

# Mycorrhizas and Soil Aggregation

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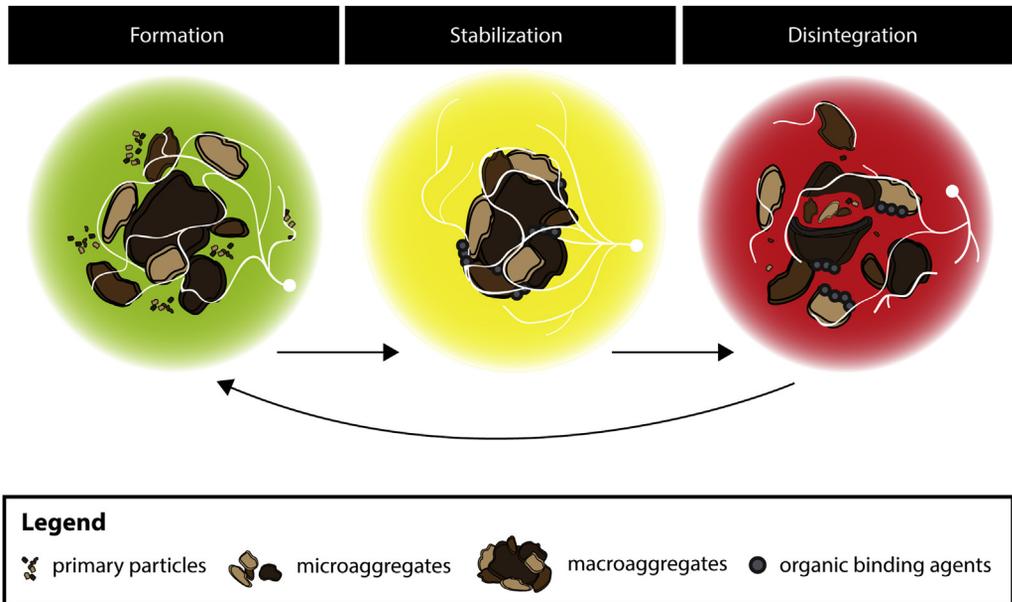
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## 14.1 INTRODUCTION: SOIL AGGREGATION, ITS COMPONENT PROCESSES, AND SIGNIFICANCE OF SOIL STRUCTURE

Soil aggregation is a dynamic and complex ecosystem process consisting of the formation, stabilization, and disintegration of soil aggregates (and associated soil pore spaces). This process is influenced by physical forces, chemical bonds, environmental factors (e.g., soil texture, freeze–thaw cycles, wetting–drying events), and biological agents, e.g., soil microorganisms and their interactions (e.g., [Tisdall and Oades, 1982](#); [Golchin et al., 1994](#); [Rillig and Mummey, 2006](#)). The basic modules in this process are the soil aggregates, which are constructs made of organic material (e.g., plant, microbial or animal derived debris), primary soil particles and minerals, adhering to each other more strongly than to surrounding particles ([Kemper and Rosenau, 1986](#)).

Soil aggregation generally is suggested to follow a conceptual, hierarchical model where primary particles (<53  $\mu\text{m}$  diameter) form microaggregates (<250  $\mu\text{m}$  diameter) via physico-chemical forces and persistent binding agents (e.g., humified organic matter and complexes of polyvalent metal cations), whereas microaggregates are assembled into macroaggregates (>250  $\mu\text{m}$  diameter) together with organic debris. Microaggregates can also form within macroaggregates. Macroaggregates are bound by relatively more transient agents including fine roots, fungal hyphae, and soil microbes ([Tisdall and Oades, 1982](#); [Six et al., 2004](#)). Macroaggregates, and to a smaller extent microaggregates, are exposed to disruptive forces (e.g., shear forces or erosion events) causing their break-down into fragments or even primary particles ([Fig. 14.1](#)). The process of disruption provides access to the otherwise encapsulated organic matter, which will either be further degraded or function as a nucleus or building block for new aggregates ([Oades, 1984](#); [Six et al., 2004](#); [Jastrow et al., 2007](#)).

Soil aggregates and the associated soil pores of different sizes and shapes, formed within and between aggregates, are essential components of soil structure that fundamentally affect soil quality, fertility, and sustainability. For example, soil pores maintain and facilitate soil gas exchange, water infiltration, habitats of soil microorganisms, and subsequently biogeochemical cycling. Furthermore, root penetration and growth in soil is facilitated by an established pore matrix. Soil erosion by water and wind is diminished in well aggregated soils. Each year 75,000 Mt of soil are



**FIGURE 14.1** Soil aggregation is a key ecosystem process, and the formation, stabilization, and disintegration of soil aggregates is influenced by physical forces, chemical bonds, and biological agents as fungal hyphae (*white lines*) maintaining a dynamic aggregate turnover. In this hierarchical process, primary soil particles are assembled to microaggregates (20–250  $\mu\text{m}$ ), which in turn build up to macroaggregates (<250  $\mu\text{m}$ ). Microaggregates can also form within macroaggregates.

removed by erosion events, causing an estimated 17,000 million dollars of damage (Pimentel et al., 1995). Soil erosion ultimately leads to reduced soil fertility and sustainability, and hence losses in plant productivity (Frye et al., 1982; Mokma and Sietz, 1992). Soil organic matter losses in eroded soil inhibit the formation and stabilization of soil aggregates, thus fueling the cycle of soil loss.

Above all, soil structure is the stage upon which life in soil plays out, and as such it is a critical aspect of the soil habitat, the loss of which could give rise to local extinctions of biota (Veresoglou et al., 2015). Given the importance of soil structure for soil biota and ecosystem functioning, it comes as no surprise that considerable research efforts have been directed at describing and understanding the effects of mycorrhizal fungi, dominant players in many soil food webs, on soil aggregation processes.

