Mycorrhizal Fungi Influence Soil Structure

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R. Michael Miller
Argonne National Laboratory

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Julie D. Jastrow
Argonne National Laboratory

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Chapter 1

Mycorrhizal Fungi Influence Soil Structure

R. M. Miller and J. D. Jastrow
Environmental Research Division, Argonne National Laboratory, Argonne, Illinois 60439, USA

Abstract: A series of closely related processes is presented, by which arbuscular
                mycorrhizal (AM) fungi contribute to the formation of relatively stable
                aggregate structures. Fibrous roots and AM fungal hyphae can be viewed as a
                "sticky-string bag" that contributes to the entanglement and enmeshment of
                soil particles to form macroaggregates, a basic building block of soil structure.
                Furthermore, AM fungi produce a glycoprotein, glomalin, that is deposited on
                their outer hyphal walls and on adjacent soil particles. Glomalin appears to be
                a rather stable hydrophobic glue that might reduce macroaggregate disruption
                during wetting and drying events by retarding water movement into the pores
                within the aggregate structure. Examples from various soil types are used to
                demonstrate the contributions of AM fungi to soil aggregation and its
                subsequent stabilization. Over a wide range of soil types, these contributions
                depend largely on broad textural characteristics and whether the soil's
                structure is hierarchical in construction, among other factors.

1. INTRODUCTION

The arbuscular mycorrhizal (AM) fungus, through its external hyphal network, provides a direct physical link between its host and the soil resource. Not only does the hyphal network contribute to the uptake of mineral ions of its host, but the fungus also represents a rather large carbon sink within the soil (e.g., 15, 26). Yet, a much-overlooked characteristic of AM fungi is the role of their external hyphae as a stabilizing agent in the formation and maintenance of soil structure (Figure 1). Recognition of the

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importance of external hyphae as a stabilizing agent for soil aggregates has focused largely on the action of hyphae through entanglement and enmeshment mechanisms (24, 38). More recent studies suggest that AM fungus hyphae might also stabilize aggregates by exuding a hydrophobic glue into the soil (45, 46). The goal of this chapter is to delineate the contributions of AM fungi to the formation of aggregates and the stabilization of soil structure, especially for soils that are hierarchically organized.

1.1 Defining soil structure

Soil structure is usually defined as the arrangement of particles and associated pores in soils (20, 29, 39). However, this definition ignores soil structure's transient nature and its architecture, where primary and secondary soil particles may be hierarchically organized into aggregates of various sizes by organic and inorganic means that can span scales of up to nine orders of magnitude (30). More recently, Tisdall (39) has tried to incorporate some of these deficiencies by defining soil structure as an arrangement of particles in soil and particles of sand, silt, and clay, bound together into aggregates of various sizes by organic and inorganic means. Structural stability is defined as a soil's ability to retain its arrangement of solids and pores when exposed to internal and external stresses (29).

The role of soil structure in controlling soil ecosystem function and the feedbacks between soil structure and soil organisms (including AM fungi) are generally recognized but not fully understood. Yet, the importance of such feedbacks cannot be understated. Studies of agronomic systems, for example, indicate that a well-aggregated soil structure is one of the primary factors controlling soil tilth, water relations, root penetration, and erosion potential. Moreover, the physical protection afforded organic debris within stable soil aggregates is a primary mechanism for organic matter accumulation in soil (8, 17, 39, 42). Even so, our understanding of the contributions of AM fungi to soil aggregation and structure has been limited by our inability to measure adequately the growth and activity of AM fungus hyphae, especially under field conditions. However, recent advances in quantifying external hyphae and associated metabolites might lead to a better understanding of the contributions of the AM fungus (e.g., 26, 31, 47).
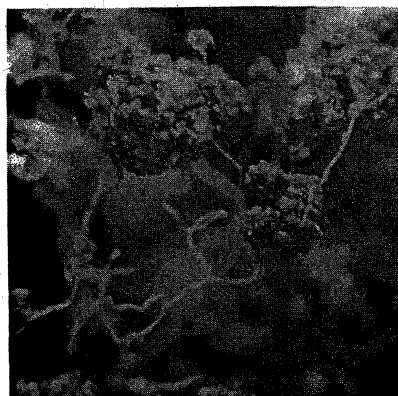
Figure 1. Photomicrograph demonstrating the entanglement of macroaggregates by AM hyphae. (Largest aggregate is about 3 mm in diameter; external hyphae are 10-15 diameter.) The soil is an Andic humitropept collected from around the roots of Piper sp. in Ecuador.

