Draft

Role of Arbuscular Mycorrhizal Soil Fungus

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Introduction

Arbuscular mycorrhizae (AM) fungi are a type of fungi that infect the root of the plant and help plants to survive. There are an estimated 100 species of AM fungi (Brady and Weil, 2009). AM fungus typically have highly branched tree-like structures that form within the root cells and branch out into the soil to search for plant nutrients. Most grasses and agricultural annual crops have an association with AM fungus. AM fungi and rhizobia bacteria evolved together and may share a common ancestor that has a fungal origin because plants utilize the same protein to communicate with AM fungus and rhizobia (Dick, R. Personal Communication). See Figure 1 for mycorrhizal networks.

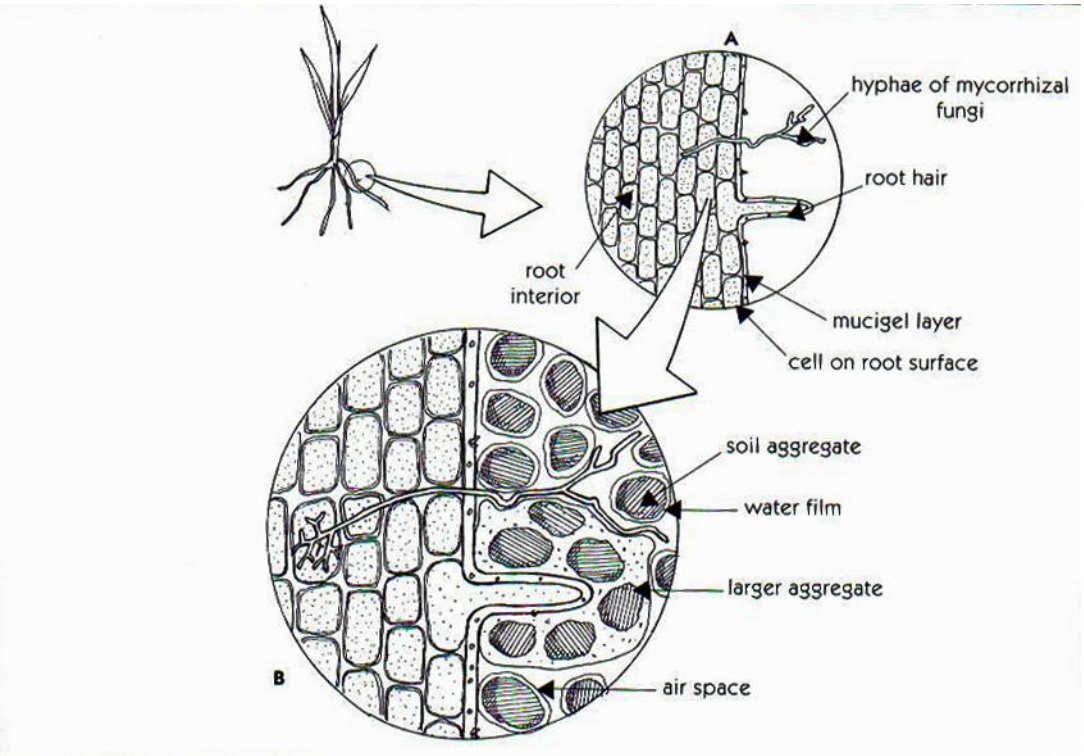

Figure 1: Mycorrhizal fungus forming a network and infecting plant roots. Photo from *Building Soils for Better Crops*, 2nd Ed., Dr. Fred Magdoff and Dr. Harold van ES. Used with permission and All Rights Reserved.

Arbuscular Mycorrhizae (AM) Fungus Functions

AM fungi have a symbiotic (beneficial) relationship with plants. AM fungi form a mycorrhizal network with plant roots, helping the plant roots be more efficient at gathering soil nutrients, especially N and P. Fungi produce enzymes such as proteases and phosphatases that mineralize and release N and P (Dick, W. Personal Communication). These enzymes are released into the environment and then the soluble nutrients are absorbed.

Most nitrogen from fungi is released as ammonium ions (NH^{4+}). Nitrifying bacteria will convert ammonia to nitrate (NO^{3-}) but since the soil conditions tend to be more acidic in fungal soils, with less nitrifying bacteria, more of the nitrogen stays as ammonium. Most grass and annual crops like corn and wheat prefer nitrates while most perennial crops like alfalfa and clovers prefer ammonia. The ammonium form of nitrogen is more energy efficient for the plant because in the plant cells, nitrate needs to be converted to ammonium to produce proteins (Lowenfels and Lewis, 2009).