## 14.2 EVIDENCE FOR INVOLVEMENT OF DIFFERENT TYPES OF MYCORRHIZAS IN SOIL AGGREGATION

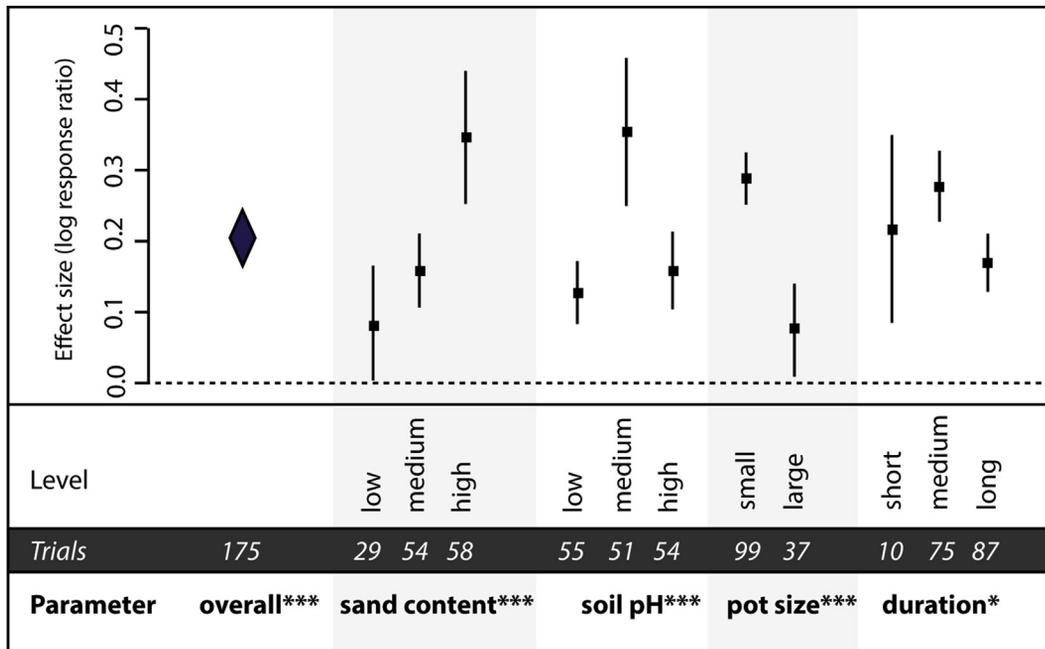
### 14.2.1 Arbuscular Mycorrhizal Fungi

Among the different types of mycorrhizal associations the arbuscular mycorrhizal (AM) fungi are the best known for their improvement of soil structure and as one of the most ancient symbioses, being estimated to originate 460–600 Ma ago (Redecker et al., 2000;

Redecker and Raab, 2006). AM fungi are members of the phylum Glomeromycota (Schussler et al., 2001) and are ubiquitous root colonizers in the majority of land plants, including a broad variety of crops (Wang and Qiu, 2006; Smith and Smith, 2011). They form characteristic intercellular and intracellular structures, mediating the intimate symbiotic interactions; the most prominent are the arbuscules. Besides its intraradical portion consisting of hyphae and storage organs, the vesicles, AM fungi support an extraradical mycelium, which is mostly relevant for nutrient acquisition beyond the depletion zone of the associated host's root (Parniske, 2008). The key property of AM fungi for stabilizing soil aggregates most likely is their extensive extraradical hyphal growth, a factor that has often been found to correlate with soil stability parameters (e.g., Wilson et al., 2009; Barto et al., 2010). Rillig et al. (2010) showed in an in vitro study in which AM fungi grew in sterilized soil that there is a direct causal link between the amount of water-stable aggregates (WSAs) and the presence of AM fungal mycelium.

The extent to which soil aggregation is promoted depends on the AM fungal species involved, because members of different families can differentially produce soil hyphae (Hart and Reader, 2002). Several studies observed variations in the soil aggregation capacity between AM fungal species (Piotrowski et al., 2004; Enkhtuya and Vosatka, 2005; Klironomos et al., 2005). Furthermore, the combination of fungal species and host plant is important for the direction and strength of the relationship along the mutualism–parasitism continuum (Johnson et al., 1997), and likewise hyphal growth and thus soil aggregation depend on this interaction (e.g., Piotrowski et al., 2004). The role of AM fungal diversity and richness has been addressed in only a small number of studies. Schreiner and Bethlenfalvay (1997) found that a mix of three species was more beneficial to plant growth promotion and soil aggregation than the single species alone. More research is required to clarify the role of species diversity for soil structure. Apart from fungal and host identity, hyphal proliferation depends on environmental conditions such as nutrient levels, soil pH, and water content (Johnson et al., 2003; Parniske, 2008; Helgason and Fitter, 2009; Pietikainen et al., 2009).

The importance of AM fungi for soil structure was uncovered during the 1950s (Martin et al., 1955; review of Six et al., 2004) and has since been well documented in narrative reviews (e.g., Oades, 1993; Tisdall, 1994; Six et al., 2004; Rillig and Mummey, 2006), as well as in a quantitative review (Leifheit et al., 2014). A meta-analysis quantitatively synthesizing studies from 1986 to 2012 examining the AM fungal impact on soil aggregation revealed a positive overall effect (Fig. 14.2) (Leifheit et al., 2014). Furthermore, it could be shown that the selection of experimental parameters can have a crucial impact on the outcome of a study testing for AM fungal effects on water-stable macroaggregates. The highest effect sizes (highest influence of AM fungi on soil aggregation) were found for pot studies, sterilized soil, sandy texture, near neutral soil pH, a pot size smaller than 2.5 kg, and a duration between 2.2 and 5 months. Lowest effect sizes were found for field studies, nonsterilized soil, fine-textured soil, and soil with an acidic pH. The effect of AM fungi on soil aggregation was independent of the fungal species richness, the soil organic carbon content, or the selected laboratory procedures for determining soil aggregation. Potential effects on soil aggregation caused by the host plant identity do not seem to be strong enough to overrule the effect of AM fungi. To further validate these findings, research should focus on studies with various AM fungal genera, richness, and diversity levels in differing contexts (e.g., soil type).