1.2 Aggregate Hierarchy

An appreciation of the hierarchical nature of many soils is necessary to better understand the contributions of AM fungi to the formation and stabilization of soil aggregates. We believe that one of the more important conceptual breakthroughs in our understanding of pedogenic processes has been the development of an hierarchical view of the mechanisms involved in the formation and stabilization of soil aggregates (6, 30, 42). In this conceptual model (Figure 2), the mechanisms and their relative importance change with spatial scale. Primary particles and clay microstructures are bound together with bacterial residues and fragments of saprophytic and AM fungus hyphal debris into stable silt-sized microaggregates (2-20 μm in diameter), which in turn may be bound together with fungal and plant debris and fragments into larger microaggregates (20-250 μm in diameter). It is currently believed that the organomineral binding agents involved in stabilizing microaggregates are relatively persistent and consist of humic substances or long-chained polysaccharides sorbed to clays, with the most persistent clay-organic associations being strengthened by bridges of polyvalent cations (39, 42). As proposed by Tisdall and Oades (42) and expanded upon by others (e.g., 30), microaggregates are bound into macroaggregates (>250 μm in diameter) by both transient binding agents (i.e., readily decomposable organic materials composed of microbial- and plant-derived polysaccharides) and temporary binding agents (composed primarily of fibrous roots and hyphae). As macroaggregates increase in size,

transient binding agents appear to be less important, and the contributions of fibrous roots and AM fungal hyphae generally increase in importance (Figures 2 and 3).
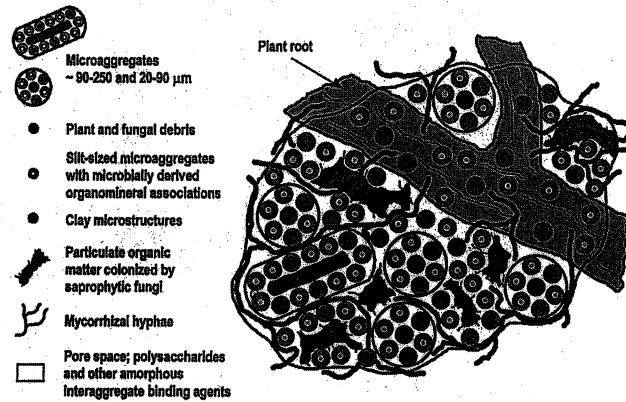

Figure 2. Conceptual diagram of soil aggregate hierarchy (17)
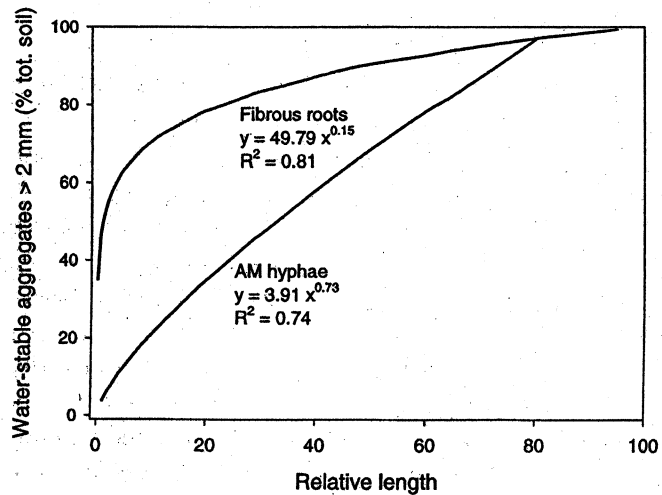

Figure 3. The relationship between water-stable aggregates and relative root and AM hyphal length in a prairie restoration chronosequence (redrawn from 24)

An important consequence of the existence of an aggregate hierarchy is the porosity exclusion principle (6). This principle is based on the premise that smaller aggregates should have smaller pores, greater contact between particles, and higher bulk densities than larger aggregates, because the latter also contain larger pores between the smaller aggregates that compose them (29, 30). Hence, the effectiveness of various binding mechanisms will

depend on their physical dimensions relative to those of the pores being bridged (20).