AM fungi enhance soybean (legume) growth and production by increasing P absorption, nodulation and N fixation. Fungi enhance and cultivate good bacteria, especially Rhizobia bacteria for nitrogen fixation, which help legume plants grow (Brady and Weil, 2009). Legumes have a taproot and are less efficient than grasses with a fibrous root system at extracting P from the soil. AM fungi make phosphorus more plant available. The AM fungus however may reduce the number of Mn^{2+} reducing bacteria in the rhizosphere by a factor of five times, reducing the availability of Mn^{2+} for soybean absorption and seed production (Sylvia et al 2005).

AM fungi produce a sticky substance call glomalin. Glomalin is an amino polysaccharide composed of sugars from the plant root and protein from the AM fungi forming a glycoprotein. In a good soil, glomalin may represent 1–5% of the total carbon in the soil and glomalin is 30% carbon, 1–2% nitrogen, and up to 5% iron, which gives it a reddish soil color (Lavelle and Spain, 2005; Sylvia, 2005). Glomalin surrounds the microaggregate soil particles and glues them together to form macroaggregate soil particles. Polysaccharides like glomalin enhance soil tilth and soil structure (Dick, R. 2009, Dick W. 2009). Mycorrhizal fungi inoculums are on the market and may be added to plant seeds at planting time to increase specific fungal populations. See Figure 2 on Mycorrhizal Production of glomalin.

Fungi increase soil structure by increasing macroaggregates in the soil. Fungal hyphae increase water infiltration and water holding capacity by forming stable macroaggregates (>250 μm). The soil particles and soil debris are physically stuck together by glomalin and other plant exudates and microbial wastes (Ingham 2009). Sylvia et al 2005 states that "there are from 1 to 20 meters of AM hyphae in each gram of soil" and there could be as much as 5 miles of AM fungi hyphae in a pound of soil". See Figure 3 on Glomalin and soil structure.

Conventional tilled soils are dominated by bacteria, which do not produce glomalin. Tillage disrupts and breaks down the macroaggregates into microaggregates and results in denser, more compacted soils, lacking soil structure. Tilling the soil decreases soil organic matter. Tilled soils are not the ideal soil habitat to main beneficial fungal populations. Fungi need well-aerated soils with large amounts of residue and cannot tolerate saturated or anaerobic (lack of oxygen) soil

conditions that occur under soils that are tilled, compacted or have poor soil structure. Tillage also injects excess oxygen into the soil, stimulating bacteria populations to expand and then consume active carbon (polysaccharides and glomalin) for food (Dick R, and Dick W, Personal Communication). Fungal populations tend to decrease with increasing depth in the soil.

