity of the mycelium. Both components are essential in determining the rate of resource uptake from a substrate. In high quality substrates with high concentrations of LMW substances directly available for uptake, the most important component of the mycelial impact is the amount of biomass. A larger or denser mycelium has a larger assimilating surface area and is therefore more efficient in uptake. The other component of the mycelial impact, the activity of the mycelium, represents the potential of the mycelium to modify its environment, rendering more resources available for uptake. This component of the mycelial impact is more important in low quality substrates that require some kind of modification before resources may be taken up.

For saprotrophic growth in low quality substrates, the degradation of polymers into assimilable substances is likely to be the rate-limiting step in

exploitation of the substrate, and the mycelial impact may primarily be expressed as the activity of degrading enzymes. In the case of necrotrophic growth, the mycelial impact is closely related to the virulence of the fungus, the ability to resist plant infection responses and subsequently to kill host tissues. For biotrophs, such as mycorrhizal fungi or endophytic fungi, the quantitative component of the mycelial impact is probably the most important, corresponding to the degree of colonisation within the host. The flexibility of biotrophic fungi to actively increase the availability of assimilable compounds within the host may be limited unless the biotroph turns into a necrotroph. For mycorrhizal fungi it remains uncertain to what extent the fungi may manipulate their hosts into providing more carbohydrates. Many ectomycorrhizal fungi may for example produce hormones that induce short root proliferation in the plant, potentially increasing the carbon supply to the fungus (Gay *et al*., 1994).

The impact a mycelial subunit may exert on its environment depends on the amounts of resources available to the subunit. The resource availability depends partly on the local uptake rate, but the local uptake rate is in turn affected by the mycelial impact. There is thus a positive feedback between the uptake rate of a mycelial subunit and its impact (Fig 3). This implies that a high initial resource quality leads to a rapidly accelerating uptake rate, as the high resource availability permits a rapid build-up of mycelial impact. Importantly, the impact exerted by a mycelial subunit also depends on the amounts of resources that may be translocated from other parts of the mycelium.

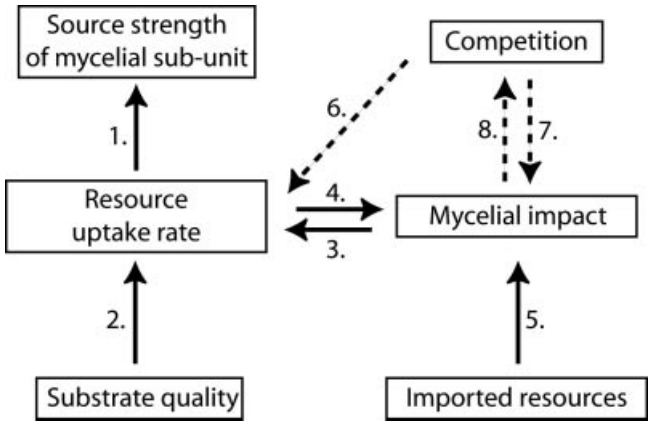

Fig 3 Schematic diagram of the major factors influencing the source strength of a mycelial sub-unit. Solid arrows indicate positive effects and dashed arrows indicate negative effects.
1. The source strength of a mycelial sub-unit is determined by the rate of resource uptake.
2. The resource uptake rate is positively correlated with the substrate quality.
3. Increased mycelial activity in the substrate - mycelial impact, increases the uptake rate.
4. The build-up of mycelial impact depends partly on local resources.
5. The build-up of mycelial impact depends partly on resources translocated to the mycelial sub-unit.
6. Exploitation competition has a negative effect on the resource uptake rate.
7. Interference competition may prevent the build-up of mycelial impact.
8. A high mycelial impact enables a mycelium to out-compete competitors from the substrate and thereby reduces competition.

