

Interactions between soil structure and fungi

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The spatial organisation of soils is crucially important in affecting belowground function, and the associated delivery of ecosystem services. Fungi constitute an important part of the soil biomass. As well as playing key roles in nutrient cycling and biotic interactions, they are also intimately involved in soil structural dynamics. Fungi mediate the formation of soil structure at a variety of spatial scales via charge, adhesive and enmeshment mechanisms. They also produce large quantities of hydrophobic compounds that affect water infiltration properties of soils. Fungi can also destroy soil structure via decomposition of organic matter that affects soil aggregation. In turn, soil structure affects fungi. The filamentous growth-form of fungi is a very efficient space-filling structure well adapted for life in a spatially heterogeneous environment such as soil, but the labyrinthine pore network ultimately regulates how fungal mycelia grow through and function within the soil. The distribution of water within soils plays a crucial role in governing fungal development and activity, as does the spatial distribution of nutrient resources. This article reviews the continual interplay that occurs between soil structure and fungi, and discusses how self-organisation mechanisms may operate in the soil system.

Keywords: soil structure, fungi, spatial organisation, foraging, hydrophobicity, biological thin section

Introduction

Life in earth is crucial for life on Earth. The wide range of organisms that inhabit soil play important roles in driving many of the key terrestrial biogeochemical cycles that underwrite primary production, via the provision of mineral nutrients to plants. The principles by which such cycles are intimately linked to fixed forms of carbon which fuel heterotrophic biological activity are well understood, and the important roles that fungi play in decomposition and cycling processes is acknowledged. However, the role that fungi play in defining the soil habitat, as a living space for all soil biota, is less appreciated but no less important. This article reviews current understanding of how fungi affect soil structural dynamics, and how the architecture of the soil in turn affects the ecology of soil fungi.

The soil habitat

The physical habitat in which all soil life resides and functions is defined by the pore networks which arise as a consequence of the spatial arrangement of the solid phases of the soil. The solid phases are comprised of

durable materials such as sand, silt and clay particles, derived from parent material, and less persistent organic matter predominantly derived from plant and animal inputs. Soil structure arises as a consequence of these components being joined together by a variety of mechanisms, a process often described as soil aggregation. As physical forces such as wet:dry and freeze:thaw cycles cause shrinkage and swelling of the soil, planes of weakness result in fracturing and the development of voids within the soil mass. Bonding forces tend to be stronger at smaller size scales, leading to an inherent hierarchy in the stability of bonded material across scale. A natural consequence of this is that over time networks of pores develop, which vary widely in their dimensions, and are ultimately always connected at some scale. The soil pore network is hence a spatially complex 3-dimensional labyrinth that forms the physical framework in and through which all soil processes occur. Since the network regulates the movement of gases, liquids, solutes, particulates and organisms, and the majority of soil processes rely upon such dynamics, soil structure plays a fundamental role in governing many soil functions.

Fungal morphology

The growth-form of filamentous (eucarpic) fungi is a

particularly effective adaptation to life in a physically structured environment such as soil. The vegetative mycelium is above all a spatially extensive structure, with a growth habit based upon hyphal extension and branching. The mycelium is hence an indeterminate structure in contrast to the precisely defined forms that, for example, soil fauna take. Hyphae grow across surfaces, absorbing nutrients from the substratum, but are also capable of growing through air and hence bridge soil pores with apparent ease (Fig 1). This simple growth form underwrites effective foraging strategies and enables sparse explorative growth where substrate is absent and a denser exploitative growth where nutrition is available. These principles apply both to saprophytes, where substrate is a variety of organic matter, and to mutualists or antagonists, where nutritional resources range from plant roots to fauna. Such responses are manifest by the majority of eucarpic species, but the most sophisticated foraging

strategies are present in the wood-decomposing basidiomycetes. Species that utilise spatially discrete resources on the woodland floor such as fallen twigs and branches form specialised foraging cords capable of fast and very extensive explorative growth, across many decametres in some instances. When pieces of wood are encountered, there is a distinct switch to a dense exploitative growth as the resource is colonised and degraded, and there is often an associated degeneration of foraging cords, with an internal recycling of nutrients within the mycelia. Other forms that utilise the more amorphous leaf litter as substrate have a mycelial form where a more or less continuous exploitative growth front permeates the litter layer, with degeneration in exploited litter behind, leading to the formation of annular mycelia more quaintly known as fairy-rings. Such growth habitats are not confined to woodlands and forests: straw-decomposing cord-formers occur in arable fields, and fairy-rings are well-

