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Review

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Mycorrhizas and soil structure

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Contents

Summary

Key words: arbuscular mycorrhizas (AM), glomalin-related soil protein, hydrophobins, microaggregate, plant and microbial communities, root system, soil mycelium, soil structure.

In addition to their well-recognized roles in plant nutrition and communities, mycorrhizas can influence the key ecosystem process of soil aggregation. Here we review the contribution of mycorrhizas, mostly focused on arbuscular mycorrhizal fungi (AMF), to soil structure at various hierarchical levels: plant community; individual root; and the soil mycelium. There are a suite of mechanisms by which mycorrhizal fungi can influence soil aggregation at each of these various scales. By extension of these mechanisms to the question of fungal diversity, it is recognized that different species or communities of fungi can promote soil aggregation to different degrees. We argue that soil aggregation should be included in a more complete 'multifunctional' perspective of mycorrhizal ecology, and that in-depth understanding of mycorrhizas/soil process relationships will require analyses emphasizing feedbacks between soil structure and mycorrhizas, rather than a unidirectional approach simply addressing mycorrhizal effects on soils. We finish the discussion by highlighting new tools, developments and foci that will probably be crucial in further understanding mycorrhizal contributions to soil structure.

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Fig. 1 Photograph of cottonwood (*Populus trichocarpa*) roots from a riparian area in Montana, USA, showing ectomycorrhizal root tips, fungal mycelium and adhering soil particles.

I. Introduction

The study of the ecology of mycorrhizas has a long tradition, with a historically heavy emphasis on the role of fungi in plant physiology. More recently, the influence of mycorrhizal fungi on plant communities has become an additional focus, and perhaps the next wave of research will aim at quantifying the contribution of these fungi to ecosystem processes (Rillig, 2004a). A salient function of mycorrhizal fungi at the ecosystem scale is their contribution to soil structure (Fig. 1).

Soil structure refers to the three-dimensional arrangement of organic/mineral complexes (aggregates) and pore spaces. This parameter is often indirectly quantified as the size distribution of aggregates or the stability of aggregates exposed to standardized disintegrating forces (Díaz-Zorita *et al.*, 2002). Aggregates are often operationally divided into different microaggregate (< 250 μm) and macroaggregate (> 250 μm diameter) size fractions. In many soils, where organic matter serves as the main binding agent, aggregates are formed in a hierarchical manner from primary particles and organic matter (Tisdall & Oades, 1982).

As the basic setting in which processes in soils take place, soil structure influences many biotic, physical and chemical aspects of soils, reviewed previously (Díaz-Zorita *et al.*, 2002; Six *et al.*, 2004). Most of these are recognized as immediately relevant to the sustainability of agroecosystems. However, soil aggregation is also important in nonagricultural ecosystems, such as in the contexts of restoration of disturbed lands, erosion prevention, global change, or soil carbon storage. It is crucial to realize that soil aggregation may change significantly in natural ecosystems on ecological time scales of a few growing seasons, for example in response to global change factors (Rillig *et al.*, 1999; Niklaus *et al.*, 2003).

Many physical, chemical and biological factors (and their interactions) contribute to soil aggregation, yet among the biological aspects, mycorrhizas are recognized as being of special importance. In this article, we first provide a review of the potential ways by which mycorrhizal fungi can influence soil aggregation in ecosystems at different scales. Subsequent discussion will be largely focused on one aspect of this influence, namely the effects of the fungal mycelium itself, as substantial progress has been made in this area not covered in previous reviews on this general topic (e.g. Tisdall & Oades, 1982; Tisdall, 1991; Miller & Jastrow, 2000; Rillig, 2004b).

Even though ectomycorrhizal fungi were considered along with arbuscular mycorrhizal fungi (AMF) in earlier conceptual contributions (e.g. Tisdall & Oades, 1982), most recent experimental work has focused on the role of AMF in soil structure, and this bias in research is also, by necessity, reflected in this review. However, many of the mechanisms discussed will apply equally to ectomycorrhizas, and important similarities, and some distinctions, between the two mycorrhizal types are also discussed.

II. How mycorrhizal fungi can influence soil aggregation at various scales

A hierarchical perspective is often useful when contemplating mycorrhizal influences on processes (O'Neill *et al.*, 1991; Rillig, 2004a), and soil aggregation is no exception. Mycorrhizal fungi can potentially influence soil aggregation at different levels (Fig. 2), namely plant communities, plant roots (individual host), and effects mediated by the fungal mycelium itself. Different mechanisms are in operation at each of these levels, and these are discussed in the following sections. Even though separated for the sake of presentation, it is important to bear in mind that these processes operate concurrently and in a hierarchical manner.