Mycelial interactions with other microorganisms

Other microorganisms sharing a substrate with a mycelium may affect the amounts of resources available for uptake as well as the impact of the mycelium. Direct competition for resources may be termed exploitation competition (Lockwood, 1992). Exploitation competition reduces the uptake rate of the mycelium and thereby the source strength. In addition, microorganisms, fungi in particular, often display antagonistic behaviour against each other resulting in a reduction in biomass of one or both of the competitors (Boddy, 2000). Such competition for space or territory rather than directly for resources may be termed interference competition. The ability to interfere successfully with other microorganisms, the combative strength, is also part of the impact of a mycelium. Interference competition frequently results in lysis of hyphae and thereby a reduction in mycelial impact of one or both of the interacting mycelia. Since a successful outcome of an antagonistic interaction may result in a decreased mycelial impact of the opponent, there is a positive feedback that may eventually lead to the exclusion of one of the competitors from the substrate (Fig 3). If a high mycelial impact is rapidly achieved, the mycelium gains a competitive advantage and may successfully exploit the substrate. On the other hand, if other fungi are more efficient in establishing a high mycelial impact, the fungus may be excluded from the substrate and the mycelial subunit will never turn into a net source.

Holmer & Stenlid (1993) studied antagonistic interactions between wood-decomposing fungi on discs of spruce wood. The discs were divided into sectors of varying sizes, which were inoculated with fungi. Sectors were then combined pair-wise to build up entire discs with two interacting fungi in each. Fungi that initially occupied a large fraction of the disc were more successful competitors and often managed to colonise the whole disc, by excluding the other fungus from the wood. Fungi that initially occupied a small fraction of the substrate were usually out-competed. These results suggest that the fungi were able to translocate resources from already colonised wood to the site of

interaction, in order to maximise their mycelial impact on the competitor.

In soil microcosms with pine seedlings and interacting ectomycorrhizal fungi, Wu *et al.* (1999) demonstrated how an unidentified ectomycorrhizal fungus not only reduced mycelial extension of the ectomycorrhizal *Pisolithus tinctorius* in the soil, but also managed to colonise root tips that were already colonised by *P. tinctorius*, excluding the latter from the roots. Landeweert *et al*. (2003) used DNA quantification to estimate the amount of ectomycorrhizal mycelium of two species; *Suillus bovinus* and *Paxillus involutus*, growing together on pine seedling hosts. Initially, the presence of *P. involutus* suppressed mycelial growth of *S. bovinus*, but at the end of the experiment, *S. bovinus* dominated the system.

Lindahl *et al*. (1999) studied antagonistic interactions between saprotrophic and mycorrhizal fungi. In oblong plastic trays, the extraradical mycelium of the mycorrhizal fungi *Suillus variegatus* and *Paxillus involutus* extended into soil from the roots of *Pinus sylvestris* host seedlings, while the mycelium of the wood-decomposing *Hypholoma fasciculare* extended into the soil from wood blocks opposite to the seedlings (Fig 4). When the soil mycelia of the fungi met, morphological interaction responses could be observed. Generally, the mycorrhizal fungi formed dense mycelial patches, as they overgrew the mycelium of the saprotroph. The interaction drastically reduced growth of the saprotrophic soil mycelium (Lindahl *et al*., 2002), indicating interference by the mycorrhizal fungi. In the experiments by Lindahl *et al.* (1999), the saprotrophic mycelium was labelled with ^{32}P and movements of the tracer isotope were monitored using electronic autoradiography. Transfer of ^{32}P could be observed from mycelium within the wood to the saprotrophic soil mycelium, from which the tracer isotope was captured by the mycorrhizal mycelium and translocated further to the host seedling (Fig 4). By interference competition, the mycorrhizal fungi not only reduced competition for soil nutrients, but also created a new substrate constituted by saprotrophic mycelium. In an additional experiment, the wood blocks colonised by *Hypholoma fasciculare* were replaced by larger blocks, presumably increasing the source strength of the mycelium within the wood (Lindahl *et al*., 2001b). When supplied with larger amounts of translocated resources, the saprotrophic fungus was able to build up a larger mycelial impact in the soil. The saprotrophic fungus was now able to interfere successfully with the mycorrhizal fungi and, in most cases, prevent mycorrhizal colonisation of the soil (Fig 5). The transfer of ^{32}P from labelled saprotrophic mycelium to the mycorrhizal seedlings was significantly lower in systems with larger wood blocks. When provided with large wood blocks, the saprotroph was able to use ^{32}P-labelled mycorrhizal mycelium as a source of phosphorus, and radioactivity could be detected in the wood block. The saprotroph captured significantly less ^{32}P from mycorrhizal mycelium, when provided with smaller wood blocks.