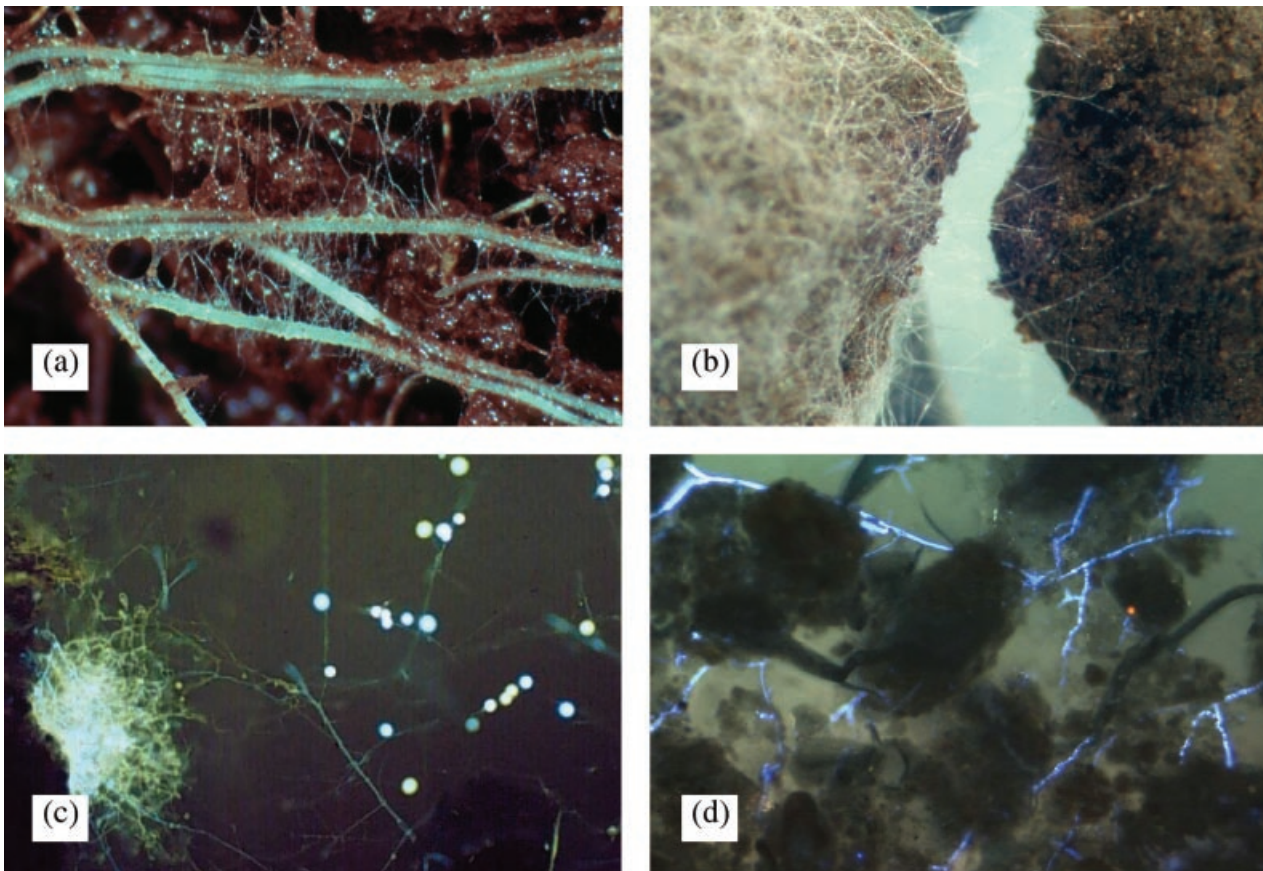


Fig 1 Fungal mycelia in the soil environment. (a) Unidentified hyphae bridging roots of *Plantago lanceolata* growing in non-sterile field soil. Note abundance of mucilage films. Image width = 2 cm. (b) Hyphae of *Fusarium oxysporum* f. sp. *raphani* colonising a pair of adjacent soil aggregates. Aggregate on left is sterile, hence extensive mycelial development. Aggregate on right is non-sterile; reduced mycelial growth is due to competitive effects of indigenous microflora and reduced nutrient levels therein. Image width = 1 cm. (c) Unidentified mycelium growing in soil pore, visualised in thin-section of undisturbed pasture soil, stained with Fluorescent Brightener 28. Note proliferation of hyphae on pore wall in left of image. Bright spherical objects are sporangia. UV epifluorescent illumination. Image width = 150 μ m. (d) Mycelium of *Rhizoctonia solani* growing in sterilised arable soil, visualised in thin-section stained with SCRI Renaissance 2200. UV epifluorescent illumination. Image width = 150 μ m. (Image sources: the authors)

known phenomena in grasslands.

The soil biomass is predominantly microbial in constitution, with the proportion that is fungal varying widely between soils and associated land-use. As a broad generalisation, soils with high organic matter content, little physical disturbance or low nutrient inputs tend to be fungal dominated, whilst the biomass in frequently tilled soils that receive high inorganic fertiliser inputs is dominated by bacteria. While the biomass of fungi in soils can range from of the order 50-1000 $\mu\text{g g}^{-1}$ dry weight (equivalent to 2-45 t ha^{-1}) or above, such values belie the potential spatial extent of mycelia, arising from associated hyphal lengths. Due to their microscopic diameters, a few μg of hyphae can be several metres long. Direct measurements of hyphal length by microscopy of dispersed soils are of the order 10^2 , 10^3 and 10^4 m g^{-1} for arable, pasture and forest topsoils respectively (e.g.; West, 1988; Frey *et al.*, 1999; Osono *et al.