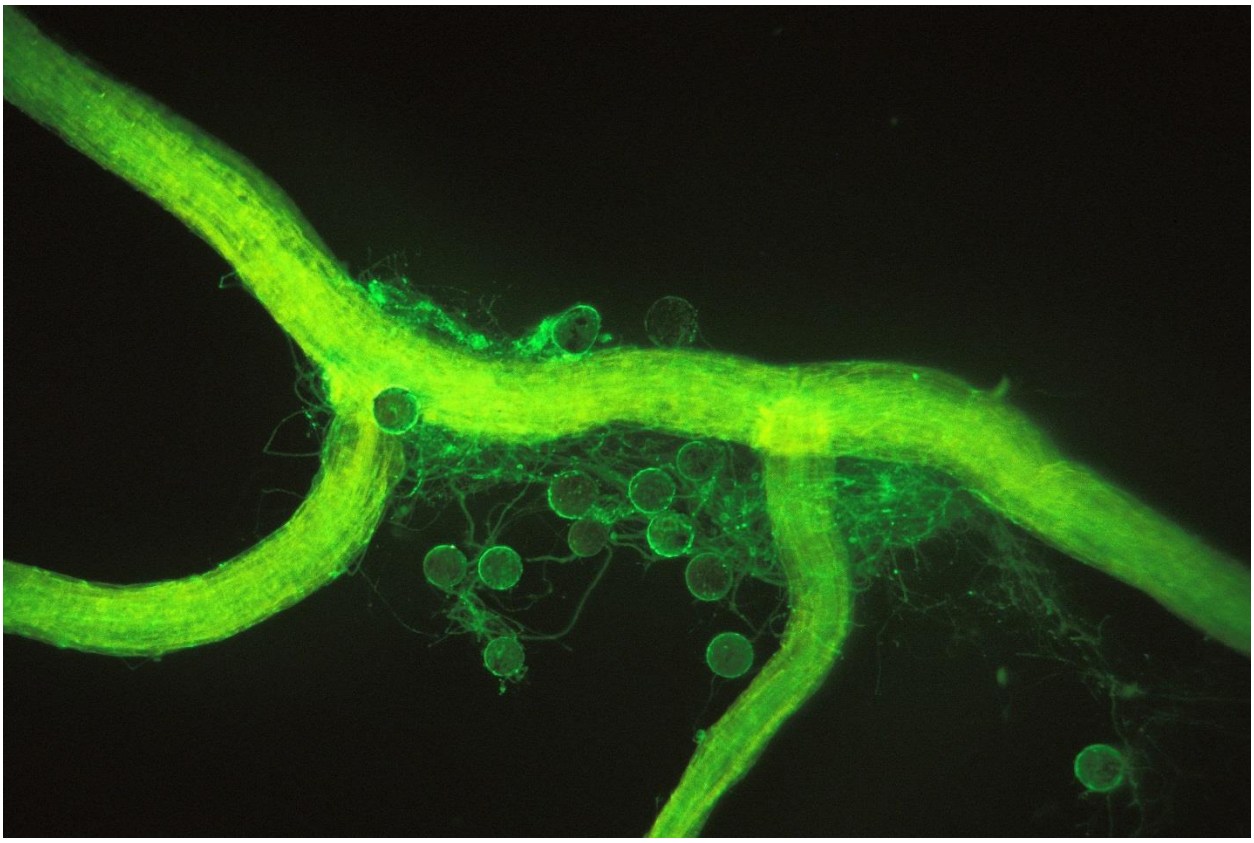

Figure 2: Microscopic view of mycorrhizal fungus growing on a corn root. The round holes are spores and the threadlike filaments are hyphae. The substance coating the mycorrhizal fungus is glomalin revealed by the green dye. Photo and cation by Dr. Sara Wright, U. S. Department of Agriculture-ARS (k9968-1). Used with permission and All Rights Reserved.