Conceptually, we can view aggregate hierarchy as the binding together of increasingly larger aggregated units; however, this does imply that aggregates are formed sequentially. Existing evidence suggests that although fibrous roots, along with saprophytic and mycorrhizal hyphae, provide the mechanical framework for forming macroaggregates, it is the decomposition process that leads to the development of microaggregates and an aggregate hierarchy (2, 8, 30, 37). Hence, microaggregates may form as a result of biological activity within or at the surfaces of relatively stable macroaggregates. They may also develop when macroaggregates turn over or fragment as the roots or hyphae binding them together are either grazed by soil fauna (e.g., 21) or are decomposed. All levels of aggregate development, however, may occur simultaneously. Furthermore, each aggregate size class forms and turns over at its own rate, depending on vegetation type, management practices, and on the degree of protection from decomposition afforded by the organomineral binding agents of each size class.

2. MYCORRHIZAE AND SOIL STRUCTURE

It has been almost 20 years since Tisdall and Oades (42) published their classic work on the hierarchical nature of soil aggregation. This view of aggregation is based on the spatial and temporal actions of various organomineral binding agents. These binding agents can be grouped into three classes on the basis of age and the degree of rendering of organic inputs. The first class of binding agents, composed of microbial and plant-derived polysaccharides and mucigels, can decompose quite rapidly and are referred to as transient binding agents. The second class, referred to as temporary agents, is composed mainly of living or dead fibrous roots and fungal hyphae and can normally persist through a growing season or even longer in perennial systems. The third class, considered to be persistent binding agents, is composed of decayed or more rendered materials having humic acid moieties in association with clays, amorphous mineral complexes, or both. Thus, in this hierarchical view, AM fungi play an important role as temporary stabilizing agents of macroaggregates.

The characteristics that allow AM fungal hyphae to contribute to the formation and stabilization of soil structure are related to a wide range of factors including soil characteristics, vegetation type, management practices, and characteristics of the fungus itself (Table 1). For example, the physical dimensions of the hyphae allow them to grow and ramify through pores the

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size of those between macroaggregates. In addition, AM hyphae are believed to persist for longer periods in soil because of their filamentous nature, coarse branching habit, and rather large diameters. Tisdall and Oades (41) reported that AM fungal hyphae could stabilize aggregates up to 22 weeks after the host plants had died. By comparison, hyphae of saprophytic fungi with their more regular branching habit and typically thin walls appear to have a more transient effect on aggregation, often lasting no more than a few weeks (e.g., 27). Another factor enabling AM fungi to contribute to macroaggregation is their obligate association with plant roots. Because AM fungus hyphae have direct access to photosynthetic carbon, they represent a direct conduit for host carbon into the soil, bypassing the decomposition process. Additionally, AM hyphae have been found to produce a very stable hydrophobic glycoprotein, called glomalin, that can act as a long-term binding agent (45). Although evidence is rapidly accumulating that the hyphae of AM fungi play a substantial role in stabilizing soil aggregates (e.g., 4, 18, 24, 34, 38, 46), the number of research papers addressing their contributions to soil aggregation does not yet reflect the importance of AM fungi in this process.

Table 1. Some examples of factors influencing the contributions of AM fungal hyphae to soil structure

Biotic factors
Host root architecture and morphology
AM fungal species composition
Architecture and morphology of hyphae
Hyphal length, tensile strength, surface charge
Types of AM fungal metabolites and their persistence and diffusion characteristics
Soil factors
Pore size, soil texture, clay mineralogy, nutrient distribution, water content
Organic matter type, amounts and types of polyvalent cations
Wetting and drying cycles, freezing and thawing cycles
Historical factors
Vegetation type, disturbance cycle, land-use, tillage and cropping practices

Many of the early investigations of hyphae and aggregation were conducted in sandy soils or sand dune systems (e.g., 3, 10, 22). These studies indicate that hyphae are the primary mechanism for binding sand particles into aggregated units (see Figures 1-5 in 22). More recent studies in sandy soils substantiate the role of saprophytic and mycorrhizal hyphae in an enmeshment mechanism (4).