*, 2003). A consequence of the highly branched nature of most mycelia is that the surface area to volume ratio of the organism is relatively high compared to morphologically determinate (more or less fixed morphology) microbes such as bacteria. Another important feature of the mycelium is that since it is effectively an interconnected tubular network, materials can be transported within hyphae between different regions of the mycelium. Such translocation is fundamental to the ability of fungi to grow through nutrient-impooverished zones and through air, for internal recycling of nutrients during degenerative phases, and nutrient supply to reproductive structures.

How fungi affect soil structure

Fungi affect the formation of soil structure (structural genesis) directly and indirectly, via a variety of biochemical and biophysical mechanisms. A vital, often overlooked, aspect of soil structure and biota interactions relates to the soils propensity to crack, and thus create voids, as described above. At a fundamental physical level, the creation of cracks in soils is strongly related to the content and type of clay (with 2:1 minerals having a greater ability to shrink and swell in comparison to 1:1 minerals). However, fungi also clearly modulate cracking properties of soils, as can be demonstrated using experimentally-controlled systems (Fig. 2).

Direct biophysical effects of fungi on soil structure are manifest at two spatial scales. At the μm scale, the physical extension of hyphae through soil can cause a mechanical disturbance and realignment of particulate materials. This can be particularly apparent with clay platelets, where surface charge phenomena may also

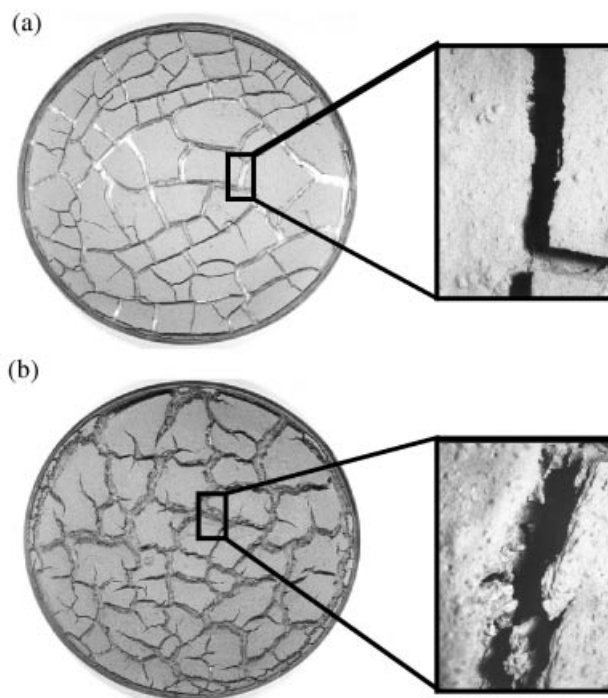


Fig 2 The impact of a fungus upon soil structural generation in a non-sterile soil slurry following drying: (a) uninoculated soil; (b) soil inoculated with *Trichoderma viride*. The fungus induces a more varied structure, manifest as greater variability in topography and in crack formation. The latter is illustrated in the enlarged boxed images from each system. Diameter of dish = 9 cm. (Image source: the authors)

interact to cause the formation of narrow clay-lined channels when the hyphae that acted as nucleation zones subsequently decompose (Fig. 3). Plant roots can mediate a similar effect, but at a larger spatial scale.