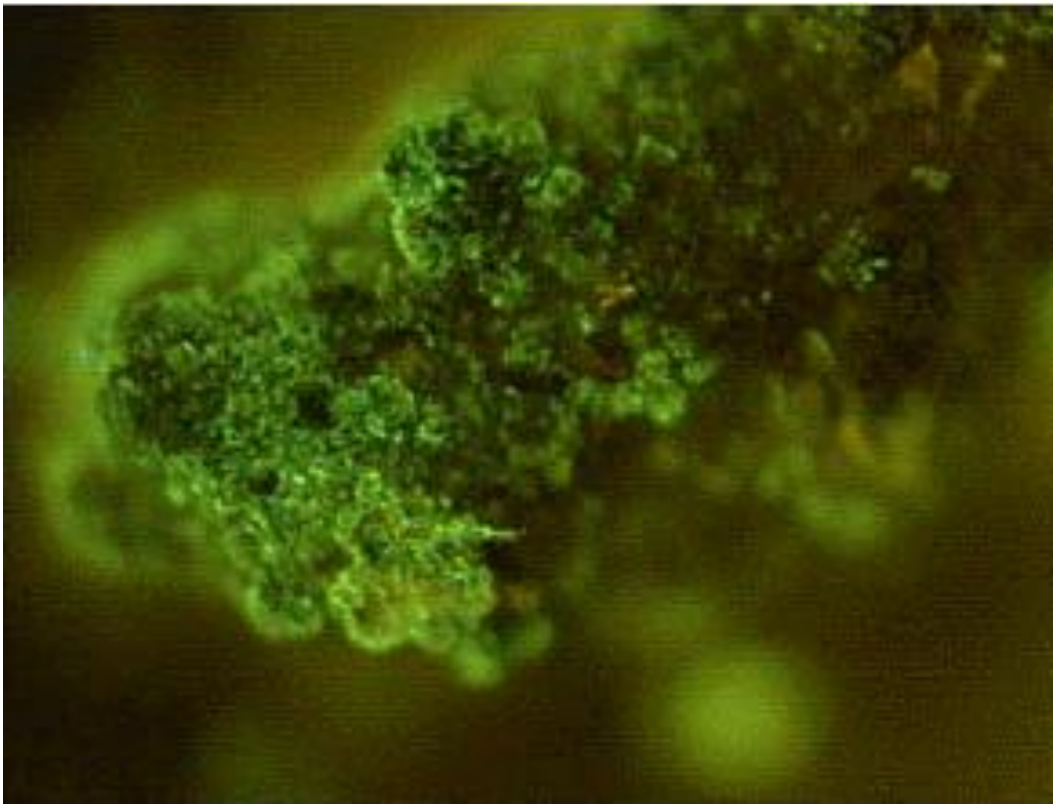

Figure 3: Glomalin in its natural state is brown. A laboratory procedure reveals glomalin on soil aggregates as the green material shown here. Glomalin glues the soil particles together into macroaggregates. In *Glomalin: A Manageable Soil Glue*. Photo, caption, and publication by Dr. Sara Wright, U. S. Department of Agriculture-ARS. Used with permission and All Rights Reserved.

Benefits of Soil Mycorrhizal Fungi

Fungi perform many functions in the soil including nutrient recycling; carbon decomposition and sequestration; water conservation; increased soil aggregate stability; produce plant hormones, antibodies, and vitamins; promote plant growth; and increase disease suppression (Ingham, 2009; Sylvia et al 2005). Mycorrhizal fungi increase the efficiency in plant and root extraction of nutrients leading to increased growth and production in nutrient poor soils and have the ability to make infertile soils more fertile (Brady and Weil, 2009, Sylvia et al., 2005).

In no-till agriculture, fungal populations dominate the soil food web (although they are less in number than the bacteria) and improve carbon sequestration. Fungi have 40–55% carbon use efficiency so they store and recycle more carbon (C) compared to bacteria. Bacteria are less efficient at retaining C and release more carbon dioxide into the air. Fungi have higher C content (10:1 C:N ratio) and less nitrogen (N=10%) in their cells than bacteria" (Islam, Personal Communication).

Due to their smaller size and much greater surface area, fungi can efficiently scavenge for nitrogen (N), phosphorus (P), calcium, magnesium, copper, iron, zinc and water (Lowenfels and

Lewis, 2006; Brady and Weil, 2009) increasing plant root nutrient extraction efficiency. Fungi share nutrients with bacteria and excrete enzymes in the soil to release soluble nutrients. For example, fungi oxidize tightly bound P to make it more available for microbial uptake. Iron and manganese are also oxidized by fungi. Fungi, unlike most bacteria, can also release N from dead microbial biomass and from insects because they have the enzymes necessary to breakdown proteins, cell walls, and chitin in insects (Sylvia et al, 2005). Once the fungus and bacteria absorb the soluble nutrients, they become like living bags of fertilizer that becomes available when they die. When the fungi hyphae die, they leave microscopic tunnels 10 µm in size throughout the soil and these tunnels serve as a haven for bacteria from many bacteria predators and the tunnels allow for the movement of air and water through the soil profile (Lowenfels and Lewis, 2006).

During a drought, fungi grow when the bacteria do not. Fungi supply moisture to the plant roots by crossing cracking dry soils to obtain water not available to plant hair roots. Fungi also supply nitrogen to plants in dry soil, by accumulating soil nitrogen to break down hard to decompose residues low in nitrogen (Ingham, 2009). Mycorrhizal networks explore up to 20% of the soil volume due to their smaller size compared to only 1% of the soil volume for a typical plant root hair. These mycorrhizal networks even connect one plant to other plants, sharing and transferring nutrients among plants (Sylvia et al., 2005, Brady and Weil, 2009). See Figure 1 on Mycorrhizal Networks.

Fungal hyphae filaments translocate and store deficient nutrients to distant parts of the soil where nutrients may be lacking, allowing reproduction and growth to continue. The plant supplies simple sugars to the fungi while the fungi supply N, P, other nutrients and water to the plant. As much as 25 percent of the plant root carbohydrates are directly exuded into the soil to feed the microbes or 5 to 10% of a plants total photosynthetic production to mycorrhizal fungal networks (Kuzyakov, 2002; Brady and Weil, 1999).

There are several factors that decrease AM fungi in the soil. When excess nutrients like N and P are supplied by commercial fertilizer to plant roots, the AM fungi stop working. Tillage also decreases the effectiveness of the AM fungi by destroying the mycorrhizal network associated with plant roots (Dick, R, Personal Communication).

