THE IMPORTANCE OF SOIL MICROORGANISMS IN AGGREGATE STABILITY

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Abstract

Aggregate stability is a soil quality factor. Water stability of aggregates is related to microbial activity. This paper reviews microbial inputs to aggregate stability. Soil fungi have long hair-like projections, hyphae that can physically entangle soil particles and exude glues. Microbial glues are discussed with special emphasis on arbuscular mycorrhizal (AM) fungi and the glue-like compound, glomalin. produced on hyphae of this group of fungi. Influences of management practices on AM fungi are discussed.

Introduction

Soil aggregates are groups of particles that bind to each other more strongly than to adjacent particles. Stability of aggregates is a measure of the resistance to disruption when outside and/or inside forces are applied. Shearing forces that occur during plowing and entry of water are two examples of forces leading to aggregate disruption. Rapid wetting of dry aggregates is especially disruptive. As water enters a dry aggregate. compressed gases are displaced resulting in aggregate break down (Fig. 1).

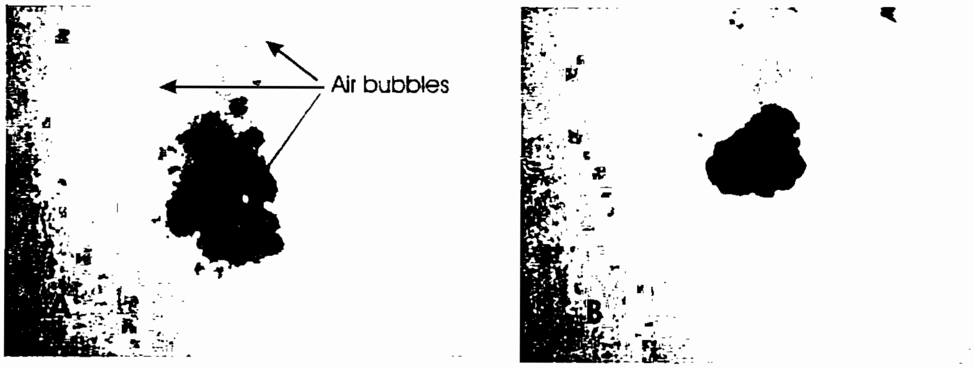

Fig. 1. Air-dried aggregates show differences in stability upon submersion in water. There was immediate release of air bubbles and breakdown of aggregate A. Aggregate B released air bubbles, but did not break apart.

Aggregate stability affects crop yield by influencing root growth, soil aeration and soil moisture. The presence of fungi is related to soil structural stability (Tisdall and Oades, 1979; Tisdall, 1994; Tisdall et al., 1997). Most fungi produce long hair-like projections called hyphae. Hyphae of arbuscular mycorrhizal (AM) fungi are recognized as important contributors to aggregate stability (Tisdall, 1994) because microscopic examination of aggregates shows physical entanglement of soil particles by hyphae (Tisdall, 1991). Tisdall (1991) also suggested the possible soil-binding mechanism of hyphae was due to secretion of extracellular cementing agents (polysaccharides).

Arbuscular mycorrhizal fungi (mycor = fungus, rhiza = root) are ubiquitous soil microorganisms that depend upon plants for growth and reproduction. These fungi colonize plant roots and obtain carbon directly from the plant cells via tree-like microscopic structures in plant cortical cells called arbuscules. Arbuscules are the source of carbon for growth of hyphae that colonize roots and extend into soil. Hyphae that extend from roots explore a greater volume of soil than roots alone can reach. Nutrients encountered by the growing tips of hyphae are transported back to the host plant. Phosphorus transport is the primary nutrient associated with activity of AM fungi. Phosphorus is an essential element that is not mobile and is in low concentration in most native soils. About 80% of land plants are hosts for AM fungi (Smith and Read, 1997), and this number includes most agriculturally important plants.

In the 1990's the discovery that hyphae of AM fungi produce copious amounts of an insoluble, hydrophobic protein with attached sugars (glycoprotein) (Wright et al., 1996) fit the concept that hyphae are producers of a cementing agent (Tisdall, 1991; 1994). The protein is named 'glomalin' because it is found on all fungi tested from the Glomales taxonomic order of fungi. All AM fungi examined to date produce glomalin.

Other fungi produce extracellular materials that bind soil particles into aggregates (Tisdall et al., 1997). There is current interest in a basidiomycete (mushroom) fungus that decomposes lignin and produces large quantities of glue (Caesar-TonThat and Cochran, 2000). Millet and lentil straw promote aggregate formation and stabilization of soil beneath the colonized litter. There is on-going research investigating the use of this fungus to stabilize surface soils after crops are harvested (T.C. Caesar-TonThat, personal communication).

