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Mycorrhizal Interactions in Sustainable Agriculture

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ABSTRACT: Vesicular-arbuscular mycorrhizal (VAM) fungi are an intimate link between the roots of most crop plants and soils, thereby affecting the development of host plants and host soils. The role of VAM fungi in improving plant nutrition and their interactions with other soil biota have been investigated with reference to host plant growth, but little is known about how these interactions affect soil structure. The impact of cultural practices and the particular role that VAM fungi play in improving soil structure are discussed in the context of sustainable farming.

KEY WORDS: vesicular-arbuscular mycorrhizae, roots, soil biota, soil structure, soil aggregation.

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I. INTRODUCTION

As the world human population continues to increase, the demands placed on agriculture to supply future food and fiber needs will be one of the greatest challenges facing the agricultural community. To meet this challenge, a great deal of effort focusing on the soil biological system and the agro-ecosystem as a whole is needed to better understand the complex processes and interactions governing the stability of agricultural land. At the present time food is (generally) not in short supply (rather there is a lack of timely distribution of foods to areas of need) due, in part, to high-input agriculture (Stewart et al., 1991). The great yield increases per unit land area have occurred over the past 40 years are a result of large increases of energy inputs, in terms of mechanization, irrigation, fertilizer, and pesticide use (Brown, 1987; Lal and Pierce, 1991). However, it is becoming increasingly clear that conventional agricultural practices cannot sustain the production base, a healthy plant-soil system (Papendick and Parr, 1992; Reganold, 1988).

Soil erosion is the primary degradative force occurring in soils in the U.S. (Board on Agriculture, 1993) and probably also worldwide (Sanders, 1992). Topsoil losses in the continental U.S. are estimated at roughly 1 billion Mg per year (Lal, 1994). The resulting loss in soil depth (rooting volume) is accompanied by losses in nutrients, in organic matter, and in the diversity of living organisms comprising the soil biota carried with the eroding sediments. In the U.S., agricultural practices are estimated to account for 64% and 57% of the pollution to rivers and lakes, respectively (Board on Agriculture, 1993). The environmental impact of erosion has shifted public opinion and federal policy toward the off-site damages of erosion (Lal and Pierce, 1991). Additionally, a number of estimates of yield reductions due to erosion over the next 100 years have been relatively small (Pierce, 1991; Pierce et al., 1984; Putnam et al., 1988), but others believe that such values have been underestimated due to omission of ephemeral and gully erosion (Board on Agriculture, 1993; Walker and Young, 1986). Therefore, soil degradation via erosion will remain a serious problem for agriculture as erosion control measures (reduced tillage) decrease productivity (Cook, 1984; Doran and Linn, 1994) and the environment experiences a disruption of ecosystem function.

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Erosion is not the only degradative process that occurs in agricultural soils and may not be the most important soil quality factor in many regions (Granatstein and Bezdicek, 1992). Compaction, salinization-sodification, acidification, and loss of biological activity are also important degradative consequences of agricultural production. These processes influence soil quality in many known and unknown ways (Arshad and Coen, 1992), rendering the soil more vulnerable to erosion (Stewart et al., 1991).

The complex nature and the multitude of both biotic and abiotic interactions that occur within soils have traditionally maintained our view of the below-ground aspects of agriculture as a black box (out of sight, out of mind). However, as we move from high-input, conventional agriculture that is production based to sustainable systems that rely more heavily on nutrient cycling and soil microbial ecology, the elucidation of the complex interactions occurring in soils will be necessary. It will be necessary to employ both reductionist research approaches to define the various functional roles of particular components of the soil-plant interface, along with holistic approaches (Coleman, 1985; Peterson et al., 1993) to integrate such information and better define the cultural conditions that govern agro-ecosystem functioning and stability.

However, the question remains: What aspects of the plant-soil interface merit extensive investigations that can be expected to contribute to the large-scale problem of agricultural stability? O'Neill et al. (1991) present a convincing argument that mycorrhizal research is one such area deserving extensive investigation for sustainable agriculture, primarily because mycorrhizal fungi are a crucial link between roots and soil. The focus of this contribution is the role that vesicular-arbuscular mycorrhizal (VAM) fungi play in the interactions between plants and soils with particular emphasis on the contribution of VAM fungi to soil structure. Some of the ideas and research discussed will also relate to the role that ectomycorrhizal fungi play in stabilizing soils, particularly for nurseries and silviculture. Ectomycorrhizal effects on soil structure have been discussed briefly by Emerson et al. (1986) and McFall (1994).