Mycorrhizal fungi may be harmed by many fungicides in the market place. So excess commercial fertilizer, tillage, soil compaction, pesticides (fungicides and fumigants that contain neonictinoides like Poncho, Cruiser, and Goucho or benzimidazoles like Benlate), short crop rotations, and long fallow periods tend to decrease fungal populations. Cereal crops and grass crops had three times higher density and length of fungi hyphae than land that was fallow (Lavelle and Spain, 2005; Lowenfels and Lewis, 2006; Sylvia et al, 2005).

Summary

Most soil fungi decompose recalcitrant organic residues high in cellulose and lignin. Fungi carbon use efficiency is about 40–55% so they store and recycle more C (10:1 C:N ratio) and less N (10%) in their cells than bacteria. Fungi are more specialized but need a constant food source and grow better under No-Till conditions. Arbuscular mycorrhizal (AM) fungi produce an amino polysaccharide called glomalin. Glomalin surrounds the soil particles and glues macroaggregate soil particles together and gives soil its structure. AM fungus store and recycle

soil N and P and generally have a symbiotic relationship with most plants, greatly increasing the N and P extraction efficiency and improving soil structure and water retention.

Acknowledgment

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14) Wright, S. Photograph (k9968-1) and caption of corn root with fungal spores and glomalin from U. S. Department of Agriculture-ARS.

Crop rotation and Management Practices Effects on Arbuscular Mycorrhizal Fungus (AMF)

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INTRODUCTION

Modern cropping rotations and management practices have an effect on microorganisms in the soil. In a typical corn and soybean rotation, live plants and active roots are present less than a third of the time during a calendar year (Magdoff and van Es, 2000). Restoring ecosystem functionality requires feeding the soil life and reducing tillage. Tillage destroys microbial habitat and the microbial food system. Almost 60% of soil organic matter (SOM) in temperate regions and 75% in the topics have been depleted by conventional tillage due to oxidation (Lal, 2004; Intergovernmental Panel on Climate Change, 1996).

A no-till (NT) system with cover crops (CC) provide more months of living roots and plants to restore C stores and improve soil ecology. Arbuscular mycorrhizal fungus (AMF) populations are associated with glomalin and water aggregate stability (WAS) aggregates. Glomalin is a glycoprotein produced by AMF (Rillig et al. 2001) and glomalin soil concentration is positively correlated with WAS (Wright and Upadhyaya, 1998), and improved soil structure. Nearly 90% of the SOM is located within soil aggregates (Jastrow et al., 2000). Current management practices (tillage, P fertilization and fallow cropping), NT, and CC affects on AMF colonization, glomalin production, and WAS are reviewed.

TILLAGE

A two year Canadian study by Kabir et al. (1997) compared conventional tillage (CT; fall plowing plus spring disking), reduced tillage (RT; spring disking) and NT with corn receiving either inorganic (N or K) or organic (liquid dairy manure) fertilizer for AMF colonization. They found that densities of total and active AMF hyphae were significantly lower in CT than RT and NT. Fertilization did not affect AMF colonization in a sandy loam soil but were abundant in manured clay soils.

Galvez et al. (2000) compared a low input (organic) system to conventional agriculture and the low input systems NT and RT had higher AMF spore populations than CT. Corn plants grown in low input NT had the highest shoot P concentrations, highest P use efficiency, and enhanced AMF colonization.

Pikul et al. (2009) compared NT to chisel-tilled (CHT) for ten years, examining the quantity and quality of SOM. Pikul et al. (2009) concluded that NT resulted in better SOM quality than CHT because the decaying plant root systems remained undisturbed favoring AMF growth. These studies show the negative effects of tillage, inorganic P fertilization, and fallow cropping on GRSP, WAS, and SOM in relation to AMF colonization. Cover crops and glomalin also effect soil aggregation and stability.

Glomalin (GRSP) produced by AMF is highly correlated with WAS (Rillig and Steinberg, 2002). Driver et al. (2004) found that about 80% of the glomalin was found in hyphal walls and was released on decomposition rather than being secreted. Hyphal turnover (5-7 days half-life) is the main pathway for glomalin deposition, released to the soil from dead mycelia fragments. Rillig and Steinberg, (2002) and Driver et al., (2004) research shows how glomalin increases soil GSRP and WAS and improves soil structure.