Bacteria also produce extracellular glues that act as binding agents in soils. Production of bacterial glues in large amounts is limited by several factors. Bacteria are active in small niches where there is digestible organic material for the particular type of bacterium, nutrients for growth, and appropriate levels of moisture and temperature. Other bacteria may digest glues produced by one bacterium. Activity of bacteria is more spatially limited than for fungi because fungal hyphae extend long distances from the source of nutrition and can re-establish colonies when additional nutrients are encountered. In addition, because of the ability to spread, fungi are not affected to the same extent as bacterial colonies by small changes in conditions within a small niche.

Aggregate stability is used as a soil quality factor that integrates microbiological activity, organic matter, soil management and texture. Glomalin is a fraction of organic matter. This paper will focus on glomalin as a relatively long-lasting (Rillig et al., 2001) contributor to aggregate stability and soil organic matter. Management practices that influence aggregate stability will be discussed.

Approach

Research on glomalin began because an antibody was developed against an unknown substance on hyphae of AM fungi. The original plan was to use the antibody as an aid to identify AM hyphae in soil. One of the first tests utilizing the antibody followed production of glomalin during the life of a plant. This experiment revealed that a layer of glomalin builds up on hyphae and then sloughs off as hyphae age (Wright et al., 1996). Extraction of glomalin from hyphae requires harsh conditions – a citrate solution at a neutral to alkaline pH and high heat. Samples are placed in 20 to 50 mM citrate and autoclaved for one to several hours (Wright and Upadhyaya, 1996). Along with insolubility and the hydrophobic nature of the molecule, glomalin appeared to be a very unusual substance that could survive in soils. The emphasis on identifying hyphae in soils was shifted to determining the function of glomalin in soils. All of the initial work indicated that glomalin had the characteristics of a recalcitrant glue present at high concentrations in soils.

Glomalin on soil aggregates is shown in Fig. 2. Hyphae of an AM fungus is shown in Fig. 3.

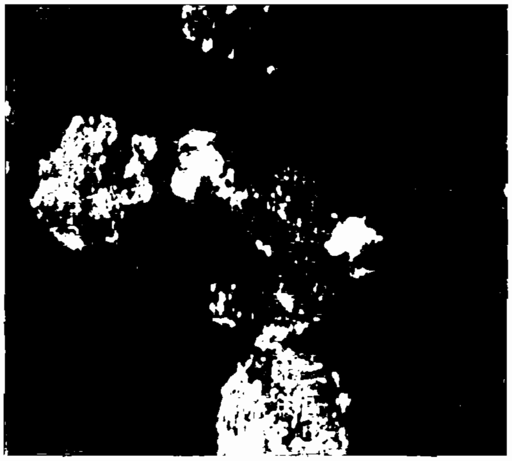

Fig. 2. Glomalin on the surface of soil aggregates. Hyphae of an AM fungus are coated with glomalin and appear as threads. Glomalin is brown in the native state but is white in this photo due to the reaction with an antibody. (Magnified 25 times.)

Fig. 3. A close-up view of hyphae of an AM fungus growing from a corn root. A microscopic view of a plant root is necessary to detect these hyphae because they are very fine and are not visible with the naked eye. (Magnified 64 times.)

Research on aggregates collected from field plots show a link between glomalin and aggregate stability. A survey of soils from various geographic areas showed a linear relationship between aggregate stability and glomalin concentration (Wright and Upadhyaya, 1998). Changes in aggregates stability and concentration of glomalin occurred during tillage management transition on a silt loam soil in Maryland (Wright et al., 1999). In the Maryland soil, aggregate stability in no-till plots was 16.7% greater than in the plowed plots, and glomalin increased in the no-till plots compared with the plowed plots during the 3-year transition. There was a linear relationship between glomalin concentration and aggregate stability. Additional research on the link between aggregates stability and glomalin is in published literature (Wright and Upadhyaya, 1998; Wright and Anderson, 2000; Rillig et al., 2002).

Recently we quantified the contribution of glomalin to soil organic matter. In soils from Colorado, Nebraska, Maryland and Georgia glomalin represents and average of 22 to 27% of soil organic carbon on a weight basis (manuscript submitted). Therefore, management practices that encourage glomalin production are valuable for soil quality and terrestrial carbon sequestration.