II. VAM FUNGI LINK PLANTS AND SOILS

VAM fungi are ubiquitous in soils around the globe and are a natural link between the roots of most plants and soil (Reid, 1990). Some form of mycorrhiza was apparently necessary for the colonization of terrestrial environments to occur (Pirozynski and Malloch, 1975). VAM fungi extend the plant's root system through an intimate relationship that permits a more direct regulation of the mycosymbiont by the plant compared with other soil biota. There is evidence that host plants regulate the extent of infection by VAM fungi, especially under high nutrient conditions (Koide and Schreiner, 1992). This fact has ecological meaning in terms of nutrient cycling in soil. For example, the accelerated mineralization of organic matter in the rhizosphere by the soil microbial biomass (SMB, defined as the soil microbial population consisting of fungi, bacteria, actinomycetes, and microfauna) may occur under conditions that result in either competition or cooperation between the SMB and plant roots for immobilized nutrients (Smith, 1994). As a result, the plant may not always derive a benefit from rhizodeposition (Lynch and Whipps, 1991) in terms of increased nutrient uptake, although it has better control of this carbon expenditure with mycorrhizal symbionts. This does not mean that plant roots do not also participate in mutualistic associations with other components of the SMB. The SMB plays a significant role in supplying nutrients to plant roots (Smith, 1994), but VAM fungi are rarely considered in the pertinent literature. Likewise, the contribution of VAM-fungal biomass is not included in some of the assays employed to estimate the SMB (Parkinson and Paul, 1982; Visser and Parkinson, 1992), although VAM-fungal hyphae may comprise the largest portion of it (Hayman, 1978).

VAM fungi are generally known to benefit plant health, the net benefit to plant health increasing as stress (particularly nutrient and water) increases (Bethlenfalvay and Svejcar, 1991; Sieverding, 1991). VAM fungi contribute greatly to phosphorus uptake (George et al., 1992; Koide and Schreiner, 1992; Smith et al., 1992), to nitrogen uptake directly (Ames et al., 1983; Azcon-Aguilar et al., 1993; Frey and Schüepp, 1993),

and to nitrogen uptake both directly and indirectly (by increasing nitrogen-fixation rates due to improved phosphorus nutrition) in associations of legumes (Barea and Azcon-Aguilar, 1983; Barea et al., 1987). Although it has been generally thought that VAM fungi increase nutrient and possibly water uptake by increasing the soil volume explored by roots, recent findings suggest that hyphal uptake is not based on increased surface area alone (Li et al., 1991). Regardless of the actual mechanisms involved, VAM fungi can increase the efficiency of phosphorus and nitrogen removal from the soil solution over that of roots alone, which has obvious implications for reducing fertilizer inputs and leaching.

VAM fungi have also been shown to be important in the uptake of other ions, including K, S, Mg, Fe, Zn, Cu, (Cooper, 1984; Sieverding, 1991; Smith and Gianinazzi-Pearson, 1988), and alternatively, in reduced uptake of certain metal ions, especially manganese (Bethlenfalvay and Franson, 1989; Kothari et al., 1991). It is unclear, however, whether the effects observed in numerous studies is due to VAM fungi alone, or due to associations with other components of the SMB. In fact, it is presently unclear how much of the literature concerning VAM fungal interactions with improved plant growth can be attributed solely to the fungus (Paulitz and Linderman, 1991). As suggested by Hetrick and Wilson (1991) and others (Schreiner and Koide, 1993), the soil microflora influences mycorrhiza formation and host growth response.

Mycorrhiza have a profound effect on the rhizosphere, altering the microbial community structure (Ames et al., 1984; Bagyaraj and Menge, 1978; Meyer and Linderman, 1986; Secilia and Bagyaraj, 1987) and leading to the concept of the mycorrhizosphere (see Linderman, 1988). Interactions of VAM fungi with other soil biota, like phosphate-solubilizing bacteria, plant growth-promoting rhizobacteria, plant pathogens, and biocontrol agents, nematodes, and microfauna have been investigated and display the manifold effects of VAM fungi in soil, which can result in significant positive and negative effects on plant growth (Paulitz and Linderman, 1991). More often than not, VAM associations with other soil organisms are associated with positive effects on plant growth (Pagyaraj, 1984; Dehne, 1982; Paulitz and Linderman, 1991), although numerous negative effects on plant growth are also known (Azcon-Aguilar et al., 1986; Staley et al., 1992). How such interactions affect soil structure is not clear, and because a majority of this work has been conducted in pots employing pasteurized soils, it is unclear how these interactions manifest themselves under field conditions.

The soil (extraradical) hyphae of mycorrhizal roots are paramount in linking the roots of plants to soil. Estimates of VAM hyphal lengths (see Miller and Jastrow, 1994) underscore the importance of soil hyphae to both nutrient uptake (O'Keefe and Sylvia, 1992; Pearson and Jakobsen, 1993) and structural stabilization of soils (Miller and Jastrow, 1990; Tisdall and Oades, 1979), although their activity, location, or architecture as opposed to length may also be important (Jakobsen et al., 1992). Few studies have measured the soil phase of VAM fungi due to the difficulty involved and the ambiguous nature of the methods (Allen and Allen, 1986; Ames and Bethlenfalvay, 1987; Sylvia, 1986).