Douds et al. (1993) found that CT yielded lower levels of AMF than low-input systems with cover crops planted between cash crops. Greenhouse bioassays showed 2.5-10 fold greater AMF colonization of plants growing in soil from low-input systems with cover crops than conventional systems. These studies show that changes in the soil ecology have a large impact on the soil quality.

INTERACTIONS WITH THE SOIL MICROBIAL COMMUNITY

Arbuscular mycorrhizal fungi modify their growth environment by producing a glycoprotein called glomain which is highly correlated with WAS. AMF under stress or less favorable growing conditions (compacted soils), poor soil structure) increased glomalin production despite smaller hyphal length (Rillig and Steinberg, 2002). Driver et al. (2004) found that about 80% of the glomalin was found in hyphal walls and was released on decomposition rather than being secreted. Hyphal turnover (5-7 days half-life) is the main pathway for glomalin deposition, released to the soil from dead mycelia fragments.

Purin and Rillig (2007) theorize that the primary role of glomalin is for fungal cell wall physiology and for defense (less palatable to grazing predators). A secondary role is in changing the soil environment associated with GRSP and WAS. Rillig and Mummey (2006) reviewed the contributions of AMF on soil structure from the soil fungus hyphae, to the individual root, and to whole plant communities. Fungal species and diversity promote soil aggregation to different degrees. The authors suggest that a multifunctional perspective be used to study AMF and feedback mechanism between soil structure and AMF arguing that the entire plant and microbial community interact to improve the soil environment.

Andrade et al. (1998a) found that roots and AMF may not associate with soil bacteria randomly, but rather in a hierarchical structure of mutual preferences. The mycorrhizal status of soils may selectively influence persistence of bacterial inoculants and affect native bacteria. Andrade et al. (1998b) showed that the plant roots and AMF enhanced WSA stability individually and additively in concert, and suggest that they affect microorganism numbers indirectly by providing habitable pore space in the WSA.

Rillig (2004) argues that research at the ecosystem level is less prominent but potentially more promising and states that too much emphasis has been put on individual plant hosts and not enough research emphasis on whole plant communities and soil ecology. Rillig notes that human-induced disturbances (global climate change and agro-ecosystem management) decrease AMF functions. He discusses four interacting routes via which AMF influence soil ecosystem processes on C cycling: 1) increasing plant species diversity and community C cycling, 2) indirect effects on soil microbial communities by changing bacteria communities in the rhizosphere, 3) individual host plant physiology (drought effects, plants as C sinks and associated ecosystem effects), and 4) direct effects of AMF and glomalin at the ecosystem level

especially on soil structure and ultimately increases in C storage. Rillig hypothesizes that AMF increases infiltration, decreases runoff, promotes AMF colonization and increased C sequestration which are the same effects observed when NT and CC are used together in the soil.

PERSPECTIVES

Current human and agro-ecosystem management practices (tillage, P fertilization, fallow cropping) may have negative effects on AMF, and impact C cycling and storage in soil aggregates. AMF were lower in CT and RT compared to NT. No-till improves AMF colonization and glomalin production and is correlated with WAS and improved C sequestration. Glomalin in AMF is primarily a defense mechanism but has major secondary effects on WAS, soil structure, and the microbial community. Further increases in C sequestration will require agricultural practices that process greater quantities of SOM. A majority of plants have an association with AMF (Fitter et al., 2000). The review of the literature suggests that major factors that affect soil aggregation include soil fauna, microorganisms, roots, and inorganic and physical processes. AMF influence ecosystem processes directly through host physiology and AMF hyphae glomalin decomposition on WAS and indirectly changing plant and soil microbial communities.

Further research is needed on no-till and cover crop's role in AMF colonization, glomalin production, and WAS. Continuous NT combined with CC may increase AMF populations and ultimately sequesters more C in the soil ecosystem. The CC supplies the carbon and the root exudates for AMF populations to produce glomalin or GRSP when the main grain crops are not being grown (in a corn-soybean rotation this may be greater than 68% of the calendar year). The AMF in the cover crops are generally of a different species than grain crops but provide many soil ecosystem services including improved soil structure, decreased bulk density, and improved water infiltration. Cover crops may provide a stable environment and a constant supply of C for AMF to process and incorporate into microaggregates and macroaggregates, where 90 percent of the C is stored. No-till and CC may mimic the natural environment, restore ecosystem functions, and restore balance to the soil ecosystem that past human activities have disrupted.

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