The effect of fungi on bacterial communities in soil can be decisive. In an experiment, where wood-decomposing basidiomycetes were growing through soil between different woody resources, it was found that the bacterial communities in the soil became characteristic for the species of fungus growing through it (Fig 6) (Tornberg *et al*., 2003). This large mycelial impact on the bacterial species composition is probably caused by a combination of stimulatory and inhibitory effects. Bacteria may be stimulated by exudation and leaking of organic compounds from the fungi, and by LMW compounds released by the activities of fungal extra-cellular enzymes. Inhibition can be caused by antibiotic substances, direct lysis of bacteria (Barron, 1988), but possibly also the generation of lignin-modifying radicals by the wood-decomposing fungi (Tornberg & Olsson, 2002).

Sink strength

The sink strength of a mycelial sub-unit depends on the rate with which the hyphae withdraw resources from the translocated pool and respire them, exude them or incorporate them into structural tissues. The rate of incorporation of resources into structural tissues depends on the growth rate of the mycelium, i.e. the build-up of quantitative mycelial impact. The build-up of qualitative mycelial impact requires exudation of enzymes and various other metabolites. Respiration-derived energy is required for all activities; growth, substrate conditioning as well as antagonistic interactions. The sink strength of a mycelial sub-unit is thus closely related to the build-up of mycelial impact in a substrate. Sink strength may also be caused by the presence of a mycorrhizal host plant that withdraws nutrients from the fungus. Allocation of resources into non-mobile storage compartments or reproductive structures may contribute to the sink strength of a mycelial sub-unit.

Leake *et al.* (2001) studied translocation of ^{14}C to the extraradical mycelium of the ectomycorrhizal fungus *Suillus bovinus* in soil microcosm where the host pine seedlings were exposed to a pulse of $^{14}CO_2$. In some of the systems, the ectomycorrhizal mycelium was challenged with the wood-degrading fungus