The soil hyphae of VAM fungi can extend well beyond the rhizosphere (Camel et al., 1991) to the bulk soil, and hence are important sources of carbon to soil organisms. It is unclear how much carbon VAM hyphal exudates contribute to the soil (Jakobsen and Rosendahl, 1990; Whipps, 1990), but observed changes in bacterial populations far beyond the rhizosphere (Kothari et al., 1991) suggest that exudation is substantial. In addition, hyphal biomass, dead or alive, represents a food source to other soil biota beyond the rhizosphere.

The functional roles of VAM hyphae that occur in the rhizosphere may be quite different from those played outside this area of root influence. Some VAM fungi may have developed methods to compete for the pool of mineralized nutrients released in the rhizosphere (Christensen and Jakobsen, 1993), whereas others may have developed alternate nutrient uptake mechanisms that function beyond the rhizosphere. VAM hyphae have been shown to alter soil properties in their immediate vicinity, thus producing a hyphosphere effect similar to the rhizosphere effect produced by roots (Li et al., 1991). The interactions with other soil microbes in the hyphosphere are yet to be defined. However, the affinity of VAM mycelium for soil organic matter (St. John

et al., 1983; Warner, 1984) and the ability to enter micropores within the soil matrix (due to their small size) may represent important niches that VAM fungi can exploit that result in increased nutrient supplies to VAM plants. The ability to access smaller pores and produce extensive networks of hyphae in the soil matrix are also important factors in the formation and/or stabilization of soil aggregates by VAM fungi.

III. SOIL AGGREGATION

Water-stable soil aggregation is a major determinant of soil structure (Hamblin, 1991; Kemper and Rosenau, 1986). Soil structure is viewed as the size distribution and spatial arrangement of various soil primary particles and organic matter into aggregates, and the associated pores within and between such aggregates (Jastrow and Miller, 1991). Edwards and Bremner (1967) proposed that soil consists of macroaggregates (>250 μm) and microaggregates (<250 μm) and that the bonds holding the microaggregates together are stronger than those in macroaggregates. The spatial arrangement of microaggregates and their conglomeration into macroaggregates governs the abiotic processes and biogeochemical cycles that determine soil fertility (Elliot and Coleman, 1988). One could argue that there are no processes occurring in soils that are independent of structure, because soil structure dictates the movement of water through the system, the diffusion of gases, and hence the activity of all the living components present. Because a well-aggregated soil structure is a prerequisite for halting the erosive forces of wind and water (Chepil, 1942, 1943: Harris et al., 1966), it is imperative that we understand the forces behind the formation and stabilization of aggregates and the cultural practices that lead to aggregate stability.

Although a considerable body of literature has dealt with soil aggregation, a generally accepted mechanism for the formation and stabilization of aggregates has not emerged (Martens and Frankenberger, 1992). A vast amount of literature was reviewed by Harris et al. (1966) who concluded that the formation and degradation of water-stable aggregates comprise a complex interrelationship of physical, chemical, and biological reactions. Numerous activities, including root growth, root exudation, production of organic acids, metabolism of root exudates, extraction of soil water by roots, entanglement and production of soil-binding agents by roots, filamentous fungi and actinomycetes, production of binding agents by bacteria, soil cover, decomposition of plant materials, organic matter turnover, earthworm activity, freezing and thawing, type and number of tillage practices, and soil moisture content play a role in aggregation of agricultural soils (Gish and Browning, 1948; Harris et al., 1966; Martin, 1971; Boyle et al., 1989).

A. Organic Matter and Soil Aggregation

It has been long known that organic matter improves soil structure (Harris et al., 1966; Jenny, 1941) and the benefits of organic amendments to agricultural land for the purpose of improving structure are well known (Alderfer, 1946; Martens and Frankenberger, 1992). VAM-fungal colonization can increase soil organic matter contents in a short period of time (Quintero-Ramos et al., 1993). Cheshire et al. (1983, 1984) found that the aggregating effect of soil organic matter was correlated to its polysaccharide content, whereas Baldock et al. (1987) did not find a significant correlation between aggregate stability and polysaccharide content in soils from various cropping treatments. Chaney and Swift (1984, 1986b) showed that humic materials stabilized soil aggregates and their effects persisted longer than polysaccharide-stabilized aggregates. However, Visser and Caillier (1988) reported that humic acids are effective disaggregating agents. An explanation for these contradictory results may be due to the ability of humic materials to aggregate soils only in the presence of polyvalent cations (Gu and Doner, 1993). Other researchers have also indicated that polyvalent cations play a crucial role in soil aggregation (Elliot and Coleman, 1988; Hamblin and Greenland, 1977; Muneer and Oades, 1989).