At a larger scale, mycelial networks bind soil together by hyphal entanglement. This mechanism is well recognised in principle, but there is little work that

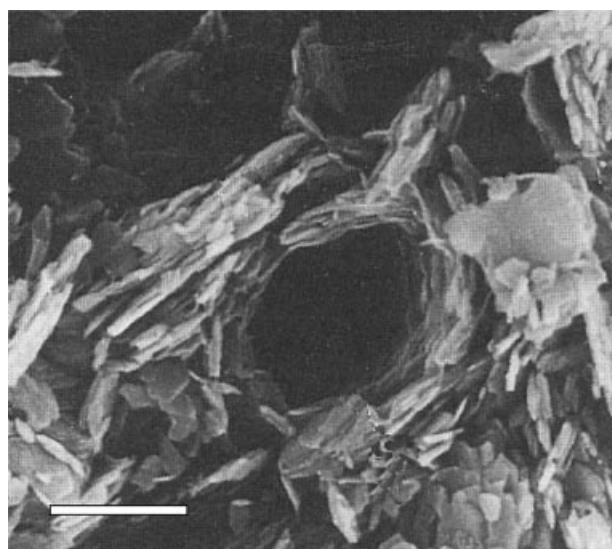


Fig 3 Orientation of kaolinite clay platelets by hyphae of *Chaetomium* sp. Scale bar = 2 μm . (Image source: Dorioz *et al.* 1993, with permission)

has analysed the detailed biophysics of the phenomenon in soil environments. A clear demonstration of the principle was provided by Meadows *et al.* (1994), who showed that *Penicillium chrysogenum* significantly increased the slope stability of experimentally inclinable beds of pure sand, and when slopes failed, hyphal trails enmeshing sand were visible. Similar phenomena under natural conditions can be observed in sand dunes. It is likely that there is a relationship between mycelial density and the efficacy of such binding, and mycelial density can vary greatly over small distances in soil (Fig. 1c). The tensile strength of individual (isolated) soil-grown hyphae is apparently unknown, but is likely to be relatively low since the hyphal structure has not necessarily evolved to possess high tensile strength, in contrast to the silks produced by invertebrates that are used in the construction of cocoons and webs. *In vitro* measures have demonstrated that hyphal aggregations grown in batch fermentation systems show changes in tensile strength over time, associated with physiological development of the mycelia (Li *et al.*, 2002). There may be a relationship between nutritional status of soils and hyphal enmeshment since mycelia will generally be denser where resources are more available, due to the mycelial foraging responses described above. Heterogeneously distributed substrate may therefore result in a localisation of soil binding by entanglement mechanisms.

Like many prokaryotes, fungi exude a wide range of compounds into their immediate environment. These include enzymes responsible for decomposing their substrates into simpler forms for subsequent uptake and utilisation, and polysaccharide and glycoprotein mucilages which form a protective and lubricating matrix around hyphae, particularly the tips. These compounds often have adhesive properties which serve to stick soil components together. Fungal glue thus provides a primary mechanism of soil aggregation. Whilst this principle is understood, we know little about the actual adhesive mechanisms of such compounds and their durability. It is likely that these compounds will have widely varying decomposition rates depending on their chemical structure and nutritional value to other soil organisms.