**FIGURE 14.2** Overall effect of arbuscular mycorrhizal fungi on soil aggregation and the impact of soil derived (sand content, soil pH) and experiment-related variables (pot size, experimental duration). For the categorical variables (parameters), the level means and 95% confidence intervals were presented, which were estimated via a random-effects model with nonparametric bootstrapping with 3999 iterations. The level categorization was: sand content (low, 7–40%; medium, 41%; high, 42–82%); soil pH (low, 5–6.7; medium, 6.8–8; high, 8.1–8.9); pot size (small, <2.5 kg; large, ≥2.5 kg); and experimental duration (short, <2.2 month; medium, 2.2–5 month; long, >5 month). Trial numbers represent the number of individual experimental systems (not synonymous to independent studies) included in the analyses. Asterisks represent significance level (\*\*\*,  $p < .0001$ ; \*,  $p < .05$ ). Redrawn from Leifheit, E.F., Veresoglou, S.D., Lehmann, A., Morris, E.K., Rillig, M.C., 2014. Multiple factors influence the role of arbuscular mycorrhizal fungi in soil aggregation: a meta-analysis. *Plant and Soil* 374 (1–2), 523–537.

### 14.2.2 Ectomycorrhizal Fungi

Ectomycorrhizal fungi (EcM) are formed between a fungal root symbiont mainly belonging to the phylum Basidiomycota, but also to Ascomycota and Mucoromycotina (Teder *et al.*, 2010), and a plant host, which are almost all perennial woody plants. This type of symbiosis was estimated to originate 50–200 Ma ago (LePage *et al.*, 1997; Berbee and Taylor, 2001; LePage, 2003). The main characteristics of EcM are the mantle encasing the host's roots, the Hartig net, and an extensive extraradical mycelium (Smith and Read, 2008).

The impact of EcM on soil aggregation is far less intensely studied than for AM fungi (Rillig and Mummey, 2006), possibly because the topic of soil aggregation is of inherently less interest in forests compared with grasslands or agricultural systems. However, there are observational and experimental studies demonstrating that they can improve soil structure. In an observational study, Thornton *et al.* (1956) found higher aggregation of a sandy soil under *Pinus radiata*, an EcM host, than under a *Leptospermum* species. Caesar-TonThat *et al.* (2013) showed

that soil adjacent (40–50 cm distance) to *Agaricus liliceps* fairy rings had higher mean weight diameter (MWD) of aggregates than soil sampled at a 1-m distance from outside the ring.

In experimental studies under controlled environmental conditions, the beneficial effect of EcM on soil aggregation was confirmed. Graf and Frei (2013) tested the EcM fungus *Melanogaster variegatus* forming mycorrhizas with *Alnus indica* and found higher water stability of macroaggregates. Similar effects could be detected by Caravaca et al. (2002) for *Pisolithus arhizus* and *Pinus halepensis*. Furthermore, Zheng et al. (2014) evaluated nine different EcM species forming mycorrhiza with *Pinus sylvestris* L. and showed that six fungal species, when in symbiosis, caused an increase in MWD and WSA, demonstrating that the effect is fungal-species specific.

### 14.2.3 Other Mycorrhizal Types

Soils may harbor a variety of mycorrhizal types besides the well-studied AM fungi and EcM, e.g., ericoid mycorrhizas (ERMs) or the newly discovered types formed by the Sebaciniales and Mucoromycotina. There is a dearth of information regarding soil aggregation effects for all of these other types.

ERMs are formed exclusively between members of the Ericaceae and fungi belonging mainly to the Ascomycota but also Basidiomycota, namely to the order Sebaciniales, which enter their hosts only at specialized distal roots. The ERMs can be seen as an adaptation to the often acidic and nutrient poor habitat of Ericaceae, growing in heathland, boreal forests, and bogs (Cairney and Meharg, 2003), and it was estimated that it originated 140 Ma ago (Cullings, 1996). Studies evaluating the impact of ERMs on soil aggregation are extremely rare. One example is the study by Tisdall et al. (1997), testing, among other saprotrophic fungi, the ErM fungus *Rhizoscyphus ericae* (synonymous with *Hymenoscyphus ericae*) but without a plant host; thus no mycorrhizal symbiosis could be established. However, in this *in vitro* experiment the fungus promoted the aggregation of a clay substrate.

For the Sebaciniales forming EcM and ERMs (Selosse et al., 2002, 2007), no data on their effect on soil structure are available, although these fungi are ubiquitously present and may occur as endophytes in a large number of plants (Weiss et al., 2011). Because there is an increasing interest in this group of fungi owing to their strong beneficial impact on plant growth performance (e.g., Barazani et al., 2005), we expect that there will soon be studies evaluating the importance of Sebaciniales species for soil aggregation.

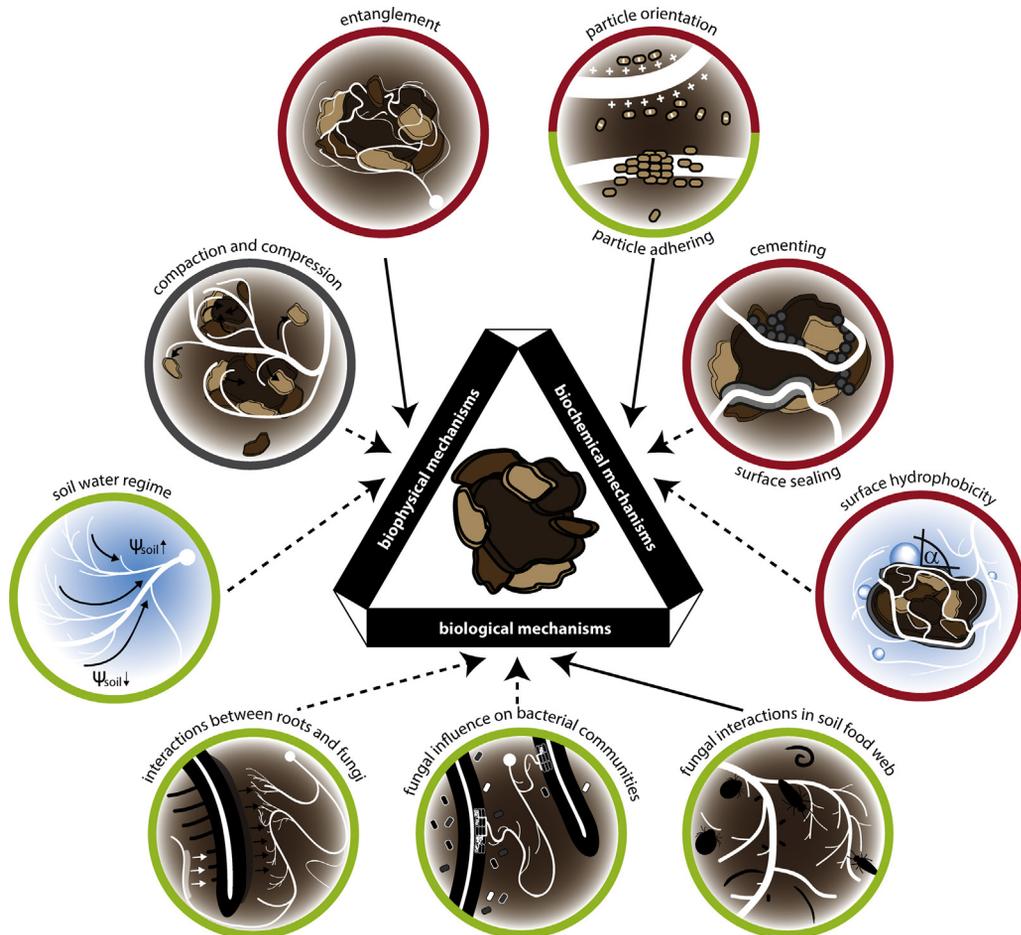
A similar lack of data can be reported for the newly discovered liverwort–Mucoromycotina symbiosis, which was potentially formed between Haplomitriopsida and Endogonales (Field et al., 2015). Along with the Glomeromycota, these fungi likely associated with the earliest land plants and facilitated their conquest of the new terrestrial habitat. Their impact on soil aggregation needs to be tested in future studies, perhaps also in association with angiosperm hosts.