It is well documented that cultivation enhances the mineralization of organic matter by exposing protected organic matter to degradation by micro-

organisms, which results in a concomitant loss of water-stable soil aggregates (Harris et al., 1966; Tisdall and Oades, 1982). A great deal of aggregate destruction in agricultural soils can be eliminated by adopting reduced tillage or no-till management through the protective action of surface residues (Chan and Mead, 1988; Lal et al., 1994) and the decrease in soil organic matter turnover (Havlin et al., 1990). Soil disturbance is known to decrease VAM-fungal colonization and nutrient uptake in corn (Evans and Miller, 1988, 1990), presumably due to the disruption of the hyphal network that exists in soils under reduced tillage. The role of the existing VAM-hyphal network has not been examined in relation to soil aggregation, but the disruption of it by tillage may contribute to the reduction of aggregate stability.

The effects of various plant species or crop rotations significantly influence aggregation in field soils. In a comparison of crop rotations, water-stable soil aggregation was greatest in corn-soybean rotation, followed by continuous corn, followed by corn-oat-meadow rotation (Lal et al., 1994). Within each of the rotation treatments, aggregation was correlated to the organic carbon content of the soils. These relationships, however, did not hold across the rotation treatments because the continuous corn rotation had the highest soil carbon contents, whereas the corn-soybean rotation had the highest level of aggregation. These result suggest that both the quantity and quality of organic carbon play a role in aggregate stabilization. Furthermore, tillage treatments employed in the above study showed that overall, reduced tillage was associated with increased aggregation, except in the case of the corn-soybean rotation where chisel-plowed plots had higher aggregate stabilities than no-till plots. Other reports have shown that alfalfa or barley cropping produced positive effects on soil aggregation, whereas corn cropping or fallow controls did not (Angers and Mehuys, 1988; Angers et al., 1992), which was correlated to the total carbon contents of the soil. Wheat, followed by sorghum, was shown to stabilize soil structure over soybeans (Armbrust et al., 1982). In corn-soybean rotations, soil losses due to erosion were greater following soybeans than following corn (Laflen and Moldenhauer, 1979; Oschwald and Siemens, 1976). Soil aggregation in this study was correlated to both root length and weight, and appeared to involve freeze-thawing effects over winter. Although tillage and cropping effects on soil structure are often associated with soil organic matter, the mechanisms and the specific fraction(s) of organic matter involved in aggregate formation or stabilization are not well understood (Gu and Doner, 1993). A step forward in our understanding of the many complex and sometimes contradictory results was made by Tisdall and Oades (1982) when they proposed the hierarchical theory of soil aggregation. An important feature of this theory is the role that VAM hyphae play in the formation and stabilization of soil aggregates.

B. Hierarchical Theory of Soil Aggregation

In the hierarchical theory (Tisdall and Oades, 1982), macroaggregates, whose stability is crucial to resisting erosion, are held together by labile forms of soil organic matter that are exposed and lost on cultivation. Tisdall and Oades (1980b) and others (Elliott, 1986; Gupta and Germida, 1988) have shown that a loss of macroaggregates due to cultivation is accompanied by an increase in microaggregates. The formation of microaggregates is similarly built on smaller structural units that are initially composed of primary clay particles held together by electrostatic bonds in association with inorganic oxides and organic polymers forming floccules. These clay floccules then encrust various small particles of organic matter forming very small aggregates (2 to 20 μm), which are combined with small sand grains to form microaggregates (20 to 250 μm). The microaggregates appear to be cemented by polyvalent cation bridges between the negatively charged clay floccules and carboxyl groups of organic matter (Edwards and Bremner, 1967; Elliot and Coleman, 1988; Muneer and Oades, 1989). The organic matter that binds aggregates of the 2 to 20 μm and the 20 to 250 μm size classes was referred to as persistent organic matter that is protected from degradation and is generally not influenced by cultivation (Tisdall and Oades, 1982).

According to the hierarchical theory, binding of microaggregates into macroaggregates occurs through the entanglement by roots and fungal hyphae, particularly VAM hyphae, which is influenced by cultivation (Tisdall and Oades, 1980b). Roots and fungal hyphae were described as transient binding agents by Tisdall and Oades (1982) that could persist in aggregates for periods of months (Tisdall and Oades, 1980a). The important role of VAM fungi was shown by Tisdall and Oades (1979) in pot experiments where VAM hyphal length accounted for most of the increase in water-stable macroaggregates (>2000 μm) in different ryegrass treatments. This was the first report showing that VAM hyphae were important soil aggregators in heavy soils, although fungal hyphae had been implicated as having primary importance in soil aggregation long ago (McCalla, 1946; Swaby, 1949). Polysaccharide binding materials were considered by Tisdall and Oades (1982) as temporary binding agents and their relative importance to macroaggregate stabilization was thought to be small. Furthermore, macroaggregates may require recolonization by roots and fungal hyphae to maintain their stability in cultivated soils (Foster, 1994).