Management practices that encourage growth of AM fungi are generally those recommended for sustainable agriculture. No-till management, in contrast with conventional tillage, allows fragile networks of AM fungal hyphae to survive until another crop is planted. To picture a hyphal network, imagine a very fine, three-dimensional tangle of hyphae (see Fig. 3) that is torn apart by plowing the top 5 to 10 cm of soil. Proliferation of AM fungi is through re-colonization of growing roots leading to renewed growth of hyphae. Cover crops extend the life of the AM fungal network because many AM fungi can colonize plants through renewed hyphal growth or spore germination. Spores of AM fungi are vulnerable to desiccation when soil is inverted and left without a cover of living plants. Extensive tillage may eliminate some species of AM fungi that depend on spore survival to re-establish root colonization.

A recent study examined aggregate stability across the Great Plains at six locations from Canada to Texas. The major factors controlling aggregate stability were glomalin and clay concentrations (manuscript submitted). Aggregate stability under no-till management was greater than under conventional tillage. These finding are in agreement with the work of Kemper and Koch (1966) who evaluated aggregate stability and correlated stability of soils from the western U.S. and Canada with constituent variables. Stability was a function of organic matter, clay and iron oxides (Kemper and Koch, 1966). Iron did not contribute significantly to the more resent work, but interestingly, iron is a part of the glomalin molecule.

Phosphorus fertilizer inhibits growth of AM fungi. There is a cost to plants in photosynthetically fixed carbon to support the transport of P through hyphae to plant roots. When phosphorus is not limiting, plants close down the association with AM fungi. Therefore, over-fertilization with P inhibits glomalin production.

An enigma associated with microbial hydrophobic glues is that these compounds may have a negative influence on hydraulic properties. Adding fertilizer nitrogen to soils may reduce sorptivity due to production of hydrophobic organic compounds on surfaces of aggregates (Hallett and Young, 1999). Increased water repellency of soil aggregates was linked to a large increase in biological activity following nitrogen additions in a laboratory experiment. In particular, an increase in fungal (non-AM fungi) activity was noted. Whether this phenomenon occurs under field conditions and the duration of increased repellency require further study.

Other questions concerning management of AM fungi or glomalin are: (1) should soils be inoculated with these fungi to promote glomalin production, (2) can glomalin be produced in a factory and added to soil to enhance aggregate stability, and (3) are some plants better than others in promoting glomalin production? Inoculation of soils with AM fungi is possible but currently is a not recommended practice. Arbuscular mycorrhizal fungi are already present in all but highly contaminated or disturbed soils. The best way to apply information we currently know about their ecology to field-scale production is to use minimal disturbance, add no more phosphorus than is required for crop production, and use cover crops. The method of addition of glomalin to soils posed by Question 2 currently is not possible or practical, and there are reasons to reject this approach. AM fungi are active in the entire 0-10 cm profile. It is unlikely that glomalin as a dried or solution amendment would penetrate much below the surface. Therefore, glomalin production by naturally occurring AM fungi should be promoted so the influence of activity will be in the entire top part of the soil profile – soil that is vulnerable to wind and water erosion. Question 3 currently cannot be answered with any degree of certainty. Much more research on specific crops in the field at various locations is required to provide generally applicable recommendations. Old and modern cultivars need to be examined for phosphorus and AM fungal interactions. An example of this is that old and modern wheat cultivars show considerable variation mycorrhizal responsiveness (Zhu et al., 2001). Modern cultivars generally have reduced dependence on AM fungi. The economic benefit to growing modern P-efficient cultivars comes from lower cost of inputs, but this may be at the expense of inputs by AM fungi. Crops in the brassicaceae are among the plants that are not hosts for AM fungi. Mustard field crops such as canola and crambe do not support AM fungi. Therefore, soil stability may be affected by growing these crops.

There are many unknown influences of management, plant selection, specific fungi, soil and the environment on production of glomalin and soil stabilizing agents from other microorganisms. A major constraint for research on microbial inputs to sustainable agriculture is lack of appropriate tools to gather accurate information under field conditions. Lack of appropriate tools greatly inhibits field-scale research on AM fungi (Millner and Wright, 2002). Many studies use soil aggregate stability to reflect changes in microbial inputs. However, microbial influences on the entire physical framework of a soil (Young et al., 2001) should be examined. There is an urgent need for multidisciplinary efforts to develop the tools for landscape-scale research and to apply them.

Summary

Soil management affects soil microorganisms, sometimes profoundly. Aggregate stability is related to production of microbial glues, and some of the glue-producing microorganisms are amenable to management. Arbuscular mycorrhizal fungi produce copious amounts of a glue-like compound that is associated with aggregate stability. Future research should focus developing and using appropriate tools to analyze landscape-scale management effects on microbes, particularly AM fungi.

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