## 14.3 MECHANISMS OF SOIL AGGREGATION

The positive impact of mycorrhizal fungi on soil aggregation has been known since the early 1900s and although intense research followed and new insights were revealed by observational, experimental, correlational and data mining approaches, the precise mechanisms

still remain unclear (e.g., Tisdall and Oades, 1982; Miller and Jastrow, 1990; Six et al., 2004; Rillig and Mummey, 2006; Leifheit et al., 2014).

The complex nature of soil aggregation with its simultaneously occurring process components (formation, stabilization, disintegration) is influenced by a multitude of interrelated factors and mechanisms mediated, among others, by soil biota. For mycorrhizal fungi, these can be loosely grouped into biophysical, biochemical, and biological mechanisms mediated directly or indirectly by their hyphae or mycelium traits (Fig. 14.3) (Rillig and Mummey, 2006). Even though these are discussed separately here, these mechanisms interact in reality.



**FIGURE 14.3** Illustration of potential biophysical, biochemical, and biological mechanisms affecting soil aggregation for which empirical evidence is either reported for mycorrhizal fungi (green circles) or for nonmycorrhizal fungi (red circles). For some potentially important mechanisms, no data was available (gray circle). The relevance of these mechanisms for soil aggregation was scarcely evaluated (solid arrow) but most often only hypothesized (dashed arrow). For further details on this topic see text of Section 14.3.

### 14.3.1 Biophysical Mechanisms

The biophysical mechanisms of soil aggregation are mediated by the direct physical interaction of individual hyphae, or the mycelium as a whole, with soil particles or aggregates. This set of mechanisms consists of enmeshment (or entanglement), alignment of particles by exertion of physical pressure, and changes in local water potential caused by the mycelium (Fig. 14.3). Each of these mechanisms is influenced by a number of mycelium traits, mostly architectural in nature.

The entanglement of soil particles and aggregates is one evident but less studied mechanism. There is correlational evidence demonstrating that with increasing length of the extraradical mycelium of AM fungi, the MWD is enhanced; thus it was suggested that with higher hyphal density per unit soil more particle surfaces can be affected and enmeshed (Tisdall and Oades, 1980; Miller and Jastrow, 1990). However, observational and experimental evidence is so far only available for nonmycorrhizal fungi (Gupta and Germida, 1988; Meadows et al., 1994; Daynes et al., 2012).

While growing, hyphae exert pressure on the surrounding soil (Money, 1994), potentially pushing and moving particles and aggregates into closer proximity and thus locally compressing the soil and aligning particles. There are no reports on experiments testing this mechanism in fungi, neither mycorrhizal nor nonmycorrhizal fungi.

Fungi can directly alter the water regime in the soil alongside their hyphae, in the so-called “hyphosphere.” Mycorrhizal fungi can transport water from soil patches to their associated hosts, whereas plants as well can transfer water by nocturnal hydraulic lift to their symbionts (Augé, 2001; Querejeta et al., 2003; Egerton-Warburton et al., 2007; Marjanovic and Nehls, 2008). This water movement could result in dampening or drying the soil in the mycorrhizosphere, potentially affecting the process of soil aggregation.

A number of fungal traits (Rillig et al., 2014; Lehmann and Rillig, 2015) influence the ability of the mycelium (or hyphae) to perform one or more of these biophysical mechanisms; including mycelium extension rate, branching patterns and angles, anastomosis ability, hyphal tensile strength, lifespan, and healing ability. These are described and discussed in the following paragraphs, mostly with examples from AM fungi and EcM in mind. However, all of these points can be applied to other mycorrhizal fungal types, and in fact to fungi in general.

The mycelial extension rate (and volume covered) determines the soil volume being exposed to fungal influence. This is an important trait, including for soil aggregation, because it determines if a fungus can even influence a given volume of soil. Little is known about how far mycorrhizal fungi colonies can reach outside their plant host in the surrounding soil. This ability will drastically vary depending on the type of considered hyphae; for explorative hyphae (e.g., runner hyphae in AM fungi), fast mycelial extension is possible compared with slow-growing absorptive hyphal structures (Bago et al., 1998).

The impact of hyphal branching patterns and angles can define the intensity of soil–hyphal interactions; branching increases the hyphal surface area-to-volume ratio, whereas narrow angles could increase the potential to move soil particles toward each other (Lehmann and Rillig, 2015). AM fungi can have quite narrow branching angles of 30–40 degrees (Friese and Allen, 1991). However, branching patterns and angles vary strongly during fungal development and with environmental cues; e.g., AM hyphal branching intensifies at close proximity to host because of the establishment of the symbiosis or at nutrient rich soil patches for

nutrient uptake (Paszkowski, 2006). The branching angle can also change during a lifetime, as was shown for the nonmycorrhizal fungus *Neurospora crassa*, for which the branching angle decreases after 22 hours of growth from 90 to 63 degrees (McLean and Prosser, 1987).