However, for soils where organomineral binding agents are important to stabilizing soil aggregates, the contributions of AM fungi go beyond the entanglement mechanism described for sand dune systems and other highly sandy soils. Rather, mycorrhizal hyphae contribute to the maintenance of a

hierarchically arranged aggregated soil structure composed of both macroaggregate and microaggregate structures in loamy textured soils of alfisols, mollisols, and vertisols (1, 18, 23, 41). Aggregates do not appear to be hierarchically organized in oxisols, where oxides are the dominant binding agent of soil particles (30). This attribute does not preclude the entanglement or enmeshment of primary and secondary particles by hyphae, but the role of the fungus may be secondary to the oxide-binding mechanism. The shrink-swell capacity of soils with a high clay content (particularly self-mulching soils) may override or minimize the contributions of hyphae to soil structure. Hence, when viewed over a wide range of soil types, the contributions of mycorrhizal fungi to soil stabilization depend largely on broad textural characteristics and whether the structure of a soil is hierarchical in construction, among other factors (Table 2).

A series of closely related processes has been proposed by which AM fungi contribute to the formation of relatively stable aggregate structures (24, 38). The first process involves the growth of hyphae into the soil matrix to create the framework that holds the primary soil particles together via physical entanglement. A second process is the creation, by roots and hyphae, of the conditions that are conducive to the formation of microaggregates. Third, hyphae and roots help to create and stabilize macroaggregates by enmeshment of microaggregates and smaller macroaggregates into larger structures.

Table 2. *Mycorrhizal and abiotic influences on soil structure for contrasting soil textures*

Property	Influence in Soil Type		
	Sand	Loam	Clay
Shrink-swell capacity	Minimal	Important	Maximum
Abiotic aggregation	Minimal	Important	Maximum
Mycorrhizal effects	Important	Important	Minimal

2.1 Contributions of Mycorrhizal Hyphae to Macroaggregates

As previously mentioned, the stabilization of macroaggregates requires organic agents large enough to bridge the voids between the microaggregates and primary particles composing macroaggregates. Because larger macroaggregates can be composed of smaller macroaggregates, their voids require even larger binding agents to stabilize them. Binding mechanisms at this scale are largely related, either directly or indirectly, to the growth and decomposition of roots and AM fungus hyphae (18, 39).

The percentage of soil in macroaggregates is often directly related to the lengths of fibrous roots and AM fungus hyphae (18, 41; Figure 3). The

effects of living roots and hyphae can be conceptualized by viewing the three-dimensional network of fibrous roots and AM fungus hyphae as a "sticky string bag" (Figure 2) that physically entangles or enmeshes smaller aggregates and particles, creating rather stable macroaggregates (30). Fibrous roots and hyphae not only form a network that can serve as a framework for macroaggregate formation, but extracellular mucilage coatings on root and hyphal surfaces can sorb strongly to inorganic materials, helping to stabilize aggregates (7, 13, 38, 40). Furthermore, roots and hyphae often become encrusted with inorganic minerals and clays which can physically slow their decomposition, thereby preserving the "string-bag" framework for a time even after the roots and hyphae senesce (30). Moreover, the pressures exerted by growing roots and by the localized drying resulting from plant water uptake are important physical forces that promote both the formation and the degradation of aggregates (20).

The types of roots and their densities, architectures, and associations with AM fungi can also influence macroaggregate size distributions. We (23) have argued that observed associations between plant species composition and the extent of stable macroaggregate formation are related to the types of roots produced by various plant species. We suggest that much of the effect of roots on soil aggregation is an indirect result of root associations with AM fungi. Hence, because plants have differing root morphologies and differing associations with mycorrhizal fungi, some plants may be more effective than others in promoting aggregation (23, 24, 29).