Not only are mycorrhizal influences on soil aggregation best discussed within a hierarchical framework, but the process of soil aggregation itself is typically viewed in a hierarchical manner (from primary particles to microaggregates and macroaggregates). Following the hierarchical conceptual model of Tisdall & Oades (1982), AMF and other fungi are hypothesized to be important for soil aggregation at the macroaggregate level, where direct hyphal involvement is thought to be most pronounced. Although a number of studies have examined the influence of AMF on macroaggregates (e.g. Miller & Jastrow, 2000; Rillig *et al.*, 2002), much less research has been devoted to the role of mycorrhizal fungi in the formation of microaggregates. Most studies examining microaggregate formation have focused on the importance of particulate organic matter (Oades, 1984; Golchin *et al.*, 1994; Angers *et al.*, 1997; Six *et al.*, 2002) and have largely ignored potentially important mycorrhizal fungal influences on the process. For example, mycorrhizal fungal mycelium products would be expected to influence, directly and strongly, aggregation at scales smaller than the macroaggregate, although direct experimental evidence is sparse. Additionally,

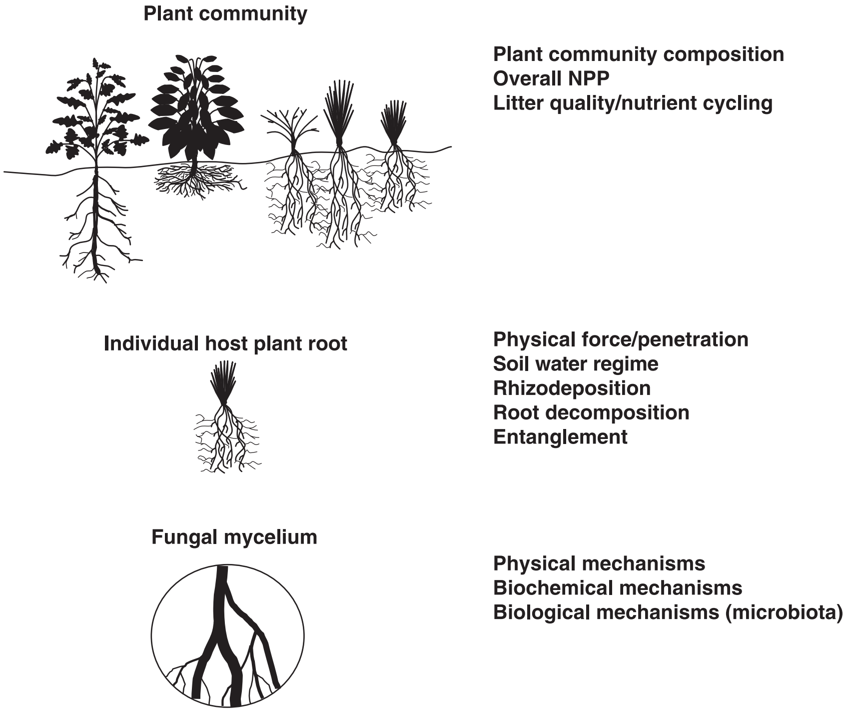

Fig. 2 Conceptual overview of the three main different scales (plant community, individual plant, and mycelium) at which mycorrhizal fungi can influence soil aggregation, as discussed in this article. Also given is a summary of the main parameters to be considered at each level. (NPP, net primary production.)

as microaggregates are thought to form most frequently within macroaggregates, AMF-facilitated stabilization of macroaggregates would be expected to result indirectly in microaggregate formation. The aggregate size hierarchy, and the potential for specific aggregate formation and stabilization mechanisms (biochemical vs biophysical, for example) to act concurrently, at different scales, and at different aggregate formation and degradation stages, is central to the following discussion.

1. Plant communities and primary production

Among the soil fungi, mycorrhizal fungi are prominent through their well-established ability to affect the composition of plant communities (e.g. Grime *et al.*, 1987; van der Heijden *et al.*, 1998; Klironomos *et al.*, 2000), for example through providing differential benefits to their members. Plant species may differ in their effects on soil aggregation, as demonstrated for agriculturally relevant plants and agroecosystems (e.g. Angers & Caron, 1998), and plants from natural communities (e.g. Eviner & Chapin, 2002; Rillig *et al.*, 2002; Piotrowski *et al.*, 2004). As a consequence, changes in plant community composition can translate into effects on soil structure. Additionally, AMF and their diversity have been shown to be important controllers of the productivity of plant communities (e.g. van der Heijden *et al.*, 1998), in part via their effects on plant community composition. Net primary production controls how much carbon may eventually enter the soil, for example as litter or as root growth, and this is, in turn, an important determinant of soil aggregation.

2. Plant roots: individual host level effects

Processes affecting soil structure that are mediated by roots can be grouped into five categories (for detailed discussion see Six *et al.*, 2004): (1) root physical force/penetration; (2) soil water regime alteration; (3) rhizodeposition; (4) root decomposition; and (5) root entanglement of soil particles. By virtue of their influence on plant biomass (or root : shoot ratios), mycorrhizal fungi can influence each of these root processes. In this section, we focus on how mycorrhizal colonization can influence these five aspects and, through them, soil aggregation, irrespective of the effects on root biomass. Many factors will strongly interact synergistically (e.g. rhizodeposition fueling microbial activity, root entanglement providing a physical net, and localized drying increasing contact between particles), and in practice these factors will be difficult to separate experimentally.