Due to the large surface area to volume ratio of the fungal mycelium, there is a particular requirement for hyphae to be well insulated from the external environment, to enable cellular homeostasis without the expenditure of prohibitive amounts of metabolic energy, particularly in relation to water. Hence fungi produce large quantities of insulating compounds in the outer wall of hyphae and a proportion of these are

invariably deposited into the soil matrix. These insulating compounds, such as melanins, are hydrophobic, sometimes strikingly so, and generally resistant to decomposition. A specific sub-class of such compounds are termed hydrophobins, which carry out a range of functional roles by mediating the hydrophobicity (water repellency) of hyphae, including aspects of morphogenesis, attachment to surfaces, and can act as elicitors in biotic interactions (Wosten, 2001). Such hydrophobic compounds can affect the rate of water infiltration into soils. Work by Hallett *et al.* (2001) using biocides to suppress fungi or bacteria, suggests that the main contribution to hydrophobicity in soils arises from the fungal community, although it is likely that hydrophobic compounds may be derived from a range of biological and non-biological sources. White *et al.* (2000) demonstrated that an increase in sub-critical repellency of a soil was strongly correlated to the growth of the basidiomycetes *Coriolus versicolor* and *Phanerochaete chrysosporium* within it.

Glomalin is a recently-characterised hydrophobic compound produced exclusively by arbuscular mycorrhizal (AM) fungi. First isolated and described by Wright & Upadhyaya (1996), it is a particularly resistant glycoprotein that is apparently abundant in a wide range of soils, and had been previously overlooked due to the specific and harsh extraction procedures required to quantify it. The subsequent development of glomalin-specific monoclonal antibodies has enabled both ELISA-based quantification and direct visualisation of the compound in soils (Wright, 2000). Application of fluorescently-labelled antibodies has revealed that abundant and extensive deposition of glomalin can occur in soils, notably on aggregate surfaces (Fig 4). Substantial quantities of glomalin have been measured in some soils, to the extent that the compound can constitute a significant proportion of total soil organic matter. For example Rillig *et al.* (2001) estimated glomalin-derived C and N constituted 4-5% of total pools of these elements in tropical forest soils. A correlation between glomalin concentration and aggregate stability has been demonstrated across a range of soils (Wright *et al.*, 1999), but any causal relationship has yet to be demonstrated. *In vitro* studies using glass beads of differing sizes have demonstrated that the quantitative amount of glomalin produced is sensitive to environmental conditions, with greater production induced under circumstances where habitat space is restricted (Rillig & Steinberg, 2002). It is hypothesised that this response may be conducive to physically structuring the environment to the advantage of the fungus via glomalin-mediated binding of structural particles, along the lines of the self-

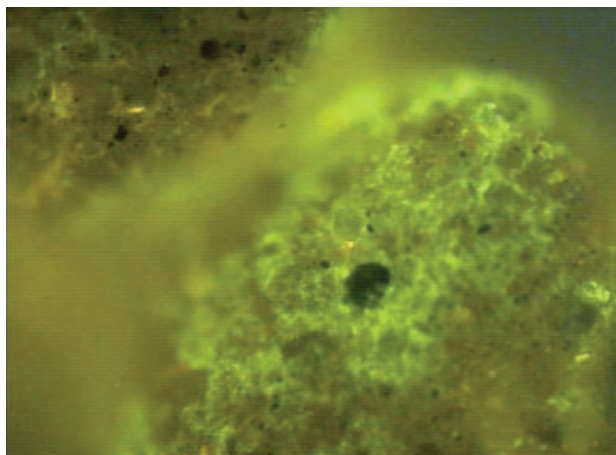


Fig 4 Glomalin, visible as green fluorescence after treatment of the soil with labelled monoclonal antibody, coats the surface of a soil aggregate. (Image source: courtesy of Sara Wright, USDA).

organisation hypothesis described below. This has yet to be proven in soil systems. It is not yet known precisely how glomalin affects soil structure, but it is likely that effects are mediated via modulation of water sorptivity and repellency as well as via adhesive mechanisms. However, there are as yet no reports of a direct correlation between glomalin concentrations and soil hydrophobicity, so the main causal mechanism is untested. The chemical nature of glomalin and exactly how it should be measured is still unclear. Nevertheless, glomalin shows potential as a bioindicator of soil structural quality, and such a diagnostic would be a highly desirable tool for application in environmental monitoring.

The organic matter that binds soil together is derived from a wide variety of sources; as we have described, compounds produced specifically by fungi constitute a proportion of such material, but other sources include bacteria, fauna, and plant material both from roots and aboveground parts incorporated into the soil via the action of fauna or cultivation. Crucially, such organic material also represents nutritional substrate for soil organisms, and if they decompose it there is an associated potential for structural degeneration. In this way, fungi (along with other decomposer organisms) can destroy as well as form soil structure. Hence there is a continual dynamic between the activity of soil fungi and the structural form of their habitat.