Resistance of the mycelial network against disturbances contributes to the stability of enmeshed soil particles and aggregates and is primarily determined by hyphal interlinkages and hyphal tensile strength. Hyphal linkages, or anastomoses, can be formed within the same or different hyphae of a genet or even between different genets of a fungal species, but no connections between different species are known for AM fungi and EcM species (de la Providencia et al., 2005; Sbrana et al., 2007; Wu et al., 2012). The intensity or number of anastomoses can vary among species; for AM fungal species, a higher number of anastomoses was found in Glomeraceae than Gigasporaceae (Giovannetti et al., 1999; de la Providencia et al., 2005).

Hyphae can confer shear resistance and tensile strength to soil units, as demonstrated for nonmycorrhizal fungi (Tisdall et al., 2012). This is partially a consequence of the tensile strength of the hyphae themselves, which is a variable property influenced among others by fungal development (Li et al., 2002). However, to the best of our knowledge, hyphal tensile strength has never been measured in soil. Hyphal tensile strength can be understood and approximated as a function of hyphal diameter, wall thickness, and septation patterns/intensity. According to this view, tear resistance of hyphae could vary depending on fungal species, developmental stage, and location of hyphae in the colony. Hyphal diameter in AM fungal species was found to range from 1 to 18  $\mu\text{m}$  (Dodd, 1994), whereas the thickness of hyphal walls varied between 1 and 4  $\mu\text{m}$ ; even further thickening of hyphal walls could be detected in AM and nonmycorrhizal fungi (McLean and Prosser, 1987; Dodd et al., 2000). Additionally, for other nonmycorrhizal fungi, wall thickness increased with increasing distance from colony margin (Trinci and Collinge, 1975) and decreased with higher branching order (McLean and Prosser, 1987).

The regenerative capability and longevity of the mycelium determines the period of functionality and integrity of the mycelial network potentially enmeshing and stabilizing soil aggregates. The lifespan of AM fungal extraradical hyphae can last 5–6 days, whereas the explorative runner hyphae were found to persist more than 30 days (Staddon et al., 2003; Olsson and Johnson, 2005), and most likely these hyphae last even much longer in soil. For EcM rhizomorphs, lifespan was estimated to average 11 months (Treseder et al., 2005).

The ability to repair disrupted hyphae after disturbance-induced injuries and breakages has been demonstrated for AM fungi (de la Providencia et al., 2005; de la Providencia et al., 2007), but such a mechanism has not been found for EcM (Taylor and Alexander, 2005). Briefly, the injury is sealed off by septa and subsequently, hyphal regrowth starts and branching from or behind the septa follows. The hyphal elongation and reorientation occurs until contact of regrown hyphae is established and hyphae can fuse. In AM fungi, the hyphal healing capability varies among species, especially for multiple injuries per hypha or long distance injuries; some species can reconnect cut hyphae with a 5-mm wide gap between the severed ends (de la Providencia et al., 2007).

### 14.3.2 Biochemical Mechanisms

The biochemical mechanisms are mainly attributed to fungal products (e.g., polysaccharides, glycoproteins, and hydrophobins) released from living or decomposing hyphae. They

are thought to attract and align soil particles, function as cements stabilizing aggregates by filling cracks, or by covering aggregate/particle surfaces (Fig. 14.3). This knowledge derives mainly from research with nonmycorrhizal fungi showing that fungal products can decrease particle detachment from aggregates and increase water stability of artificial aggregates amended with fungal exudates (Griffiths and Jones, 1965; Caesar-TonThat and Cochran, 2000; Daynes et al., 2012; Tisdall et al., 2012). A variety of polysaccharides can be produced by AM fungi and EcM during their lifecycle (Bonfante Fasolo and Gianinazzi Pearson, 1982; Hooker et al., 2007); thus it seems plausible that for mycorrhizal fungi this mechanisms also applies to soil aggregation.

Observational studies also revealed that AM fungi have clay and sand particles adhering to their hyphae and thus increase particle attachment in colonized roots compared with uncolonized roots (Sutton and Sheppard, 1976; Tisdall and Oades, 1979). In nonmycorrhizal fungi, it could further be demonstrated that the zone of orientation of clay particles by fungal hyphae can be 1–5 μm thick and can be established within 3 days. Besides the hyphal influence on clay particles via surface charges, exudates as well can cause particle orientation, as demonstrated for the polysaccharide scleroglucan (Chenu, 1989); this exudate additionally formed fibers linking the surfaces of particles, further increasing the potential stabilization effect.

Among fungal exudates, hydrophobins are of special interest. They are ubiquitous proteins found in filamentous fungi (Wessels, 1997; Wosten, 2001) with highly conserved cysteine residues (Linder et al., 2005) that are essential for mediating interactions of hyphae and their hydrophobic/hydrophilic environment with aqueous/aerial phases. They are hypothesized to increase aggregate stability toward water as a disintegrating force by sealing of cracks or simply enhance their water repellency; hence hydrophobins can slow down or even prevent the wetting of aggregates or the filling of their small cracks and cavities, thus encapsulating the enclosed air and keeping the aggregate from breaking and falling apart (Sullivan, 1990; Piccolo and Mbagwu, 1999). The surface sealing by fungal mucilages and the resulting smoothing of the otherwise rough aggregates can be well studied by scanning electron microscopy (Gupta and Germida, 1988; Daynes et al., 2012). Soil water repellency was further shown to increase in the presence of EcM and AM fungal hyphae (e.g., Schantz and Piemeisel, 1917; York and Canaway, 2000; Rillig et al., 2010); however, so far no hydrophobins could be identified in AM fungi, although analogues likely exist.

Other proteins of fungal origin may also be involved in soil aggregation (Rillig et al., 2007). For AM fungi, for example, glomalin-related soil protein (GRSP) (Rillig, 2004b) has been discussed as an agent involved in soil aggregation based on the assumption that it is mostly of AM fungal origin. However, it is unclear whether glomalin(s) are produced by AM fungi and to what extent extracted GRSP fractions really are of glomeromycotan origin (e.g., Rosier et al., 2006).