Root entanglement and physical force/penetration Root morphology and architecture (e.g. degree of branching, thickness of roots, etc.) influence each of these five mechanisms, perhaps particularly strongly through root entanglement and exertion of physical force. Ectomycorrhizal fungi generally invoke extensive change in root architecture through the formation of a root-tip enveloping mantle (Smith & Read, 1997), hence architectural influences are particularly obvious in this case. The net effect for soil aggregation has not been studied to our knowledge (i.e. is the loss of root surface area inconsequential in view of mycelium proliferation?). That infection with arbuscular mycorrhizas (AM) can result in root morphological changes, albeit comparatively more subtle ones, is known (e.g. Berta *et al.*, 1993) and is the subject of ongoing research to determine both the mechanisms involved and the consequences for plant and ecosystem function (e.g. Berta *et al.*, 2002; Gamalero *et al.*, 2002; Oláh *et al.*, 2005). Roots can create compressive and shear stresses that may reach 2 MPa (Goss, 1991), thus resulting in localized soil compression (Dexter, 1987) and reorientation of clay particles along root surfaces (Dorioz *et al.*, 1993). Localized soil compression serves to eliminate spatial constraints on microaggregate formation (Six *et al.*, 2004). Differences in root architecture also determine the overall influence of root penetration (Carter *et al.*, 1994) and root entanglement (Tisdall & Oades, 1982; Miller & Jastrow, 1990).

Changed soil water regime Soil structure is influenced by soil water content and its variation with time, and plant growth can strongly influence the magnitude and frequency of wetting and drying cycles. Decreased water content typically increases contact points between primary particles and organic matter, resulting in increased soil cohesion and strength (e.g. Horn & Dexter, 1989; Horn *et al.*, 1994). Localized drying of soil, in close proximity to roots, promotes binding between root exudates and clay particles (Reid & Goss, 1982), directly facilitating microaggregate formation. Not only can mycorrhizal fungi influence plant growth overall (and hence soil water regimes), but mycorrhizal plants exhibit different water relations from their nonmycorrhizal counterparts (Augé, 2001, 2004). For example, higher stomatal conductance and transpiration can occur in the mycorrhizal situation (Ebel *et al.*, 1997; Augé *et al.*, 2004). More efficient exploration of water by mycorrhizal fungi may lead to more extreme wet/dry cycles, which could have very strong consequences for soil aggregation (see Six *et al.*, 2004). Additionally, because the symbiosis can allow leaves to fix more carbon during water stress (Duan *et al.*, 1996), carbon inputs into the soil would be expected to be increased, which might be especially important in more arid environments.

Rhizodeposition Rhizodeposition – the release of compounds from living roots – can be strongly influenced by mycorrhizal fungi (Jones *et al.*, 2004), because these fungi can affect plant carbon metabolism (e.g. Douds *et al.*, 2000), while representing a sizeable sink for plant-derived carbon. In addition to quantitative changes, qualitative shifts in rhizodeposits have also been documented (reviewed in Jones *et al.*, 2004). Root exudates provide much of the carbon known to stimulate the formation of aggregates; for example, root mucilages can stick particles together, leading to the short-term stabilization of aggregates (Morel *et al.*, 1991). Additionally, rhizodeposited carbon can fuel microbial activity (giving rise to the rhizosphere), which in turn contributes largely to aggregate formation.

Root decomposition Through the delivery of organic material, the decomposition of roots also contributes to soil aggregation. Mycorrhizal colonization, in addition to altering root morphology (e.g. altered proportion of fine roots), can influence below-ground litter quality by inducing changes in root chemistry (Langley & Hungate, 2003), which could influence both the rates of root decomposition and the nature of decomposition products. Ectomycorrhizal hyphae themselves can also directly negatively influence litter decomposition rates, an observation known as the 'Gadgil effect' (after Gadgil & Gadgil, 1971, 1975); this is probably caused by combined nutrient and water effects (discussed in Bending, 2003).

3. Effects mediated by the fungal mycelium

Mycorrhizal fungi contribute significantly to soil microbial biomass in many terrestrial ecosystems, often representing a dominant fungal biomass fraction. The effects of this abundant soil mycelium on aggregation are discussed in the following section in greater mechanistic detail.

III. Effects of fungal mycelium: a mechanistic discussion

Figure 3 provides an overview of the various, in part hypothetical, mechanisms by which the mycorrhizal fungal mycelium may influence soil aggregation. These can be loosely divided into biophysical, biochemical and biological processes, but they clearly are strongly interrelated. Further elucidating these processes and their interactions is important for an eventual mechanistic understanding of fungal-mediated soil aggregation, which is currently based mainly on correlative evidence. Even though this has received relatively little experimental attention, there is an important distinction between the stabilization of aggregates and the formation of aggregates in the first place (Six *et al.*, 2004). Different aspects of the fungal mycelium may have different roles in these respective processes, hypotheses for which are presented in Table 1. These distinctions are important to bear in mind in the following sections.

1. Biochemical mechanism: fungal mycelium products

Fungal products – either secreted into the environment or contained in the hyphal walls (and then secondarily arriving in the soil via hyphal turnover and decomposition) – have long been implicated as an important mechanism in soil aggregation (Tisdall & Oades, 1982). Recently, there have been several developments concerning novel compounds and their biochemistry, which are summarized below.