How soil structure affects fungi

As described in the Introduction, it is the pore network that fundamentally governs how organisms operate in the soil. The reticulate nature of the pore network and

the generally patchy distribution of organic matter (particularly at the microbial scale) means that distances between food resources can be substantially increased compared to their literal distance in three-dimensions. This has large implications for foraging patterns in soil organisms, since energy expenditure increases with distance. Otten & Gilligan (1998) have demonstrated the importance of geometry to soil fungi, showing how the distances covered by *Rhizoctonia solani*, when reliant upon a point-source of substrate, decrease markedly in the three-dimensions of a soil volume as opposed to more or less planar growth across a soil surface. The intrinsic bulk density of the soil can also have a large big impact upon the extent of fungal growth. At greater bulk density, there are fewer larger pores, and a smaller net pore volume. Intuitively, one might hypothesise that higher bulk densities, with concomitantly less pore volume, would tend to curtail biota, but it appears that this is not necessarily the case for microbes. Harris *et al.* (2003) demonstrated that the extent of colonisation of an arable soil by *Rhizoctonia solani* was reduced at lower bulk densities (Fig 5).

There is a crucial second factor that regulates the soil biota, which is water. All soil microbes are aquatic in the sense that they require the presence of moisture to function. Prokaryotes, protozoa and nematodes require water films for motility, unlike sessile eucarpic fungi which generally deal with such spatial matters via the mycelium, as we have discussed. Water distribution in soils is also fundamentally governed by the pore network, and described by the so-called moisture release characteristic. The basic principle here is that water is held more strongly in small pores compared to large ones, such that when suction is applied via drainage, large pores will become air-filled sooner. Crucially for life, gas diffusion in water is orders of magnitude slower than in air, and hence even extremely thin films of water occluding small pores will act as valves, curtailing gas exchange within the local volume of soil. If microbial activity is high in such circumstances, then microaerophilic or anaerobic microsites may develop, curtailing microbial activity. Air-filled pore volume is a significant factor in dictating fungal spread in soils, with fungi apparently less able to grow where air-filled porosity is reduced (Otten *et al.*, 1999).

When growing in porous media, the mycelium is intrinsically a three-dimensional space-filling structure. Hence it might be expected that the orientation of pores might have little impact upon fungal growth in soils. However, there is an inherent polarity to hyphal growth, and Otten *et al.* (2004) have demonstrated how the size and orientation of pores