Other reports support the hierarchical theory, showing that the organic matter associated with macroaggregates was less complex (Dormaar, 1984) or less highly processed (Elliot, 1986) than the organic matter associated with the more stable microaggregates. Additionally, the nutrient contents (organic C, N, P) of macroaggregates is greater than that of microaggregates leading to the suggestion that "cultivation results in a smaller proportion of soil containing high-nutrient macroaggregates and a larger proportion of soil containing low-nutrient microaggregates" (Elliott, 1986). These findings were supported by Gupta and Germida (1988) who showed that 69 years of cultivation resulted in a decrease of macroaggregates and of the nutrients (C, N, S, P) they contained, when compared with virgin soil. The decline in aggregation was associated with a large decrease in fungal biomass, but not with bacterial plate counts, supporting the important role played by fungal hyphae in aggregating soils. The hierarchical theory may not apply to all soils (see Tisdall, 1994), as organic matter is not the primary binding material in some soils (Greenland, 1971) and macroaggregates from different soils may not be composed of similarly sized microaggregate fractions as described by Tisdall and Oades (1982). Many soils under cultivation (Edwards and Bremner, 1967; Elliot, 1986; Elliot and Coleman, 1988; Miller and Jastrow, 1990; Oades and Waters, 1991) appear to involve aggregate size classes and binding agents similar to the red-brown earth (alfisol) described by Tisdall and Oades (1982).

A clearer picture of the organic matter constituents and other soil components involved in soil aggregation may be achieved by isolating particular aggregate size fractions before attempting to identify the specific binding agents involved in stabilizing such aggregates. Studies that employ whole soil samples not separated into different aggregate size classes may lead to inconclusive results because the primary binding components of a particular aggregate size class may be spatially separated from those of other size classes. The enriched labile fraction (ELF) isolated by Cambardella and Elliot (1994) from macroaggregates may be the fraction of soil organic matter that is involved in binding macroaggregrates in a mollisol. The ELF appears to be of microbial origin and it is particularly labile, but is physically protected from degradation inside macroaggregates (Cambardella and Elliot, 1994). Future work in this area will help clarify the roles of various soil chemical and biological constituents that are involved in binding soil aggregates.

C. Roots, Soil Microbes, and Soil Aggregation

Roots affect both aggregate formation and degradation, depending on conditions. The physical forces of root growth and the production of acids and chelating agents can be associated with aggregate destruction (Harris et al., 1966; Reid and Goss, 1982; Reid et al., 1982). The production of mucigel, rhizodeposition, increases of polycations in the rhizosphere, and soil water extraction by plant roots have been implicated in the formation or stabilization of soil aggregates

(Gish and Bowning, 1948; Harris et al., 1966; Lynch and Whipps, 1991; Perfect et al., 1990; Pojasok and Kay, 1990; Reid and Goss, 1981). Even though root activities can disaggregate soil under some circumstances, whenever roots die they will contribute to aggregation by supplying organic matter for eventual degradation by the soil biota. Root fragments, hyphal fragments of VAM fungi, and dead VAM spores and sporocarps may act as nucleation sites in the formation of soil aggregates by supplying substrates to the microbial community. However, while active, VAM hyphae may also enhance aggregation in the same way as roots, due to water extraction that causes a parallel reorientation of embedded clays on root surfaces (Boyle et al., 1989).

The ability of numerous soil organisms to stabilize aggregates has been demonstrated *in vitro* and typifies the complexity of interactions that may be involved in soil aggregation in the field. Glucose addition accelerates the formation of stable aggregates due to the production of microbial binding agents (Harris et al., 1966; Martin, 1971), but such treatments do not last and the aggregate stability declines as the microbial products are degraded (Chaney and Swift, 1986a). More slowly consumed substrates, like decaying plants and fungal and arthropod tissues, stabilize soil aggregates more slowly, but with more persistent effects (Chaney and Swift, 1986b; Martin, 1971). In a study comparing the abilities of fungi, bacteria, and actinomycetes to stabilize soil aggregates, it was shown that different binding materials were produced by different microbes including lignin, humic materials, polysaccharides, and waxes. Some of the microorganisms examined in this study produced a combination of binding materials. In addition, the mechanical stability of aggregates stabilized by different organisms was highly variable and was affected by soil type (Aspiras et al., 1971). Chitin and humic materials decompose more slowly in soils than polysaccharides like cellulose, pectins, and xylans (Martin, 1971), supporting Tisdall and Oades' (1980a) observations on the persistence of VAM hyphae in macroaggregates for periods of months.