Glomalin and glomalin-related soil protein Glomalin (Wright & Upadhyaya, 1996) is a fungal protein (or protein class) that is operationally quantified from soil as glomalin-related

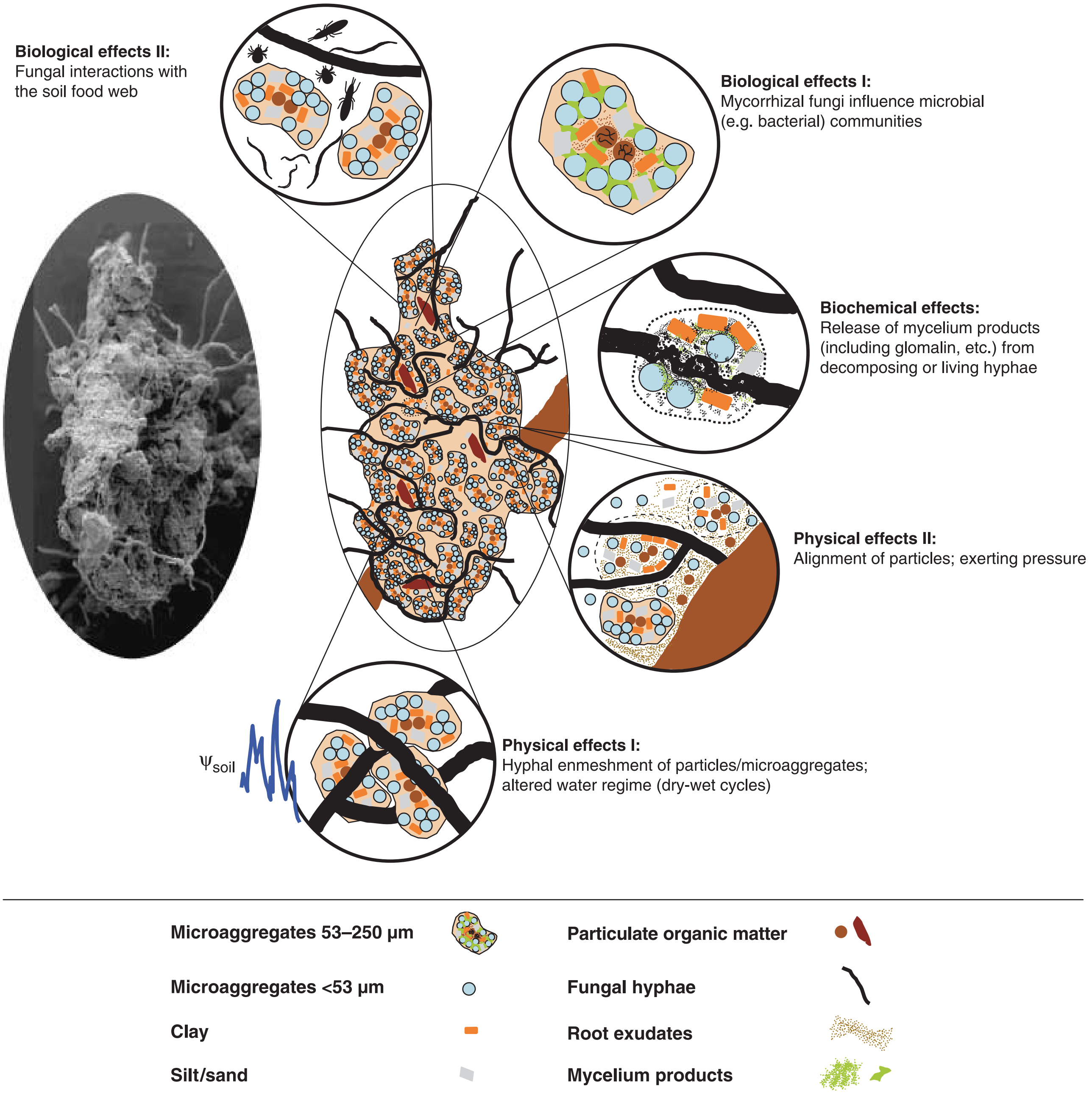

Fig. 3 Overview of various mechanisms (including hypothesized processes) that are hyphal mediated and influence the formation or stabilization of soil at macroaggregate and microaggregate scales. Mechanisms are divided into physical, biochemical and biological processes; these are discussed separately in the text, and also their interactions are highlighted.

soil protein (GRSP; for a detailed discussion on nomenclature and various issues of quantification, see Rillig, 2004b). Glomalin, the actual gene product, and GRSP (the soil organic matter pool) need to be separated in this discussion, as it is not clear whether the soil-extraction and quantification tools only capture material of AMF origin; in fact, recent evidence suggests that this is not the case (Rosier *et al.*, 2006). GRSP has received attention in the context of soil aggregation owing to the frequently observed correlation between GRSP and soil aggregate water stability (Wright & Upadhyaya, 1998, reviewed in Rillig, 2004b). However, evidence linking GRSP to soil aggregation remains correlative, and the mechanisms involved are still unclear. Glomalin is hypothesized to act as a 'glue' with hydrophobic properties, but direct biochemical evidence for this is lacking. Contrary to original expectations, glomalin (in a sterile hyphal culture system) has recently been shown to be mostly tightly bound in the fungal mycelium, rather than being secreted into the medium

Table 1 The role of fungal mycelium in aggregate formation or stabilization

Mycelium aspect	Formation role	Stabilization role
Overall hyphal abundance	Carbon input to nucleation sites; degree of particle alignment	Degree of aggregate surficial cover (i.e. mesh size of an aggregate enveloping 'network')
GRSP/other protein or exopolymer deposition	Organic matter for binding, protein–mineral association (proteins as versatile molecules at mineral surfaces)	Changing aggregate surface polarity (e.g. hydrophobicity)
Mycelium growth rate	Exertion of physical force (pressing particles together)	Continued delivery of plant-derived carbon to aggregate surface; rapidly bridging planes of weakness
Mycelium architecture	Absorptive mycelium contributes to primary particle alignment and enmeshment	Runner hyphae provide 'backbone' of stabilizing network on aggregate surface; provision of tensile strength
Hyphal decomposition	Provision of nucleation sites for microaggregate formation	Carbon input to aggregate surface/surficial pores (coating)

The same aspects of the fungal mycelium can be important to both formation and stabilization, but we hypothesize that there will be differences in the main roles of mycelium characteristics for each. Experimentally these roles will be difficult to disentangle, but it is important to note the conceptual distinction.
GRSP, glomalin-related soil protein.