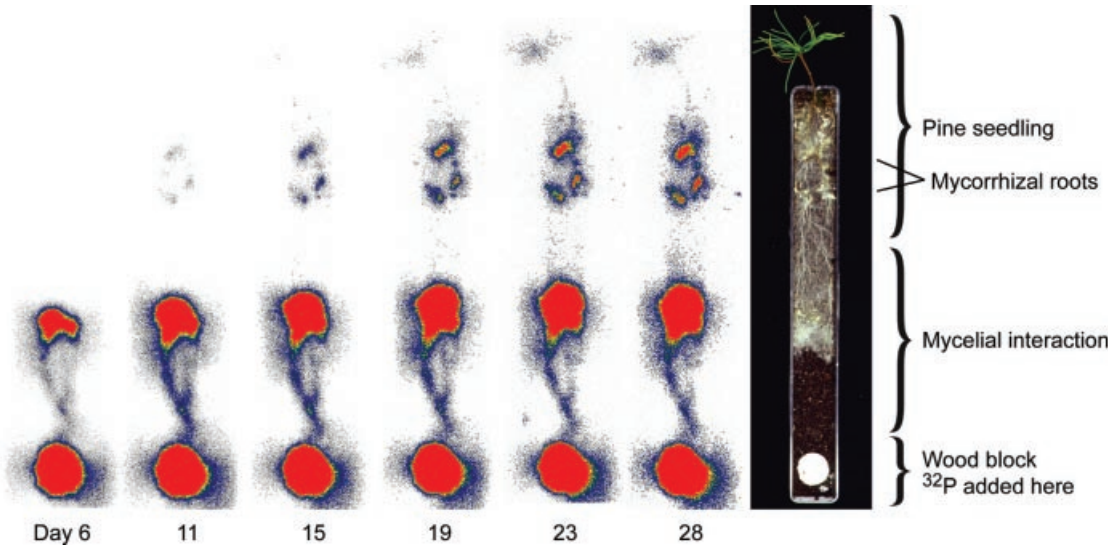

Fig 4 Autoradiographic images and photo of a soil microcosm containing interacting mycelia of *Suillus variegatus*, growing from pine roots and *Hypholoma fasciculare*, growing from a wood block. A patch of dense mycorrhizal mycelium is formed in the area where the two interacting mycelia overlap. The figure shows a time sequence of the spatial distribution of radioactivity in the microcosm following addition of ^{32}P. Blue-yellow-red colours represent increasing levels of radioactivity with the colour scale adjusted to correct for isotope decay. Following addition of ^{32}P to the mycelium colonising the wood block (day 0), label was rapidly detected in the saprotrophic soil mycelium. After 11 days, radioactivity could be detected in the mycorrhizal roots. One month after ^{32}P addition, on average 13% of the activity in the saprotrophic soil mycelium had been transferred to the mycorrhizal seedlings, and radioactivity could be detected in the plant shoots (from Lindahl *et al.*, 1999, with permission).

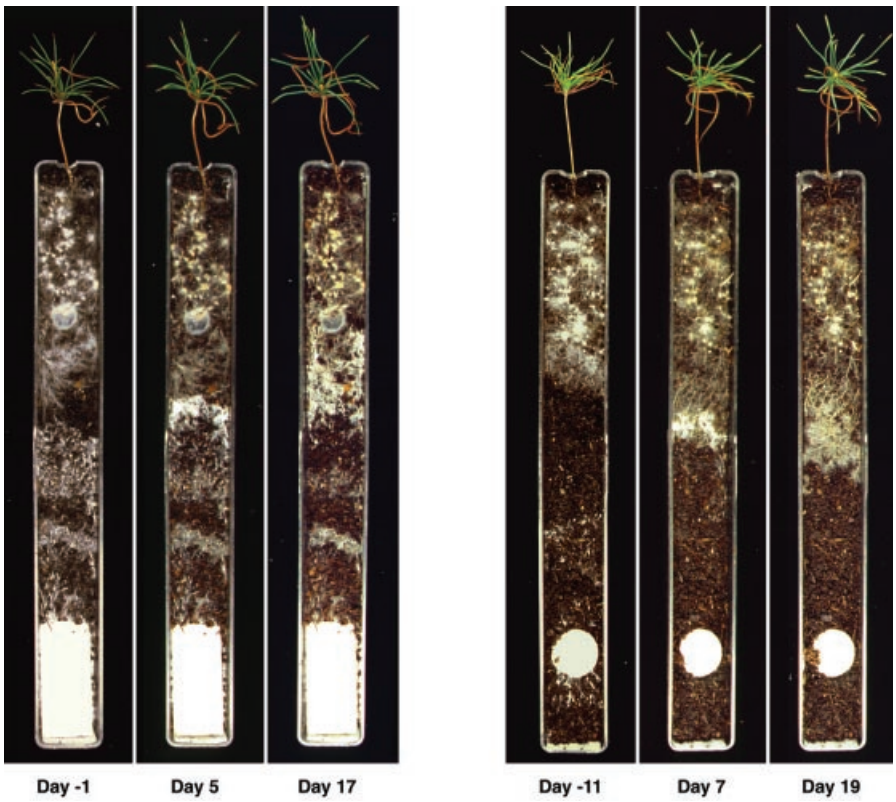

Fig 5 Time series of photographs of two soil microcosms with interacting mycelia of *Suillus variegatus*, growing from pine roots, and *Hypholoma fasciculare*, growing from differently sized wood blocks. Day 0 represents the day of physical contact between the two mycelia. Soon after mycelial contact, a morphological interaction response could be observed in both systems, with the wood decomposer forming a dense mycelial barrier at the site of interaction with the mycorrhizal mycelium. Left: When the saprotroph was supplied with a larger wood block, it overgrew the mycorrhizal mycelium with a dense mycelial patch. Right: When the saprotroph was supplied with a smaller wood block, it was overgrown by a dense patch of mycorrhizal mycelium (Lindahl *et al.*, 2001b, with permission).