Mycorrhizal fungi that are not obligate biotrophs need enzymes for the degradation of extracellular organic compounds. ErMs and EcM produce extracellular enzymes capable of degrading organic substances such as cellulases, hemicellulases, and polyphenoloxidases (Read and Perez-Moreno, 2003; Read et al., 2004; Talbot et al., 2008); these enzymes could be needed for decomposition of plant litter (Read and Perez-Moreno, 2003) or might even potentially degrade mucilaginous substances on aggregates acting as cements. However, the amounts produced and the activity of these enzymes is much lower than, for example, in

saprobic fungi (Read and Perez-Moreno, 2003); hence there is more research needed to evaluate what impact on aggregate destabilization mycorrhizal fungi really have compared with saprobic fungi.

Another potential, but so far not studied, (bio)chemical mechanism relates to mycorrhizal fungi changing the hyphosphere pH; AM fungi can reduce soil pH from 5.9 to 3.5 within 18 weeks (Bago et al., 1998). By locally acidifying the soil, AM fungi could prevent clay lixiviation and with it the loss of clay particles to lower soil layers; clay particles are important building blocks of soil aggregates. The process of lixiviation is characterized by dispersion of clays at alkaline conditions and/or reduced salt concentrations and the relocation of dispersed clay particles downwards in the soil profile. Finally, the process gets stopped by for example, flocculation, encapsulated air, or a stagnating water flow (Scheffer and Schachtschabel, 2002). Whether AM fungi or other mycorrhizal types can contribute to the reduction of this process by acidification of their hyphosphere remains unclear.

### 14.3.3 Biological Interaction Mechanisms

Mycorrhizal fungi do not exist in isolation, but are in intense relationships with roots of their associated host, are integrated in the soil food web, and also shape and interact with the soil microbial community (Fig. 14.3). For example, they can modify soil microbial communities in their hyphosphere and thus influence soil aggregation by indirect, strongly inter-related, biological mechanisms (Andrade et al., 1997).

Hyphosphere communities are dynamic systems determined by the growth and decay, fragmentation, and reconnection of the mycelium. The community composition depends on fungal species, hyphal vitality, and their developmental stage, affecting the attraction and attachment of soil microbes toward the fungal hyphae (Toljander et al., 2006; Scheublin et al., 2010). For bacteria, there is strong evidence that their abundance and richness is increased in the hyphosphere compared with bulk soil (Ames et al., 1984; Meyer and Linderman, 1986; Secilia and Bagyaraj, 1987; Warmink and van Elsas, 2008) and that their chemotactic responses are altered depending on the colonization state of plant roots (Sood, 2003). These effects were suggested to be driven by fungal exudates, but no hard evidence is available (Jansa et al., 2013). Hyphal-associated bacteria are known to affect soil aggregation by particle alignment (Caesar-Tonthat, 2002).

For fungi, the potential consequences of species interactions on soil aggregation are clearly underexplored, although they can represent a dominant fraction of soil microbial biomass in organic soil layers (Joergensen and Wichern, 2008). Depending on the biome, mycorrhizal fungi can comprise 30% of microbial and 80% of fungal biomass, respectively (Hogberg and Hogberg, 2002). Few studies investigated the interaction of mycorrhizal fungi with other fungi in terms of ripple-on effects on soil aggregation. In two studies testing the interaction of a mycorrhizal and a nonmycorrhizal Ascomycete for their effect on soil aggregation, a nonadditive increase in macroaggregate stability in the combined compared with the single treatments could be found for EcM but not AM fungi (Caravaca et al., 2004, 2005). Further research is needed to identify the mechanisms behind these soil structure improvements.

Another biological component affected by mycorrhizal fungi are roots; with those they maintain intense chemical “cross-talks” resulting in morphological and physiological changes in both symbiosis partners, indirectly influencing soil aggregation. There is evidence that this cross-talking affects specifically hyphal and root branching patterns. From the EcM fungus *Pisolithus tinctorius* an indole alkaloid (hypaphorine) can be isolated that

can reduce lateral root development of the host (Beguiristain and Lapeyrie, 1997; Ditengou et al., 2000). Conversely, the host (*Eucalyptus globulus*) can increase the colony diameter or intensify the branching pattern of this EcM fungus by exuding flavanols and cytokinins, namely rutin and zeatin, respectively (Lagrange et al., 2001; Martin et al., 2001). In arbuscular mycorrhizas, both symbionts can induce intensified branching in their partners; for AM fungi, the mechanism is not known, but for plants this phenomenon is induced via the plant hormone strigolactone (Yano et al., 1996; Paszkowski and Boller, 2002; Paszkowski, 2006; Harris, 2008). Not surprisingly, the cross-talking also affects quantity and quality of exudates such as amino acids and carbohydrates (Leyval and Berthelin, 1993; Azaizeh et al., 1995). Thus the amount and quality of biochemical compounds acting as potential glues could also be affected by this biological mechanism.

Furthermore, mycorrhizal fungi are suggested to indirectly affect soil aggregation via their interplay with fungivores. Although AM fungi are of lower nutritional value compared with other soil fungi, their sheer abundance contributes to an extensive fungal-based energy channel in the soil food web (Holtkamp et al., 2011). Even though fungi are typically assumed to be not predominantly top-down controlled, i.e., controlled in their abundance by consumers, it is quite clear that fungal hyphae are differentially consumed, and that therefore such food web interactions could also have important consequences for mycorrhizal effects on soil aggregation (Rillig and Mummey, 2006). Fungivores can be found among all major soil biota taxa, including microarthropods, bacteria, mites, nematodes, and protists (Hunt et al., 1987; Geisen et al., 2016), where some taxa/species are found to be facultative or even obligate fungal feeders (e.g., Old and Darbyshire, 1978; Okada et al., 2005). There is very little research on the possible consequences of the interplay of fungi and fungal grazers for soil aggregation. Rillig and Mummey (2006) suggested that fungivores could have several possible effects: (1) they could alter fungal community composition by preferential feeding, thus potentially shifting the abundance of fungi with differential impact on soil aggregation; (2) they could induce shifts in fungal traits related to soil aggregation (e.g., mycelial architecture and exudate quantity/quality); and (3) fungal communities could shift fungivore abundance and communities. For microarthropods (e.g., collembola), it was hypothesized that they can positively affect fungal growth and respiration by grazing-induced stimulation at moderate densities of grazers (Fitter and Sanders, 1992; Lussenhop, 1992; Fitter and Garbaye, 1994); such an induced mycelial growth should have positive effect on soil aggregation. In the only two studies available, testing the combined impact of AM fungi and collembola, a nonadditive increase in the combination treatment compared with the two single treatments was found (Helgason and Fitter, 2009; Siddiky et al., 2012a,b). This was likely caused by complementarity in-soil aggregation mechanisms between fungi and collembola, and by the fact that collembola appeared to preferentially graze on saprobic fungal hyphae, preferring them over the AM fungal hyphae in these greenhouse experiments.