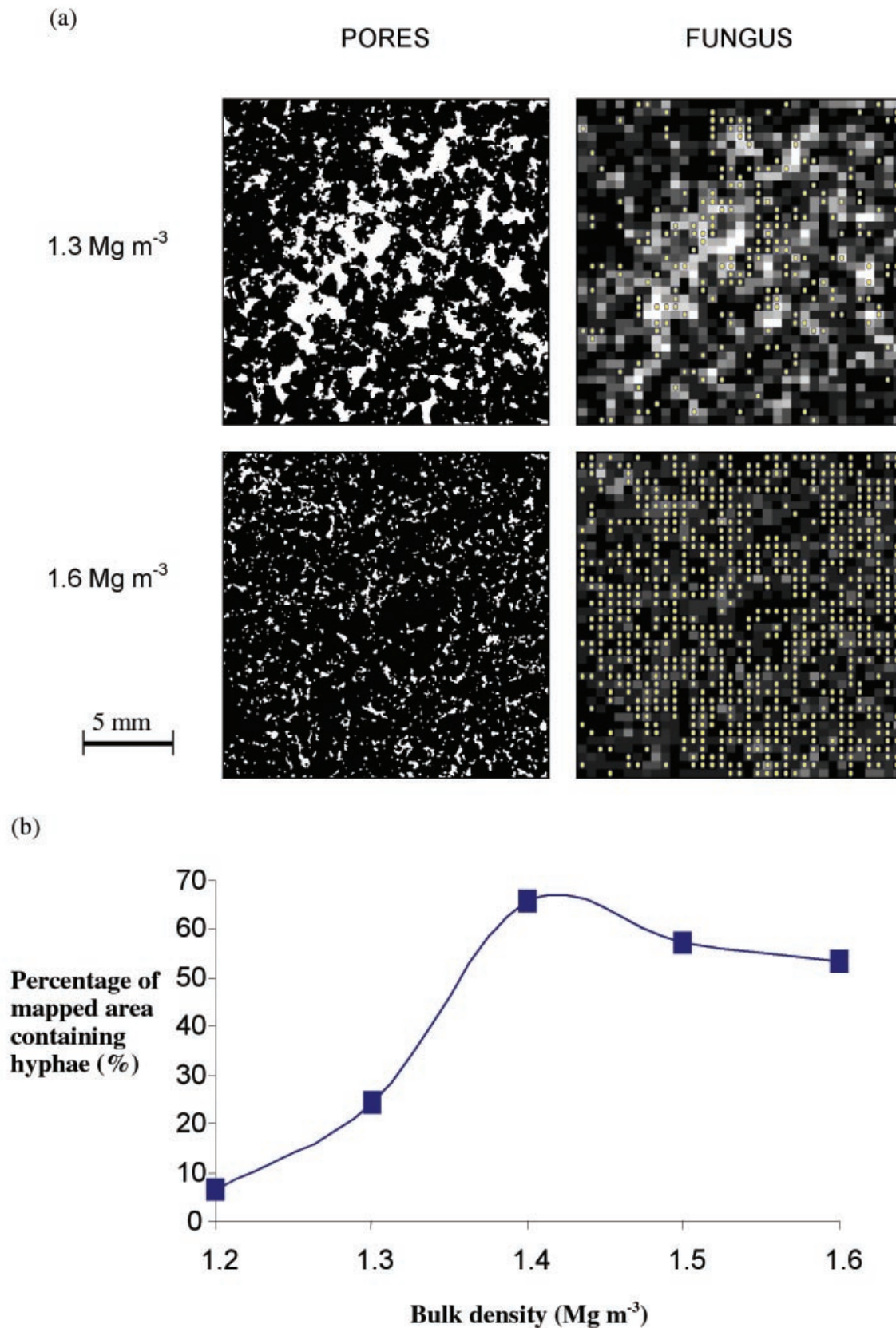


Fig 5 Effect of bulk density upon spatial organisation of *Rhizoctonia solani* grown in sterilised soil. (a) Maps of pore networks (left column) and associated distribution of hyphae (right column) as visualised in thin-sections of soil. In fungal maps, yellow spots denote presence of hyphae in underlying region of the section; grey scale relates to mean porosity in associated region (black=>90% porosity, white =<10% porosity). (b) Relationship between bulk density and fungal extent. (Derived from Harris *et al.* (2002))

affects the growth of *R. solani* in porous media. Using an experimental system where synthetic macropores were introduced into sand and soil microcosms, they showed how growth *along* such macropores was significantly greater than growth *across* (i.e. tangential to the primary growth front). This suggests that while hyphae can bridge air-gaps in pore networks, there may be a metabolic cost associated with such growth, and that ultimately surface-associated growth is more efficient. This may be related to more efficient nutrient acquisition via contact with the substratum. Aerial growth requires substrate delivery to the growing tip more or less exclusively via translocation. These observations are important in considering how soil structure might modulate the growth of soil fungi; for example, in the context of the epidemiology of plant disease caused by *R. solani* (Otten *et al.*, 2004).

Soil structure can confer physical protection to organisms via size exclusion mechanisms. Fungal hyphae are consumed by a variety of nematodes, insects, mites and worms. If hyphae are located in soil pores that are smaller than the body size of such grazing organisms, they will be protected from ingestion. Grazers may also be excluded from pores that could otherwise accommodate them if connecting pores are too small to permit entry. The indeterminate nature of fungal mycelia means that it is highly unlikely a mycelium will be entirely consumed by grazing, since it is inevitable that some hyphal fractions will be physically protected by soil structure. As is the case for other aspects of fungal growth in soils, these principles are understood, but there is little experimental validation of such hypotheses.

Fungi can show remarkably sensitive responses to the physical structure of their local environments. For example, developmental responses in foliar pathogens have been demonstrated where the production of infection structures is clearly induced by the local topology of the physical surface. Using artificially constructed surfaces it was found that topographical signals alone could induce a reproducibly high percentage (83-86%) of germ tubes to differentiate to form infection structures (Read *et al.*, 1997). There are no reports of thigmotropic responses in soil fungi, but given the nature of the soil habitat we hypothesise such phenomena are likely. A striking example of physically-appropriate organisation we have observed in an arable soil relates to the positioning of the orifice of a perithecium in a root (Fig 6).