(≈ 80% of glomalin was bound in the mycelium; Driver *et al*., 2005). Given that it appears to not be secreted primarily, this implicates glomalin to have a role in the living fungus; functionality in the soil would then be only secondarily arising, perhaps by virtue of its relatively slow turnover rate in the environment (e.g. Steinberg & Rillig, 2003). We recently sequenced the putative gene for glomalin, showing homology to a class of stress-induced proteins (broadly found amongst fungi) with a known cellular function (V. Gadkar & M. C. Rillig, unpublished); this provides additional evidence for effects observed in soil arising secondarily, and may provide clues about its mode of action in the soil. Research on glomalin provides an exciting possibility, especially with the molecular biology data available, to link fungal physiology specifically with soil aggregation.

Mucilages, polysaccharides and other extracellular compounds Soil microbes produce a variety of extracellular polymeric compounds for several purposes, including attachment, nutrient capture and desiccation resistance (an overview is provided in Rillig, 2005a). For example, Chenu (1989) demonstrated the involvement of fungus-derived polysaccharides in soil aggregation. Even though not dealing with a mycorrhizal fungal species, work on a specific saprobic lignin-decomposing Basiomycete (russuloid clade) has further highlighted the importance of fungal-derived mucilages, including polysaccharides, in soil aggregation (Caesar-TonThat & Cochran, 2000; Caesar-TonThat *et al*., 2001; Caesar-TonThat, 2002). As part of this work, polyclonal antibodies were developed and directed at quantifying mycelium products involved in soil aggregation. While it would be surprising if there were not similar contributions from mycorrhizal fungi, specific evidence is sparse. Extensive qualitative and quantitative analysis of exudates derived from different AMF species, produced by *in vitro* cultures, for example, is clearly needed to clarify AMF roles in soil aggregation (Tisdall, 1991).

Hydrophobins and related proteins Filamentous fungi are known to produce hydrophobins, which are recently discovered small proteins involved in various functions from mycelium attachment to surfaces, alteration of biotic or abiotic surface properties, and lowering water tension (Wösten, 2001; Linder *et al*., 2005). This work has concentrated on biochemistry and molecular biology, and very little is known, by contrast, about hydrophobins in the environment, specifically the soil (Rillig, 2005b). Hydrophobins have not yet been described for AMF, but are known to occur in ectomycorrhizal fungal species (e.g. Tagu *et al*., 2001; Mankel *et al*., 2002). Given their importance in helping to attach fungal mycelium to various surfaces, and their role in altering surface polarity (e.g. making surfaces hydrophobic), a strong functional role in soil aggregation can be hypothesized, but there is presently no evidence for this. Hydrophobin-like effects can also be caused by fungal proteins not related to hydrophobins, such as SC 15, which mediates formation of aerial hyphae and attachment (Lugones *et al*., 2004), or in general by many proteins that can form amyloid-type structures (Gebbink *et al*., 2005). Examination of the importance of hydrophobins and related proteins to soil aggregation processes remains an exciting area for future research.

2. Biological mechanisms: mycelium-influenced microbiota and the soil food web

When thinking about the contributions of mycorrhizal fungi to soil aggregation, it is important to realize that these fungi do not occur in the soil in isolation, but rather interact with numerous other organism groups, in addition to roots. Many of these interactions have been mostly ignored in the context of understanding the mycorrhiza-related mechanisms of soil aggregation.

Microbiota The microbial ecology of the AMF symbiosis is still in its relative infancy (Hodge, 2000; Johansson *et al.*, 2004). While it is clear that AMF influence soil microbial communities (e.g. Andrade *et al.*, 1998a,b; Artursson & Jansson, 2003; Artursson *et al.*, 2005a,b; Rillig *et al.*, 2006), how and where within the soil matrix these changes are mediated, and the significance of these changes to soil aggregation and other processes, is poorly defined. Unlike AMF, which exert a strong influence at the scale of macroaggregates, bacteria and archaea would be expected to influence the formation and stabilization of microaggregates in a more direct manner. Thus, AMF-facilitated alteration of prokaryotic communities may indirectly influence aggregation processes at scales smaller than the macroaggregate. There are several ways in which AMF communities can affect microbial community changes, leading to the alteration of soil aggregate distributions and turnover.

First, AMF can directly influence bacterial communities via the deposition of mycelium products that serve as substrates for bacterial growth. For example, Filion *et al.* (1999) showed that AMF exudates influence the abundance and activities of specific fungal and bacterial species. Interestingly, bacteria (such as *Paenibacillus* spp.) have recently been isolated from AMF mycelia which appear to be important in soil aggregation (Budi *et al.*, 1999; Bezzate *et al.*, 2000; Hildebrandt *et al.*, 2002; Mansfeld-Giese *et al.*, 2002). Additionally, AMF deposition products may also contain bacteriostatic or fungistatic agents, a possibility suggested by the results of Ravnskov *et al.* (1999).