## 14.4 RELATIVE IMPORTANCE OF MYCORRHIZAS

Soil aggregation is a process that is influenced by a range of abiotic factors (e.g., wet-dry cycles, freezing-thawing), site characteristics (e.g., texture), but also by a range of biotic factors, of which mycorrhizas are but one. Studies that aimed at examining and quantifying mycorrhizal effects have often been carried out under circumstances in which their effects are

expected to be largest, or in which effects by other players are mostly excluded. This has been and still is necessary in order to establish mechanism and causality. However, from an ecological perspective it is also important to ask about the relative importance of mycorrhizas, either in comparison to effects of other soil biota or site factors or, ideally, the effect of mycorrhizas given all other biotic and abiotic components.

#### 14.4.1 In Relation to Other Biota

Effect sizes mediated by mycorrhizas can be modified by other soil biota, which necessitates interaction studies in a common experiment. Depending on the organism, species interactions are scarcely explicitly covered in experiments and hence our understanding of the relative importance of mycorrhizas on soil aggregation is quite limited.

An omnipresent organism group in experiments focusing on AM fungi is, of course, plant roots; this is because of the obligate status of this mycorrhizal symbiosis. Hence it is not surprising that mycorrhizal effects are typically conceptualized as including roots (e.g., [Rillig and Mummey, 2006](#)). As a matter of fact, only a limited number of studies have used root exclusion compartments to disentangle root and fungal contributions to soil aggregation. From such studies, it is known that the combination of root and mycorrhizal hyphae can lead to a nonadditive increase in WSA compared with root- and hyphae-only treatments ([Thomas et al., 1993](#); [Andrade et al., 1998](#)). The application of hyphae-only (or hyphosphere) compartments or sterile *in vitro* growth systems ([Rillig et al., 2010](#)) revealed that the soil aggregation ability of mycorrhizal fungi can be comparable to that of roots ([Thomas et al., 1993](#); [Andrade et al., 1998](#)).

Microbiota, including nonmycorrhizal fungi (e.g., saprobic fungi) and eubacteria, share the same habitat with mycorrhizal hyphae and influence each other in a number of ways, including competition and alteration of the surrounding soil and its structure ([Andrade et al., 1998](#); [Rillig, 2004a](#); [Rillig and Mummey, 2006](#); [Nottingham et al., 2013](#)). Thus it is not straightforward to disentangle experimentally the relative importance of mycorrhizal fungi and associated microbiota, because this necessitates the existence of sterile culture systems. There is so far evidence that the co-occurrence of mycorrhizal fungi and bacteria promotes soil aggregation and that this effect is species specific ([Rillig et al., 2005](#); [Caesar-TonThat et al., 2013](#)). [Leifheit et al. \(2015\)](#) went one step further and examined the soil aggregation potential of AM fungi and a natural soil microbial community. They found that both organism groups applied as individual treatments improved water stability of macroaggregates, whereas in the combination treatment a nonadditive increase was detected, i.e., the level of soil aggregation when the two treatments were combined was comparable to that of the single-additions. However, those experimental results are context dependent and many more studies are needed before general conclusions can be reached.

A well-studied organism group affecting soil aggregation are earthworms, whose effects on soil aggregation can mainly be related to disturbance and the production of casts and biopores ([Shipitalo and Le Bayon, 2004](#)). Depending on the species, soil conditions, and experimental duration, earthworms can process up to two-thirds of litter-amended artificial soil and convert it into macroaggregates ([Ziegler and Zech, 1992](#)), demonstrating their enormous potential impact on soil structure. There are only limited reports available on the combined examination of earthworms and mycorrhizal fungi. [Milleret et al. \(2009\)](#) found no significant

change in water stability of macroaggregates for either the individual AM fungi treatment or the combined AM fungi and earthworm treatment. Thus further research is needed to disentangle both biotic components and to evaluate their individual contributions to soil aggregation.

Under natural conditions, mycorrhizal fungi are exposed to fungivores, which themselves affect soil aggregation—to what extent is rather unclear. [Maaß et al. \(2015\)](#) addressed this topic and summarized potential mechanisms by which microarthropods, with a focus on collembola, could affect soil aggregation. Beside production of organic materials (e.g., egg clutches, integuments, necromass, and fecal pellets) their main contribution could be related to the interaction with other soil biota (e.g., grazing on fungal hyphae). Grazing by microarthropods is one of the most researched fungal feeding interactions, but only two studies tested the impact of collembola on soil aggregation in combination with mycorrhizal fungi. [Siddiky et al. \(2012a\)](#) were the first to empirically test the effects of collembola on soil aggregation. They showed that collembola contribute comparably to soil aggregation as AM fungi when used as separated biota treatments; although in the combination treatment a non-additive increase in WSA could be detected. Because of the nature of the experiment, non-AM fungi were also present in the soil, which was the preferred fungal food source for collembola. Hence further research is needed to evaluate the relative impact of mycorrhizal fungi on soil aggregation when grazed. This is also true for other groups of soil fungivores, including nematodes and protists, for which there are no studies available for consequences on soil aggregation.

#### 14.4.2 Across Different Settings

Gauging the relative effect of mycorrhizal fungi on soil aggregation given all other factors (e.g., biotic and abiotic) is very difficult to achieve experimentally, and therefore research has so far relied on observational approaches. Here, data are typically collected in the field and subsequently used to disentangle mycorrhizal effects through tools such as structural equation modeling ([Jastrow et al., 1998](#)). This method is uniquely suited to this question, because it takes into account the hierarchical nature of predictor variables and different hypothesized causal pathways. With such approaches it was possible to reveal the overall importance of mycorrhizal fungal hyphae and roots for soil aggregation over a range of different systems. In both natural ecosystems (arid and mountain grasslands) and managed sites (managed grassland and woodland), roots and extraradical mycelia of AM fungi had a strong impact on aggregate stability ([Miller and Jastrow, 1990](#); [Chaudhary et al., 2009](#); [Owen et al., 2009](#); [Li et al., 2015](#)).