Extracellular mucilage coatings of roots and hyphae most likely constitute the "sticky" part of the string bag. Most of the evidence for such coatings is based on microscopy and selective staining of ultrathin sections (e.g., 11, 12, 13, 30, 40). Until recently, these mucilages were generally believed to consist mainly of polysaccharides and, in some cases, polyuronic acids and amino compounds (11, 39). A small body of research also suggests that proteinaceous materials are important in soil structural stability. For example, Emerson et al. (9) described hydrophobic organic surface coatings on sand-sized particles, which appeared to be proteinaceous in nature and of apparent fungal origin. In fact, recent studies have shown that Ericoid and ectomycorrhizal fungi produce extrahyphal, glycoproteinaceous slimes (5) and that a hydrophobic glycoprotein occurs on the surface of the hyphae of AM fungi (44). This glycoprotein, named glomalin, was identified by using monoclonal antibody techniques and appears to be exuded from both intraradical and external hyphae and deposited on soil surfaces (44, 45). Evaluation of a limited number of AM fungal isolates for the presence of glomalin suggests that it is produced by the majority of AM fungi; however, isolates vary considerably in the amount they produce, with differences occurring largely along generic taxonomic

ranks (Table 3). Glycoproteins, and especially glomalin, may be an important new class of soil binding agent that was probably not detected previously because of the extreme conditions (autoclaved in citrate buffer for 30-90 minutes at 121°C) needed to solubilize this compound (44, 45).

Table 3. Comparison of yields for the immunoreactive protein extracted from AM hyphae (data from 44)

Culture	Hyphal wt. (mg)	Total protein (μg)	Yield (μg mg⁻¹)
Gigaspora gigantea MA453A[1]	2.4	152	63
Gigaspora rosea UT102	1.3	79	60
Glomus etunicatum UT316	5.1	61	12
Glomus intraradices UT126	1.2	35	21
Glomus intraradices FL208	44.6	767	17

[1] International culture collection of AM fungi isolate number.

The ability of fungi to grow across the voids between aggregates is a trait that differentiates fungi from other microbes. The coating of hyphae with glomalin may be a mechanism enabling the fungus to cope with gas-water interfaces during aerial growth across the soil pore spaces between and within macroaggregates. In this case, the glycoprotein could serve to adhere the essentially hydrophilic fungal wall to hydrophobic surfaces located on soil particles and particulate organic matter. Although the primary function of the glycoprotein may be as a hydrophobic coating for the fungal wall, other hydrophilic surfaces (e.g., polysaccharides associated with microbial residues and soil particles) may also be coated by the exuded glomalin.

The placement of hyphae within the soil matrix may be related to the amount and quality of organic debris. Some evidence suggests that AM hyphae exhibit foraging behavior when they encounter organic-rich microsites (e.g., fecal pellets, rhizodeposition) by proliferating or branching into or near these sites (14, 19, 24, 28, 33). The ability of AM fungi to respond to microsite differences may be an underlying mechanism behind the physical entanglement of soil particles and the enmeshment of smaller aggregates to create larger ones (24).

2.2 The Contributions of Mycorrhizal Hyphae to Microaggregates

The contributions of AM fungal hyphae to the development of microaggregates and an aggregate hierarchy appear to be primarily an indirect consequence of their role in the enmeshment mechanism of stabilizing macroaggregates. Hyphae of AM fungi help to create the conditions that are conducive to the formation of microaggregate structures

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by contributing to the formation of stable soil macroaggregates (24). These conditions are produced primarily through their effects on the growth and activity of other soil organisms. For example, organic substances exuded from both living and senescing hyphae can serve as substrates for the microbial community. In the presence of clays and silts, these substrates, along with hyphal fragments, can act as nucleating points for the formation of microaggregates. The stability of microaggregates depends mostly on the strength with which clays and other inorganic components of the soil are sorbed to particulate organic matter, AM and saprophytic fungal hyphal fragments, bacterial cells, and a variety of other organic colloids and compounds primarily of microbial origin (Figure 2). Clays are generally the mobile component, with much of their movement and reorientation around organic debris resulting from localized drying and the mechanical actions of plant and fungal growth. For example, controlled-environment studies and micrographs of fungi growing in pure clays and clay soils show compaction and reorientation of clay particles along the surface of mycorrhizal and saprophytic fungal hyphae and demonstrate hyphal enmeshment of mineral particles and organic debris to form stable microaggregates (7, 43).
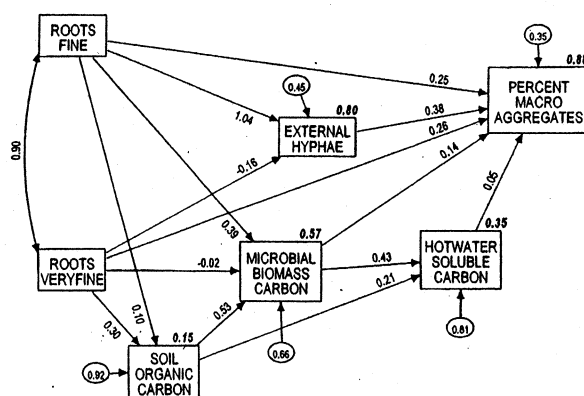