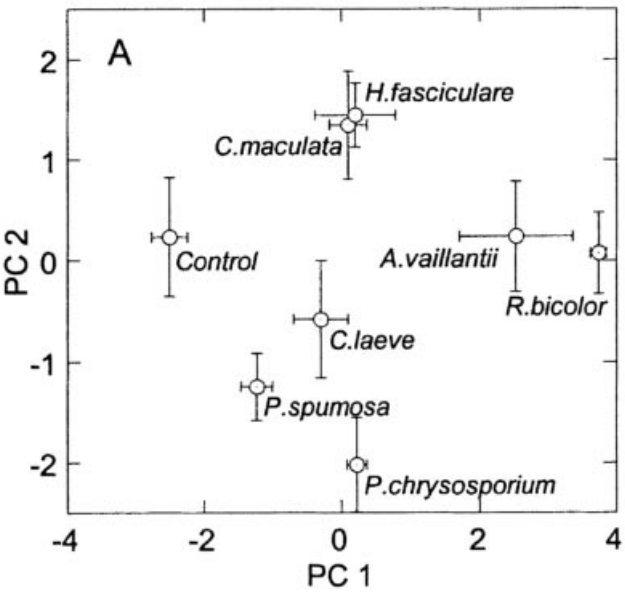

Fig 6 Principal component analysis (PC axis 1 and 2) of bacterial communities in soil samples inoculated with different wood-decomposing fungi (mean and standard error bars, n =6). The analysis is based on the occurance of different bacterial phospholipid fatty acids (PLFAs) in the soil. The control represents PLFA composition in non-inoculated soil (from Tornberg *et al*., 2003 with permission).

Phanerochaete velutina, growing out from wood blocks. In systems with *P. velutina* present, the rate of ^{14}C translocation to the extraradical mycelium of *S. bovinus* was much lower than in systems where the ectomycorrhizal fungus was growing alone. Presumably, the presence of the competing saprotroph prevented the build-up of mycelial impact by the mycorrhizal fungus, thereby reducing the sink strength of the extraradical mycelium.

Source-sink interactions

Whether a mycelial sub-unit constitutes a net source or a net sink for resources depends on the relation between its source strength and its sink strength. If the uptake of resources together with mobilisation from storage reserves is more rapid than the sum of exudation, respiration and incorporation of resources into structural tissues, the sub-unit is a net source and may support other parts of the mycelium with resources. If the sub-unit is a net sink, however, it will be dependent on translocation of resources from other part of the mycelium to maintain its activities. The relation between source strength and sink strength changes during the colonisation and exploitation of a substrate. High initial sink strength admits the rapid build-up of a high mycelial impact within the substrate. Due to efficient exploitation of the substrate and a high competitive ability, a high mycelial impact results in a high source strength. There is, however, a lag in time between the investment - high initial sink strength, and the profit - subsequent high source strength. A mycelial sub-unit is thus likely to be a net sink for resources during the establishment in a substrate, but a net source once exploitation of the substrate has intensified.

Wells *et al*. (1998) introduced wood blocks sequentially to soil microcosms containing mycelia of *Phanerochaete velutina*. Radioactive phosphorus (^{32}P) was supplied to the fungus at centrally located colonised wood blocks, and the dispersal of radioactivity throughout the mycelia was monitored over time. Mycelium in recently colonised wood blocks accumulated ^{32}P, and the accumulation rate was highest in wood blocks that had been colonised for 40-50 days. Thereafter, the ^{32}P accumulation rate decreased, as degradation progressed. Mycelium in wood blocks that had been colonised for more than 80-90 days exported ^{32}P that had earlier been accumulated. The source-sink dynamics for ^{32}P, added at one part of the mycelium, do not accurately reflect the source-sink dynamics for non-labelled phosphorus (Lindahl *et al*., 2001a). Still, this experiment demonstrates how mycelium in recently colonised wood may be a sink for a substance but turn into a source, as degradation progresses. In field experiments, where plant litter is incubated in nylon mesh bags on the forest floor, import of nitrogen and phosphorus into the litterbags is commonly observed at early stages of decomposition, while at later stages of decomposition, these elements are exported from the litterbags (e.g. Staaf & Berg, 1982).

Finlay & Read (1986) found that ^{14}C, initially supplied as $^{14}CO_2$ to the shoot of an ectomycorrhizal pine seedling, accumulated in the mycorrhizal roots of another seedling connected to the labelled seedling by a common ectomycorrhizal mycelium. More radioactivity accumulated in the mycorrhizal roots of the seedling that were shaded, indicating an increased dependence on carbohydrates translocated from other parts of the mycelium, as the local supply was diminished.