Second, AMF modification of rhizodeposition products, both quantitatively and qualitatively (see the paragraph above), results in alteration of the composition of the bacterial community. Elegant experimental approaches to address this aspect include split-root systems, in which a nonmycorrhizal portion of a mycorrhizal plant is examined (e.g. Marschner & Baumann, 2003).

Third, location within the soil matrix is thought to represent a salient control on microbial community structure and functional attributes, and a number of studies have reported contrasting distributions of microbial biomass, community composition, as well as functional attributes, in different aggregate size classes (e.g. Gupta & Germida, 1988; Hattori, 1988; Mummey *et al.*, 2006). All AMF activities, resulting in the alteration of soil structure, influence the nature and extent of pore spaces available for microbial habitation. Alteration of pore distributions would result in alteration of the salient controls on bacterial community composition and function, namely substrate, nutrient, water, and oxygen concentrations, as well as predator/prey relations.Very few studies have attempted to address experimentally the direct consequences of AMF-altered microbial communities on soil aggregation. A study using heat-inactivated AMF inoculum suggested that symbiosis-influenced microbial communities (inferred from phospholipid fatty acid patterns) could influence soil aggregate water stability in an AMF-species dependent manner (Rillig *et al.*, 2005). However, in this experiment, only the microbial communities themselves were present, and more research is needed that specifically addresses the interactions of AMF and microbial communities in soil aggregation. There is also ample opportunity for research on altered physiological states of hyphae-associated microbes (in addition to community changes) that may be very relevant for soil aggregation. Examples include exopolysaccharide production by bacteria, which is controlled by microenvironmental conditions that are probably affected by mycorrhizal fungal hyphae (e.g. localized soil moisture and nutrient concentrations).

Soil food web; microarthropods Fungi form the basis of an important energy channel in the soil food web. The fungal energy channel fuels populations of microarthropods and other mesofauna (Hunt *et al.*, 1987). Mycorrhizal fungi contribute to this flow, even though AM fungi appear to be of lower resource quality compared with many saprobic fungi (Klironomos & Kendrick, 1996). Microarthropods have important roles in organic matter processing via physical, chemical and biological mechanisms (Lee & Foster, 1991; Wolters, 2000). However, it is not known how interactions between microarthropods and mycorrhizal fungal communities affect soil aggregation. Potential mechanisms include: preferential fungal grazing leading to altered fungal communities, and hence changes in average soil-aggregation processes; secretion of compounds by fungi (which could also be important in soil aggregation) in response to grazing; effects of fungi on microarthropod abundance and community composition (via food quality effects); and alteration of mycelium architecture in response to grazing. It is clear that soil microarthropod interactions, and interactions with other soil biota (earthworms, nematodes, etc.), in relation to mycorrhizal fungal influences on soil structure, present an exciting, yet under-explored, area of research.

3. Biophysical mechanisms: enmeshment, alignment, altered water relations

Enmeshment Similarly to the action of roots, albeit at a smaller scale, hyphae serve to enmesh and entangle soil primary particles, organic materials and small aggregates, facilitating macroaggregate formation, while potentially eliminating spatial constraints on microaggregate formation (Table 1; Fig. 3). Also similar to roots, hyphal morphological characteristics would be expected to influence strongly the extent to which fungi stabilize soil aggregates and the scale at which this occurs. Hyphal morphology varies greatly amongst mycorrhizal fungi (width, wall thickness, branching patterns, septation). Even within single AMF species, external hyphal morphology can be highly variable (e.g. Hart & Reader, 2005). Hyphae may also differ in tensile strength as a function of diameter or wall thickness/chemistry, but we know of no study measuring the tensile strength of hyphae in soil. How these differences influence soil aggregation processes, however, is almost completely unknown. In order for enmeshment to be most effective in stabilizing aggregates, this cannot be a very ephemeral phenomenon; however, enmeshment may also enable other mechanisms to come into play secondarily. Even though AMF hyphae as a whole may turn over quite rapidly (5–6 d; Staddon *et al.*, 2003), some mycelium components, presumably runner hyphae, can persist (most C assimilated by AMF remained in the mycelium 32 d after a labeling event; Olsson & Johnson, 2005), and continue to stabilize aggregates for several months after plant senescence or death (Tisdall & Oades, 1980). This may be even more pronounced for rhizomorphs formed by some ectomycorrhizal fungi; rhizomorph life spans in soil have been estimated to average 11 months (Treseder *et al.*, 2005), even though it is not yet established how these structures interact with soil aggregates.

Alignment Primary particles, such as clay, can be aligned along growing hyphae (Tisdall, 1991; Chenu & Stotzky, 2002:). Hyphae, having been conceptualized as tunneling machines (Wessels, 1999), can exert considerable pressure on adjacent soil particles (Money, 1994), and might be physically able to force organic matter and clay particles together, leading to microaggregate formation in a manner similar to the physical action of roots.

Water relations In analogy to the role of roots at larger spatial scales, in inducing wet–dry cycles in the rhizosphere that are important for aggregate formation, one could hypothesize this to occur on the smaller scale of hyphae. This might contribute to the increased binding of root and fungal exudates onto clay particles. Interestingly, Querejeta *et al.* (2003) have shown that in oak, nocturnal hydraulic-lift related water transfer can occur from the plant to the mycorrhizal (AMF and ectomycorrhizal) fungal hyphae in the top soil layer. This, again, might induce a dampening or exacerbation of wet–dry cycles in the mycorrhizosphere. The relative importance of this potential mechanism is unknown.