McCalla (1946) and Swaby (1949) concluded that soil fungi were the most effective soil-binding microbes, followed by actinomycetes and certain gum-producing bacteria. Also, Bond and Harris (1964) concluded from microscopic investigations that fungal mycelium persisted in well-aggregated soils, but not in poorly aggregated ones. Other researchers have also concluded that fungi are more important than other soil microbes in the formation or stabilization of aggregates (Foster, 1994; Gupta and Germida, 1988; Molope et al., 1987; Tisdall and Oades, 1979, 1982). Physical entanglement by filamentous organisms was proposed as the major soil aggregating mechanism (Swaby, 1949; Tisdall and Oades, 1982). However, the obvious role that polysaccharides play in aggregation (Martin, 1971), coupled with the findings by Cheshire et al. (1983, 1984) and Chaney and Swift (1986a,b) regarding the resistance of soil polysaccharides to periodate cleavage, indicates that the involvement of polysaccharide cementing agents in the stabilization of macroaggregates by roots and fungal hyphae has been underestimated.

D. VAM Fungi and Soil Aggregation

Many of the studies mentioned above did not consider the role that VAM fungi play in the interactions between plants and soils. Yet agricultural practices (e.g., tillage and crop rotations) are known to effect VAM fungal communities (Johnson and Pfleger, 1992; Johnson et al., 1991) and function (Evans and Miller, 1988, 1990) and the fungi, in turn, are a crucial component of plant and soil development (Bethlenfalvay, 1992; Miller and Jastrow, 1992). The effects of VAM fungi on soil development, in particular, reaches from the establishment and maintenance of aggregates in sand dunes (Clough and Sutton, 1978; Koske et al., 1975; Sutton and Sheppard, 1976) to the stabilization of natural and disturbed ecosystems (Barea and Jeffries, 1994; Bethlenfalvay and Schüepp, 1994).

The effects of VAM fungi on the stability of agricultural soils began with the pioneering work of Tisdall and Oades (1979), who showed the importance of VAM soil hyphae in determining the level of water-stable aggregation. The binding of soil aggregates by VAM soil hyphae does not appear to be dependent on their viability (Tisdall

and Oades, 1980a). Rothwell (1984) observed the binding of individual sand grains and loose aggregates by the external mycelial network of *Glomus clarum* in a sandy-loam mine spoil. Both the VAM hyphae and the sand grains in contact with them stained red with periodic acid-Schiff reagent indicating the presence of polysaccharides. Thomas et al. (1986) demonstrated that onion roots colonized by *Glomus macrocarpum* increased the aggregation of a calcareous silty-clay loam, when compared with non-VAM roots. Both root mass and VAM-hyphal density were significantly correlated to macroaggregation but the correlation with root mass was greater, suggesting that roots may have been more important in aggregating this soil. However, in a later study by Thomas et al. (1993), the separation of root and VAM fungal contributions to soil aggregation showed that both roots and external VAM hyphae contributed equally to water-stable, soil aggregation, whereas roots and VAM fungal hyphae together had an additive effect. In addition, it appeared that the main effect of VAM fungi and roots in this experiment was to stabilize existing aggregates present in the initial soil, based on the quantity of fine sand (mixed with the initial soil) present in aggregates at the end of the experiment. However, as noted by Thomas et al. (1993), the arbitrary standard of aggregate stability set by the wet-sieving procedure may have biased the results, such that newly formed aggregates, which would have incorporated the fine sand, were not yet stable enough to withstand the forces of slaking in the method employed.

Miller and Jastrow (1990) reported that the root lengths of fine roots (0.2 to 1 mm), the lengths of both fine and very fine (<0.2 mm) roots colonized by VAM fungi, and the external hyphal lengths of VAM fungi were correlated with the geometric mean diameter (GMD) of water-stable aggregates from field soils (mollisols and an alfisol) of prairie restorations and cultivated sites. A multiple regression path analysis was then employed to determine the relative importance of the measured variables on the GMD. The results showed that the length of VAM soil hyphae had the greatest impact on GMD, followed by fine root length. Both fine and very fine root lengths were significantly correlated with GMD whenever the path included VAM fungal parameters, but the very fine root lengths did not significantly correlate with GMD directly.