Figure 4. Path model of hypothesized causal relationships among lengths of AM hyphae and roots, three soil carbon pools, and the percentage of water-stable soil aggregates in a chronosequence of prairie restorations (from 18). Fine roots are 0.2-1 mm dia; very fine roots are. <0.2 mm dia. Single-headed arrows indicate direct causal relationships, and double-headed arrows indicate unanalyzed correlations. Numbers are path coefficients and proportion of total variance explained (r2; shown in bold italics) for each endogenous (dependent) variable. The numbers within ellipses represent the proportion of unexplained variance [(1-r2)1/2] and, thus, indicate the relative contributions of all unmeasured or unknown factors to each dependent variable.

2.3 The Role of AM Fungi with Respect to Other Mechanisms of Aggregation

Few studies have investigated concurrently the contributions of differing mechanisms to the aggregation process. We have used a prairie restoration chronosequence to investigate the relative contributions of various mechanisms to the formation of water-stable macroaggregates in mollisols (e.g., 16, 18, 23). Direct and indirect mechanisms were examined by using path analysis techniques. Path analysis is a statistical approach that enables the heuristic examination of causal processes underlying observed relationships. After construction of a conceptual model of the interrelationships among multiple independent and dependent variables, the total correlations between independent and dependent variables can be partitioned into direct and indirect effects and noncausal components (Figure 4).

Table 4. Partitioning of the Pearson product-moment correlations between selected organic binding agents and the percentage of water-stable aggregates (>212 indirect, and total causal effects on the basis of path analysis (n=49).

Measured parameter	Direct effect	Indirect effect	Total effect	Product-moment correlation (r)
Fine root length	0.25	0.47	0.72	0.91
Very fine root length	0.26	-0.04	0.22	0.85
External hyphal length	0.38	0	0.38	0.89
Microbial biomass carbon	0.14	0.03	0.17	0.65
Hot-water-soluble carbohydrate carbon	0.05	0	0.05	0.55
Soil organic carbon	0	0.09	0.09	0.43

Adapted from 18.

The hyphae of AM fungi had the strongest direct effect on the percentage of water-stable macroaggregates in the restoration chronosequence (Table 4). Fibrous roots exhibited the next strongest direct effects on macroaggregation, with essentially equal contributions for each of two measured diameter size classes. However, the indirect effects of the two root size classes differed, with fine roots (0.2-1 mm in diameter) having the overall largest total effect of all binding agents evaluated. The indirect effect of fine roots on macroaggregates was due primarily to strong positive associations of this root size class with mycorrhizal hyphae and microbial biomass. Hence, the path analysis approach strongly supported the importance of the various contributions of roots and AM fungal hyphae to the stabilization of macroaggregates in aggrading grassland systems. In this system, the roles of microbially derived extracellular polysaccharides and of soil organic carbon in stabilizing macroaggregates were dominated by the

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contributions of roots and AM fungus hyphae via the "sticky string bag" mechanism. Although it was not specifically measured by this study, much of the total effect of roots and hyphae on aggregation is probably the result of their turnover and decomposition.

3. CONCLUSIONS AND FUTURE DIRECTIONS

We need to recognize the role of photosynthate-derived carbon as the energy source that enables AM hyphae to grow and ramify through the soil when considering the contributions of AM fungi to soil aggregation. The growth of AM fungus hyphae will cease without a growing root system. It is this association between endophyte and host that differentiates the contributions of AM fungal hyphae from those of saprophytic fungi, which acquire their energy from mineralization of organic matter. Hence, the strength of the contributions by different types of fungal hyphae to aggregation vary, depending on inputs from either an actively growing host or the turnover of plant materials to fuel decomposition processes.