Soil tillage is a management practice in agriculture that affects soil structure and hence modifies the physical environment of the soil biota (for review, see Young & Ritz, 2000). Physically disruptive and

repetitive tillage practices generally result in reduced fungal biomass due to repeated disruption of mycelia which compromises fungal integrity. Excessive tillage often results in a general degeneration of soil structure due to enhanced decomposition of organic matter, principally by bacteria, driven by the removal of physical protection mechanisms. The corollary is that reduced or no-till systems tend to be fungal dominated, with an associated fungal basis to structural generation and integrity. This demonstrates how manipulation of soil structure provides a means of managing soil communities via a modification of habitat space.

Conclusions

Mankind has relied upon soil for millennia, and will continue to do so for the duration. Since the development of farming and the associated foundation of civilisations, we have developed reasonably sophisticated systems by which we can grow crops at the yield and quality that we demand. However, the generally accepted view is that the ecosystems that modern farming methods have produced are detrimental to the sustainability of a productive soil ecosystem: we have unequivocal increases in erosion (once lost the soil is effectively gone forever), and increases in soil compaction leading to significantly reduced yields. Fungi have an important role to play in underwriting the sustainable management of soils, as we have discussed in this article. However, as we have also highlighted, there are many gaps in our detailed understanding of the mechanisms governing the feed-forward and feed-back processes that occur between fungi and the wider physical, chemical and biological

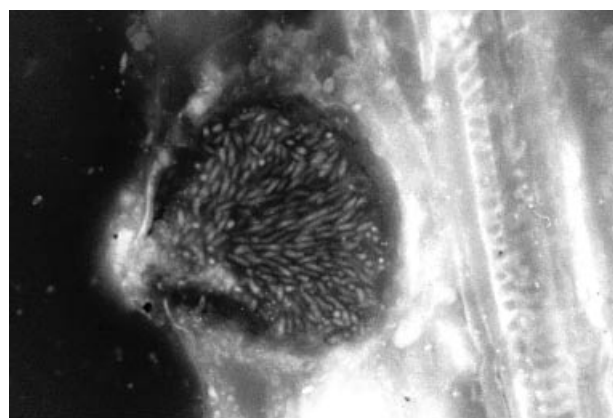


Fig 6 Perithecium of unidentified fungal species in cortex of root, visualised in thin-section of undisturbed grassland soil. Root vascular tissue is to right of image. Note alignment of the perithecial pore toward the soil pore, with the consequence that released spores stand a greater probability of dispersion through the soil, via transmission through the pore network. Image width = 120 μm . (Image source: the authors)

properties of soils.

There is the intriguing possibility that fungi are implicated in the self-organisation of soil systems. Consider the situation of a sterile soil. Initially devoid of life but containing potential substrate, the three-dimensional arrangement of the pores and their connectivity constrain the flow paths, and reactive sites of fluids and gases. Now into this sterile environment we add fungi. With sufficient substrate, the fungal biomass increases, as does the production of exudates. Within a short time, probably within a day or so, the microstructure is altered both in geometry and with increased stability. The fungi at this stage act as interior architects, and painters and decorators; painting proteins onto the walls of pores and altering the pore shape and design. This will have an immediate impact on the pore geometry and connectivity which will lead to a significant alteration in the structure's ability to retain water and the rate at which fluids and gases are transported through the system. In essence the fungi have altered the energy pathways of their own environment and thus within a relatively short time span, they will then have to react to the different environment that they have created. Thus, they self-regulate their own environment. These concepts provide a new framework to think about soil structure-biota interactions, as it offers a more mechanistic approach to the management of the soil ecosystem.

To conclude, we will put these concepts beyond Earth. It is not trite to postulate that to take advantage of the recent observations on Mars by the planetary rover Spirit, of seemingly sterile loose soil, the promise of planetary colonisation will require such a new conceptual grasp of Earth's soil resource in order that we can start to plant the planets. The key to the exploration of planets has as much to do with the ability of soil being able to sustain life in it, as it has to do with rocket science. Interplanetary mycology might have a future!

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