Interactions between roots and VAM hyphae, as observed by Thomas et al. (1993), may have contributed to the observed differences between the fine and very fine roots in the experiments of Miller and Jastrow (1990). The lack of a direct correlation between the GMD of water-stable aggregates and the very fine roots was hypothesized to be due to the greater dependence of coarser than of finer roots on VAM associations (as suggested by Tisdall, 1994). Alternatively, an interaction between root exudates and VAM hyphae (or hyphal exudates) might explain these results. If the differences between the fine and very fine roots isolated by Miller and Jastrow (1990) can be attributed to root age, differences in the chemical composition of root exudates produced by fine and very fine roots may have occurred in their respective rhizospheres (Campbell and Greaves, 1990). For example, the production of secondary metabolites (e.g., phenolics, tannins) by older roots could have contributed to the stability of aggregates by cross-linking the polymers holding aggregates together. Rothwell (1984) suggested that reactions between root phenolics and glucosamine residues in VAM hyphal walls could be a stabilizing mechanism for soil aggregates. Although we know of no evidence in support of aggregate stabilization by secondary metabolites exuded by roots, the long-term stability of aggregates in polysaccharide-treated soils was shown to be greatly increased by the addition of tannic acid (Griffiths and Burns, 1972).

The above studies show that VAM fungi enhance soil aggregation. Yet many questions remain unanswered. Do all VAM fungi contribute to aggregation or are some isolates better adapted to increase aggregation than others? Is entanglement of soil particles the main function performed by VAM fungi that leads to improved soil structure? Or does the production of extracellular gums or mucigel play a major role? What kinds of extracellular materials are exuded by VAM hyphae? How do interactions with other soil microbes influence soil aggregation by VAM fungi? Many of these questions and others were dis-

cussed by Tisdall (1991, 1994), and much work will be required to define the best strategies for preserving soil structure through the management of VAM fungi.

With regard to VAM-fungal species comparisons, we examined plant and soil responses of pot-grown pea in Chehallis silty-clay loam to treatment combinations of different VAM fungi and fungicides. Seed yield was significantly improved by all VAM-fungal treatments (Figure 1A), even though the soil studied was relatively high in phosphorus (28 mg kg^{-1} P, Olson). The soil response (water-stable aggregates, 1 to 2 mm) to VAM-fungal treatments showed that *Gigaspora rosea* was more effective than either *Glomus etunicatum* or *Glomus mosseae* (Figure 1B). Treatments containing a mixture of all three fungi caused significantly greater water-stable aggregation than any of the individual isolates (Figure 1B). Relative spore abundance of *G. rosea* in the mixed inoculum at the end of the experiment was very low and the number of *G. rosea* spores per gram of soil was reduced more than fivefold in the mixed inoculum treatment vs. that of the individual *G. rosea* treatment. Unfortunately, spore production is not a reliable indicator of soil or root colonization. Therefore, no valid inference can be drawn from low *G. rosea* spore densities as to the hyphal contribution to soil aggregation. However, comparisons among the individual VAM-fungal isolate treatments in this study support findings by Miller and Jastrow (1992) who showed that increases in soil aggregation over 5 years in prairie restorations were associated with increases in the relative spore biovolume of *Gigaspora gigantea* and decreases in that of two *Glomus* spp.

Multiple colonization by different VAM fungi is often associated with more consistent benefits to plant growth over a range of environmental conditions, than associations with a single mycosymbiont (Daft and Hogarth, 1983; Koomen et al., 1987) and a diversity in the VAM fungal population, capable of responding to environmental stresses, has been proposed to account for the high productivity of some soils (Ellis et al., 1992).

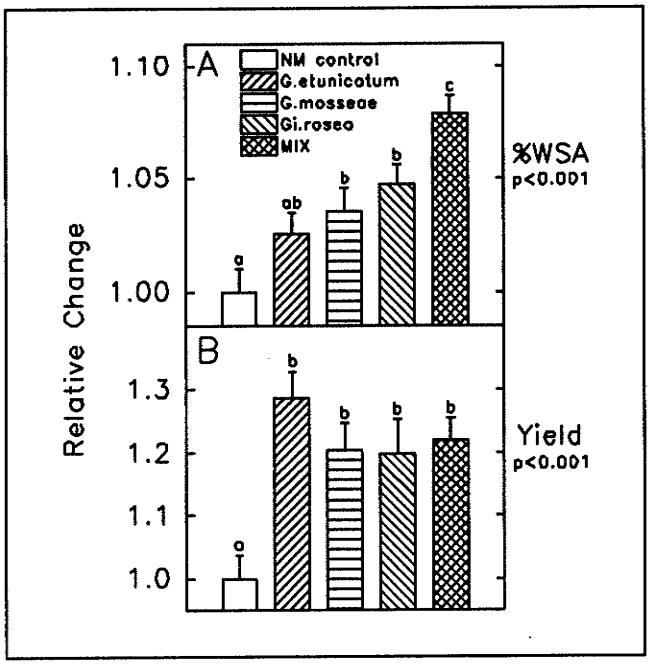

FIGURE 1. Effects of VAM-fungal inoculation on (A) percentage water-stable aggregates, 1 to 2 mm and (B) seed yield in pot-grown pea. Relative change as function of NM control (n = 20).