It is difficult to assign one structure or mechanism more importance than another in the formation and stabilization of soil aggregates. Even though this chapter has taken a mycocentric view of soil aggregation, the effects of primary producers on aggregation dominate in soils where organic binding agents are the primary mechanism of aggregation. Furthermore, aggregation requires the continued inputs of the relevant organomineral binding agents, and soils decoupled from vegetation favor the breakdown of soil structure.

Vegetation effects on aggregation can be through biomass allocation, litter inputs, the kinds and amounts of roots produced, and, of course, the allocation of photosynthetically derived carbon to the AM hyphal network. Indeed, controlled environment studies have demonstrated how difficult it is to separate the effects of roots from those of hyphae (35, 36). Also, much of our knowledge of mycorrhizal influences on soil aggregation has come from experimental approaches emphasizing end points (tilled vs. virgin soils) rather than the dynamic processes of soil aggregate formation, stabilization, and degradation. Those studies that have incorporated a gradient approach by using different tillage and crop rotations (41) or a chronosequence study (16, 18, 23) have allowed for data interpretations that emphasize the interactive nature of the effects of land management practices, vegetation, and soil biota on soil structure.

Biotic factors that influence soil aggregation are listed in Table 1. Unfortunately, very little is known about their management. We have not yet elucidated the determinants of AM fungal species composition. Indeed, even the basic characteristics of hyphal architecture and morphology of

isolates of AM fungi have not been determined in a general sense, let alone in light of their contributions to soil aggregation. However, some research directions show promise. For example, the yield of the hyphal metabolite glomalin appears to be strain specific (Table 3), suggesting a trait that could be used to identify superior isolates of AM fungi for use in soil conservation and restoration programs. Also, a side benefit of depositing glomalin on soil particles is that it is a glycoprotein and, hence may represent an unrecognized pool of somewhat labile nitrogen in the soil. Glomalin may account for about 10-15% of the total nitrogen pool in a prairie soil (R.M. Miller, S.F Wright, J.D. Jastrow and A. Upadhyaya, unpublished data). We note that the isolates of AM fungi with the strongest correlations with the percentage of water-stable macroaggregates in prairie soils were *Gigaspora* spp. (24), the genus thus far found to produce the highest yields of glomalin (Table 3). Other investigators have found a concomitant increase in both glomalin and soil aggregates in annual grassland soils exposed to enhanced levels of atmospheric CO_2 (32).

In summary, the contributions of AM fungus hyphae to soil structure are substantial. Hyphae and roots can be viewed as a "sticky-string bag" from a mechanistic point of view. Basically, the hyphae of AM fungi contribute to the entanglement and enmeshment of soil particles to form macroaggregates, the basic building blocks of soil structure. Furthermore, the glycoprotein glomalin, deposited on the cell wall of the AM fungus, is a rather stable hydrophobic glue that might enable the fungus to cope with gas-water interfaces during aerial growth. In addition, the hydrophobicity of the deposited glomalin may reduce macroaggregate disruption during wetting and drying events by retarding water movement into the pores within the aggregate structure, thereby allowing the nondisruptive escape of displaced gases from the pores. Finally, but not discussed directly in this chapter, an increase in the proportion of soil held as macroaggregates should result in an increase in the accumulation of soil organic matter (see 16). Although the growth of AM hyphae might contribute directly to soil carbon pools, the indirect paths, such as hyphal influences on macroaggregate stabilization, could be of greater importance to soil carbon accrual than the accrual measured by their standing crop. Mycorrhizal fungi may increase the residence time of organic debris found between and within macroaggregates via the contribution of the AM fungi to macroaggregate stabilization. However, because of the nonlinearity of the relationship between aggregation and organic matter protection, as well as interactions with other factors (e.g., soil texture, clay mineralogy, vegetation), care must be taken in assuming that an increase in aggregation results in a corresponding increase in carbon accrual. During the coming decade, the association between macroaggregation and organic matter accumulation in soils will be an

important area of research. The contributions of AM fungal hyphae will no doubt be an important aspect of this relationship.

Hence, the challenge before us is both conceptual and methodological, requiring us to better elucidate and measure the contributions of AM hyphae to the formation and stabilization of soil structure over a wide range of soil types, evaluated at relevant temporal and spatial scales.

4. ACKNOWLEDGEMENTS

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