Biotic effects, including those of mycorrhizal fungi, have also been examined at larger spatial scales (e.g., Germany), integrating across differences in soil characteristics, e.g., soil texture. [Barto et al. \(2010\)](#) showed in their study, which included 27 different sites across Germany with different land use intensity and site characteristics, that such abiotic factors can override the role of mycorrhizal fungi in soil aggregation. Many more studies are needed to arrive at a thorough understanding of the relative role of mycorrhizas across complex landscapes; of course, results are also prone to be very strongly influenced by the biotic and abiotic factors included in measurements, because only those can be considered in the statistical models.

## 14.5 AVENUES AND NEEDS FOR FUTURE RESEARCH

The mediation of soil aggregation by mycorrhizas is a critical process, especially given the ever-increasing demands on soils and threats to sustainable management of this resource in agroecosystems. Soil aggregation is clearly an under researched process compared with the more “classical” functions such as nutrient uptake. Therefore it is important to keep in mind clear paths for research, which we outline here.

### 14.5.1 Mechanisms

There is quite an appalling lack of mechanistic understanding of how mycorrhizal fungi or roots really build up and stabilize (or disintegrate) soil aggregates. We should not be satisfied with “just-so” stories, as appealing as they may be, but strive to replace this with a thorough process understanding. This requires a new approach that employs a combination of a variety of methods. These could include advanced imaging, direct observation in time-lapse videos, or novel soil-on-a-chip approaches (Stanley et al., 2016) coupled with more informed correlational approaches based on measurement of a number of traits in a large set of fungi (and roots).

A promising approach to make inroads toward mechanistic understanding is to systematically adopt a trait-based approach, as has been proposed by Rillig et al. (2014) and Lehmann and Rillig (2015). A first step is to disentangle soil aggregation process components (Fig. 14.1) and to identify related fungal characteristics influencing them. Rillig et al. (2014) addressed this task for a broad range of potentially important fungal traits, as discussed previously. These potentially relevant traits have to be evaluated for their explanatory value. In order to do so, dedicated experiments enabling the separation of the soil aggregation process components have to be designed. As suggested by Lehmann and Rillig (2015) specific soil aggregate formation and stabilization assays could be utilized to test fungal ability to form new aggregates out of primary particles using soil powder or slurry (Tisdall et al., 1997) and to stabilize (artificially produced) macroaggregates (e.g., Caesar-TonThat and Cochran, 2000). Then correlations of trait and assay-derived data will reveal the important fungal characteristics for each soil aggregation process component.

Rigorously adopting such a trait-based approach for a large number of species of mycorrhizal fungi would be an ambitious task. Like trait-based approaches for plants (Cornelissen et al., 2003; Perez-Harguindeguy et al., 2013), this requires a collaboration of researchers. An important step toward an effective collaboration would be to agree on standardized measurement conditions and methods. This is necessary to ensure comparability of experimental results, because plant and mycorrhizal fungal growth strongly respond to environmental conditions; for example, in nutrient-rich soil patches, fungi show intense hyphal branching, whereas for plant hosts the dependence on their fungal partner can be diminished and carbon (C) translocation can be reduced (Olsson et al., 2002; Grant et al., 2005; Paszkowski, 2006). The vision would be to collate all these pieces of information in public, curated databases, which should also capture variability in the expression of mycorrhizal fungal traits and with it their effect on soil aggregation.

### 14.5.2 Relative Importance and Greater Coverage of Ecosystem Types

The systematic study of the relative importance of mycorrhizas, given other factors, requires a large research effort, especially if such data are to be integrated in global models.

It should include a wide parameter space, including various ecosystem types, not just the much-researched agricultural systems and grasslands. Variance partitioning and structural equation modeling can then be used to estimate the relative importance of mycorrhizal mycelium in these various settings, and lessons learned from this will be very important for management of mycorrhiza for this specific process.

Another related research focus should also be trying to better understand the interaction of mycorrhizas and other factors, especially abiotic factors such as wet–dry or freeze–thaw cycles. For obvious reasons, most studies have focused on understanding mycorrhizal contributions to soil aggregation in a given abiotic setting, keeping such factors constant. But efforts should move beyond demonstration of the fact that mycorrhizal fungi can aggregate soil, with particular choices of study parameters optimized for detection of such effects; this has been convincingly shown already. We now need to move to a new mode of experimentation that critically challenges our knowledge: under what conditions (biotic and abiotic) does the importance of mycorrhizas fade?

### 14.5.3 Conceptual Advances: Functions and Ecosystem Engineering

Even though soil aggregation is often thought of as a “function” of mycorrhiza, it is worth pondering whether this is really the case in the narrow sense; i.e., considering that the “proper function of a trait is the effect for which it was selected by natural selection” (Neander, 1991). Even though it is fully appropriate to regard soil aggregation (or its process components) as an ecosystem process probably notably under the influence of mycorrhizas, it seems unlikely that this has been selected for; rather it appears more probable that this is a process that arose as a consequence of functions such as nutrient uptake and foraging. However, this does not mean that there could not be interesting feedbacks between fungi and soil aggregation (e.g., Rillig and Steinberg, 2002), perhaps best viewed within the framework of ecosystem engineering. Work aimed at conceptually clarifying the soil aggregation function of mycorrhizas and other soil biota could therefore be enlightening.

### 14.5.4 Model Integration

Integration of soil aggregation and mycorrhizas together in process models is a very pressing need. Very few models consider soil aggregation from an organismic perspective (Caruso and Rillig, 2011), and this includes mycorrhizas. On the other hand, models of mycorrhizal function are focused on nutrient delivery and do not consider the soil aggregation effects. This is a large gap, and future effort fueled by the targeted collection of data is required to close it. Success in this endeavor is crucial, because otherwise soil aggregation risks being an overlooked process at larger scales (e.g., global models), at least as mediated by mycorrhizas.

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