4. Interactions of hyphal-mediated processes

The biological, biophysical and biochemical-based mechanisms discussed above (Fig. 3) probably interact strongly (and of course hyphae-mediated mechanisms, as a whole, will also interact with roots and their products at similar scales). We illustrate this with a few examples. The hyphal-enmeshment process can be made more efficient by hyphae possessing the means to attach strongly to the surfaces; this can be accomplished by biochemical agents, such as hydrophobins, and perhaps glomalin (‘sticky string bag’; Miller & Jastrow, 2000). The alignment and grouping of particles will be enhanced by biochemical compounds (serving as binding agents), and perhaps also by more drastic localized drying affected by the hyphae. Localized enrichment of bacteria with contributions (e.g. polysaccharides) to soil aggregation can act synergistically with other biochemical compounds released by hyphae, or the bacterial communities can process/modify any such biochemical compounds secreted. Microbial communities will also mediate the decomposition that leads to the further release of hyphal-wall bound compounds, including glomalin (Driver *et al.*, 2005) or hydrophobins. Given these tight interrelations, it will be a major challenge to the experimental soil ecologist to disentangle the relative contributions of these hyphal-mediated processes, especially at such small spatial scales in a dynamic system.

IV. Role of fungal diversity

Through much of the discussion thus far we have compared a hypothetical situation of reduced or eliminated mycorrhizal fungal activity with one where mycorrhizas occur. In addition to its conceptual value, this is a situation that might occur after severe soil disturbance at the outset of restoration, in early succession, or as a consequence of adverse management and soil losses. There is, however, another important dimension to mycorrhizal research, namely that of the diversity of fungal isolates and species. Changes in the composition of the fungal community could occur as a consequence of far lesser disturbances, and hence a situation where different fungal communities are compared is more common in practice than considering the complete elimination of the symbionts. As a consequence, the functional role of fungal diversity has received much recent research attention (e.g. Hart & Reader, 2002; Klironomos, 2003; Munkvold *et al.*, 2004). Patterns of functionality are emerging at the level of phylogenetic groupings of AMF (Hart & Reader, 2002). A very limited number of studies have examined the role of diversity (richness or community composition) of fungi in soil aggregation (Schreiner & Bethlenfalvay, 1997; Klironomos *et al.*, 2005). It is better established that AMF isolates can differ in their effects on soil aggregate water stability (Schreiner *et al.*, 1997; Piotrowski *et al.*, 2004; Enkhtuya & Vosatka, 2005).

The discussion of the previous sections of this article can be integrated into the context of fungal diversity by recognizing that fungal species (and communities) can differ in the extent to which they promote processes at the various scales (examples are given in Table 2). As fungal species may differentially contribute to these functions, a mechanism exists for potential synergistic effects. AMF have been described as ‘multifunctional’,

Table 2 Examples of how different species of mycorrhizal fungi or fungal diversity differentially affect processes or mechanisms related to soil aggregation at the three main levels discussed in this review

Level of contribution/example	Reference
Plant community level	
AMF community richness influences plant community composition	van der Heijden *et al*. (1998)
AMF species differentially affect plant community composition	Klironomos *et al*. (2000)
Individual root system level	
ECM fungal species differ in their effects on root hydraulic conductivity (and causing different amounts of soil to adhere to roots)	Bogeat-Triboulot *et al*. (2004)
AMF communities differ in affecting plant water use in the field	Querejeta *et al*. (2006)
AMF differentially influence root biomass	Klironomos (2003); Piotrowski *et al*. (2004)
ECM richness influences root biomass	Baxter & Dighton (2001)
Mycelium level	
AMF differ in hyphal patterns of spread and activity in relation to host root	Abbott & Robson (1985); Smith *et al*. (2000)
AMF differ in hyphal production	Klironomos (2000); Piotrowski *et al*. (2004)
AMF differ in mycelium architecture (e.g. runner hyphae, absorptive hyphae, diameter size distribution)	Drew *et al*. (2003); Hart & Reader (2005)
ECM species differ in mycelium architecture (e.g. cord, fan formation)	Donnelly *et al*. (2004)
AMF differ in associated bacterial communities	Rillig *et al*. (2005, 2006)
AMF differ in GRSP yield	Wright *et al*. (1996)
AMF species are grazed differentially by microarthropods	Klironomos *et al*. (1999)

AMF, arbuscular mycorrhizal fungi; ECM, ectomycorrhizal fungi; GRSP, glomalin-related soil protein.

from a phytocentric perspective (Newsham *et al.*, 1995). Soil aggregation can be viewed as another functional axis, even though not necessarily at the level of the plant, but rather for the soil and ecosystem. Some 'trade-offs' among functions residing at the level of the fungal species are tentatively beginning to emerge. For example, fungi that allocate carbon preferentially to the extraradical mycelium might be more important in nutrient uptake, whereas fungi that allocate preferentially to the intraradical hyphae could protect the root better against pathogens (Klironomos, 2000). However, properties related to soil aggregation have not been integrated into this framework; they may be largely related to allocation to the extraradical mycelium. It is important to recognize soil aggregation as another 'functional axis', because otherwise a fungus with a large investment in soil hyphae, but with limited contribution to nutrient translocation, may be viewed just as a parasite from a phytocentric perspective (Johnson *et al.*, 1997).