Our results indicate that the benefits of multiple inocula are also applicable to soil responses. Differences in hyphal density and morphology among VAM isolates may account for our divergent soil responses. Morphological restrictions of different VAM fungi could result in the colonization of different microsites within soil that may enhance aggregation whenever multiple fungi are colonizing the soil. Because the spatial distribution of soil hyphae can vary among fungal species (Jakobsen et al., 1992), an increase in the overall hyphal density of VAM mycelium around roots may also result from multiple VAM-fungal infections, compared with single species. Alternatively, different VAM fungi may produce different types and/or amounts of soil binding agents and the interaction of these agents within aggregates may result in a synergistic effect on soil stability. Also, if soil microbe-VAM fungus interactions are specific and preferential (Kothari et al., 1991; Meyer and Linderman, 1986), their derivative products could lead to a synergistic enhancement of the aggregation process. One can envision that the path analysis of aggregate size distribution carried out by Miller and Jastrow (1990) could be extended beyond the soil hyphae of VAM fungi (the last link in the path) to include other soil microbes.

The interaction of VAM fungi with other soil biota, particularly bacteria, has been shown to alter both fungal and host-plant responses to each other (Paulitz and Linderman, 1991), and we expect it to affect the soil response also. Recent experiments investigating the interactions between a rhizobacterium (*Bacillus* spp.), a VAM fungus, and *Rhizobium* nodulation in pea plants showed the variation in both plant and soil responses that can occur whenever three rhizo-organisms are manipulated (Table 1). The biomass of non-nodulated pea plants that received nitrate fertilizer increased when colonized by VAM fungi and decreased when inoculated with *Bacillus.* However, no differences in biomass occurred in nodulated plants. Soil structure responded positively to both VAM fungal inoculation and *Bacillus* inoculation, but the relative importance of the VAM fungus in promoting aggregation was greater than that of the *Bacillus* treatment (Table 1). the soils without VAM fungi disaggregated during the course of the experiment, and this slaking was greater in the nodulated plants. An important finding from this experiment was that the positive effects of VAM fungal inoculation on soil aggregation were associated with either no above-ground response (nodulated plants) or an increased above-ground response (nitrate-fertilized plants), whereas the positive effects of the rhizobacterium on soil aggregation were associated with no effects (nodulated plants) or negative effects (nitrate-fertilized plants) on plant growth. These findings indicate the role that can be played by soil microbes in mitigating the responses of plants and soils to VAM fungi and the need to integrate the soil biota in VAM experiments to determine the ultimate response of the agrosystem to VAM fungal manipulations.

TABLE 1
Plant and Soil Responses to N Nutrition and Rhizo-Organisms in Pot Culture

		Rhizobium		Nitrate	
Parameters	**ASAR**	**–VAM**	**+VAM**	**–VAM**	**+VAM**
Plant					
Biomass (g)	+*Bacillus*	3.5	3.5	2.9	3.6
	–*Bacillus*	3.4	3.5	3.1	5.2
Root/shoot	+*Bacillus*	0.14	0.17	0.22	0.23
	–*Bacillus*	0.14	0.018	0.19	0.15
Soil					
pH	+*Bacillus*	6.7	7.2	7.4	7.5
	–*Bacillus*	6.7	7.2	7.5	7.6
% Δ WSA	+*Bacillus*	–20	14	–18	33
	–*Bacillus*	–33	2	–26	28

IV. CONCLUSIONS

VAM fungi are effective soil aggregators and therefore management of VAM fungi can be considered as a biological technique for the purpose of improving soil structure. Whenever VAM fungi have been examined in relation to soil structure, they have been shown to enhance aggregation in both pot and field experiments. The exact mechanisms of VAM fungus-mediated soil aggregation are little known, but seem to result from the binding of small particles into microaggregates and the entanglement of microaggregates into macroaggregates. The ability of VAM fungi to extract water from small pores within the soil matrix may contribute to the stabilization of soil aggregates created by entanglement and cementing mechanisms.

More aggregated, stable soils produced through management strategies that promote healthy VAM-fungal development will not only decrease the off-site damages of erosion, but will also become more productive. The creation and stabilization of soil aggregates results in the protection of soil organic matter within aggregates, decreases in soil nutrient losses through leaching, and increases in the plant's ability to rely on mineralization to supply future needs.

Isolates of VAM fungi differ in promoting soil and plant responses as influenced by environmental conditions. Because soil response may or may not be related to plant response, VAM-fungal treatments (isolates or mixtures of isolates in conjunction with other microbes) may be identified that result in a net benefit (balancing agricultural production and soil conservation) to particular agrosystems. Therefore, the inclusion of the soil response in the evaluation of "efficient" VAM fungi is needed. Application of VAM fungi in future agricultural management will depend to a large degree on our ability to identify the specific functions that VAM fungi are performing within particular field systems and to integrate these findings into management strategies.

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