Dowson *et al*. (1989) observed mycelia of the wood degrading fungi *Phanerochaete velutina* and *Hypholoma fasciculare*, as they grew out from wood blocks into soil microcosms. When the mycelium encountered a fresh substrate (wood, leaves or needles), most of the mycelium in the soil regressed, leaving only a thick mycelial cord connecting the fresh substrate to the initial wood block. Presumably, the large sink strength, associated with the build-up of mycelial impact in the recently colonised substrate, decreased the resource

availability in other parts of the mycelium, preventing further growth.

Eventually, as the quality of the substrate decreases due to resource depletion, the source strength decreases and the resource unit is expended. By degrading structural components into mobile LMW compounds and replacing the cytoplasm with vacuoles, the senescing mycelium maintains a source strength, which, in combination with minimal sink strength, leads to net translocation out of the mycelium. By doing so, the fungus minimises losses of valuable resources associated with mycelial death, in much the same way as deciduous trees withdraw resources from leaves before abscission. This is exemplified by conidiation in *Aspergillus nidulans* which is triggered when the substrate is finished. As the conidia are formed, the vegetative mycelium becomes a net source and vacuolizes. The vacuolization process show similarities to programmed cell death in animal cells, since caspase-like protease activity is initiated during the process (Thrane *et al*., 2004). It can thus be assumed that the recycling of resources in filamentous fungi involves both programmed cell death and the recycling of cell constituents through the general eukaryotic process of autophagy, which has been extensively studied in yeast (Klionsky & Emr, 2000).

Interaction between different resources such as C and N

In order to simplify the discussion above, mainly carbohydrates have been considered as desirable resources. A fungus, however, needs more than carbohydrates to grow and survive. Mycelial sub-units with high carbohydrate source strength do not necessarily have high source strength with respect to nitrogen or phosphorus.

Olsson (1995) cultivated fungi on agar in oblong Petri dishes. The agar contained opposing concentration gradients of glucose and nitrogen, so that one end of the dishes had a high concentration of glucose while the other end had a high concentration of nitrogen. By translocating carbohydrates to the mycelium growing on glucose deficient medium, and nitrogen to the mycelium growing on nitrogen deficient medium, many of the tested fungi were able to grow well throughout the whole dishes. Other fungi were unable to translocate and only grew in the middle parts of the dishes, where both glucose and nitrogen were present.

Spatial separation of sources for carbohydrate and mineral nutrients is most obvious in mycorrhizal fungi, where the mycorrhizal root tips usually are net sources for carbohydrates, while a high nitrogen and phosphorus source strength may be achieved primarily in the extraradical mycelium. Mycelium within mycorrhizal root tips usually turns into a net source for carbohydrates, once a high mycelial impact in the form of a high colonisation level is achieved within the root, but remains a net sink for mineral nutrients for all its lifespan, due to the high sink strength caused by nutrient transfer to the host plant. In contrast, hyphae within the extraradical mycelium of mycorrhizal fungi remain net sinks for carbohydrates for all their lifespan, but may turn into net sources for mineral nutrients such as phosphorus and nitrogen, once a high mycelial impact is achieved within the soil.

Conclusions

Many fungi translocate resources, such as carbohydrates, amino acids and phosphate, throughout their mycelia. Translocation enables growth and activity in substrates where available resources are scarce or absent. Fungi may use translocated resources to build up 'mycelial impact' in a substrate, thereby conditioning the substrate to increase resource availability. A high mycelial impact also enables fungi to interact with other microorganisms; to interfere with other fungi in order to monopolise the substrate, and to modify the composition of the bacterial community. The capacity to translocate makes fungi well adapted to colonise solid substrates where diffusion and mixing is limited. The benefit of translocation is likely to be highest in environments with a high degree of spatial heterogeneity, such as forest soils. A wider knowledge and recognition of how, when and where fungal translocation takes place may radically change established models of processes where fungi are involved, such as decomposition, plant nutrition and plant disease (Lindahl *et al*., 2002), and may eventually lead to a better understanding of fungus-dominated ecosystems.

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