Not only is it important to understand the 'independent' (more accurately: normalized to one host) biology of different fungi, but it is also clear that fungal functioning depends strongly on host plant identity (Klironomos, 2003). Recently, Piotrowski *et al.* (2004) demonstrated, in an experiment using all combinations of nine plant and five fungal species, that soil aggregation also responded sensitively to the actual combination of fungi and host plant. There are consequences of this from an applied perspective (e.g. there is probably no 'super-aggregator' AMF species that could be used in restoration contexts), but if soil aggregation is a primary goal, a tailored inoculum or mix could be made for a particular crop or other target species.

V. Emerging foci, new directions and tools

1. Aggregate turnover – rare earth labeling

Largely owing to methodological constraints, most studies pertaining to soil structure and biotic interactions view aggregates as static entities. However, accumulating evidence indicates that the soil structure is highly dynamic. Aggregate turnover dynamics probably represent a primary control of the relationships between soil organic matter occlusion and decomposition dynamics, and a determinant of microbial community structure and processes. Although mycorrhizal fungi may play a central role in the regulation of aggregate turnover, the extent to which they influence aggregate turnover rates has yet to be experimentally determined. Recently, a number of different tracer methods have shown promise for analysis of aggregate formation and breakdown at different scales (Denef *et al.*, 2001; Plante & McGill, 2002; Plante *et al.*, 2002; De Gryze *et al.*, 2005). The recent rare earth oxide-based method of De Gryze *et al.* (2006) shows promise for direct determination of aggregate turnover. This method involves a preincubation step, which allows different rare earth oxides to be individually incorporated into forming aggregates. Labeled soils are then fractionated to isolate individually labeled aggregate fractions of different sizes and are reconstituted in such a way that each aggregate size class contains a different tracer. After a second incubation period, in which treatments thought to influence aggregate turnover dynamics (such as the presence of mycorrhizal fungi) are applied, the soil is again fractionated and the transfer of each label between different aggregate size classes is measured.

2. Molecular methods

Molecular methods, based on the analysis of ribosomal genes, provide a powerful means to examine AM species interactions, both in relation to host plants and at multiple scales in the soil that are relevant to aggregation processes. However, genetic and phenotypic variability is pronounced in at least some AMF species (Koch *et al.*, 2004) and more research is clearly needed to determine the degree to which phylogeny, based on ribosomal genes, correlates with functional attributes influencing soil aggregation and other processes. The application of qualitative and quantitative analysis tools to functional genes related to soil aggregation, such as genes for glomalin and hydrophobins, is an exciting possibility that may result in further progress, but these analyses are still in the developmental stages.

In addition to the analysis of mycorrhizal taxonomic relationships with processes, the use of molecular methods for the analysis of relationships between AMF and the organisms that AMF influence, which are potentially involved in soil aggregation processes, is very promising. For example, bromodeoxyuridine (BrdU) immunocapture-based methods for determination of microorganisms exhibiting increased growth in response to specific stimuli, including AMF presence (Artursson & Jansson, 2003; Artursson *et al.*, 2005, 2006) or exudates, will probably yield important information concerning AM/bacterial interactions in aggregation processes.

3. Feedbacks of soil structure on mycorrhizas: closing the loop

This review has only addressed the unidirectional chain of causality from mycorrhizas to soil structure. However, if one were to appreciate fully the interplay between mycorrhizas and soil structure, the effect of aggregation on the fungus or the colonized host cannot go unaddressed. Yet, the physical arrangement of pores and solid particles is very difficult to disentangle from other factors, such as organic matter content, microbial communities, etc., that would change concurrently. In soil biology, the approaches followed to date have involved the use of surrogate systems that aim to model the physical aspects of growing space, for example using glass beads of various sizes (e.g. Parr *et al.*, 1963). Attempts in this regard have also included AMF (Rillig & Steinberg, 2002), with the conclusion that AMF exhibit a strongly positive response to conditions simulating increasingly ‘aggregated’ soil. Interestingly, the protein glomalin (see ‘Glomalin and glomalin-related soil protein’) was produced in greater concetrations in conditions simulating a ‘poorly aggregated’ soil; this points to the existence of interesting feedback between fungal growth and soil structure that needs to be further explored mechanistically. If mycorrhizas can, as it seems, modify their physical growing environment to their advantage, the relationship between mycorrhizas and soil structure could be conceptualized as physical ecosystem engineering (Jones *et al.*, 1997).

VI. Conclusions

We have presented a hierarchically structured view of the role of mycorrhizas in soil aggregation, with particular emphasis on the contribution of the mycorrhizal fungal mycelium.

Given the importance of soil aggregation to the functioning of ecosystems and the role played by mycorrhizas in this context, it is nothing short of shocking how comparatively little work is dedicated to this topic. For example, in a database search (Scopus®, Elsevier B.V., the Netherlands), ≈ 20% of all articles dealing with mycorrhizas had phosphate or phosphorus in the title, abstract or key words, compared with ≈ 1% that mentioned soil aggregation or soil structure. Even more drastically, only 0.8% of all articles on soil aggregation/structure deal with mycorrhizas. Clearly, awareness of this symbiosis for this function has to be increased all around, and we hope to have made a contribution with this report.

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