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POSSIBLE ROLE OF ARBUSCULAR MYCORRHIZAL FUNGI IN DEVELOPMENT OF SOIL STRUCTURE

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INTRODUCTION

Soil consists of particles of sand, silt and clay held together into aggregates of various sizes by organic and inorganic materials. In the field, the stability of these aggregates to water and the pores between them affect infiltration, drainage and storage of water, the activity of biota in the soil, erosion of the top soil and the growth of crops. To keep an agricultural system sustainable and profitable, we must manage it as an ecological system, in order to provide the best soil structure for plants. Soil aggregates, composed of primary particles and binding agents, are the basic units of soil structure (Batey, 1974). The size, shape, and stability of soil aggregates control the pore size distribution which, in turn, affects soil physical properties. Aggregate stability is a way to estimate the ability of a soil to maintain good water infiltration rates, good tilth and adequate aeration for plant growth (Emerson et al., 1986; Kemper and Roseman, 1986). Soil aggregation is a complex process that begins with consolidation of soil particles into microaggregates (0.25-mm diameter) and progresses towards formation of macroaggregates from these smaller units (Tisdall and Oades, 1982). Several authors have proposed models of aggregates of different sizes held together by different organic, inorganic materials and micro-organisms (Tisdall and Oades, 1982; Elliott and Coleman, 1988; Oades and Waters, 1991).

Arbuscular mycorrhizal (AM) fungi colonize plant roots and the surrounding bulk soil. They transport mineral nutrients from the soil to the plant and carbon compounds from the plant to the soil, and have pervasive effects on plant form and function, and on the composition of the

soil microbiota. Under the growing plants, the hyphae of AM fungi were shown to bind microaggregates of an alfisol into water stable macroaggregates (Tisdall and Oades, 1979). The AM hyphae appeared to entangle microaggregates physically and to secrete polysaccharides to which the microaggregates firmly adhered. Miller and Jastrow (1992) proposed that AM hyphae form and stabilize aggregates of soil through three distinct processes: (1) The AM hyphae physically entangle primary particles of soil; (2) roots and AM hyphae create conditions that enable microaggregates to form in soil; and, (3) roots and AM hyphae enmesh and bind microaggregates and smaller macroaggregates into larger macroaggregates.

INVOLVEMENT OF AMF IN SOIL STRUCTURAL DEVELOPMENT

In soil under plants, the macroaggregates are stabilized mainly by roots and AM hyphae (Tisdall and Oades, 1982). The relative effect of roots and AM hyphae on the stabilization of macroaggregates could be determined in soil compartmentalized by a screen which allowed hyphae to grow but not the roots (Camel et al., 1991). Roots and AM hyphae form an extensive network in soil and are covered with extracellular polysaccharides to which microaggregates are firmly held (Fig.1). In fact,

Fig. 1: Showing extensive network of hyphae in soil aggregation.

network of encrusted roots and hyphae hold the macroaggregates, so that they do not collapse in water. The clay on the surface protects the roots and hyphae from microbial decomposition, but once the roots and hyphae die the network is broken by fauna or tillage, and the macroaggregates are disrupted in water; the encrusted fragments remain as microaggregates (Oades and Waters, 1991).

AM fungi form mutualistic association with most species of plants and produce spores or sporocarps in soils (Harley and Smith, 1983). Most AM fungi produce simple branched hyphae or hyphal strands in soil and extend the root systems of plants. The stability of macroaggregates of several soils was related to the length of these hyphae in soils (Tisdall and Oades, 1979, 1980b; Elliott and Coleman, 1988; Miller and Jastrow, 1990). Within each macroaggregate, fungal hyphae form a network with up to 50 m of hyphae per g of stable aggregates, or up to 14 m of external hyphae per cm of root (Barea, 1991; Tisdall, 1991). However, the stability of macroaggregates of an alfisol under grassland was directly related to the length of external AM hyphae and to the length of fine roots (0.2-1 mm dia); the stability was not directly related to the length of very fine roots (<0.2 mm dia), but was indirectly related through the external hyphae supported by the very fine roots (Miller and Jastrow, 1990). The different effects of fine and very fine roots on stability were probably because plants with mainly very fine roots (< 0.1 mm dia) formed fewer mycorrhizas than those with mainly coarse roots (> 0.5 mm dia) (Barea, 1991). Bethlenfalvay and Barea (1994) observed a 400% improvement in soil aggregation by inoculation of *Glomus mosseae* in a gray-silt loam and 50% increase in soil aggregation in yellow clay loam (Table 1). In one soil, root and soil colonization by an AM fungus did not enhance seed yield, but markedly improved aggregation compared with AM control. In another soil, the same AM fungus improved soil aggregation only slightly but enhanced seed yield significantly. Thus, the AM fungus affected the development of both plant and soil hosts. Thomas et al. (1993) showed that the presence of AM roots, non-AM roots, or AM hyphae alone differently affected the water stable soil aggregate (WSA) status of the soils (Table 2). With both roots and hyphae present, there was a significantly greater incidence of WSA than in any of the other three treatments. The incidence of WSA was statistically the same (p > 0.05) when only AM hyphae or non-AM roots were present in the four-chambered growth container, suggesting a comparable effect on water stability of the soil by roots and hyphae alone; other saprophytic fungi may have contributed to the greater abundance of WSA in the AM root chamber.

Table 1. Seed yield, root development and soil aggregation status of potted pea plants inoculated with *Glomus mosseae* (Bethlenfalvay and Barea, 1994)

Parameters	Silt loam			Loam		
	+ AM	-AM	p-value	+ AM	-AM	p-value
Seed dry mass (g)	2.2	2.0	0.120	2.3	1.3	0.001
Soil aggregates						
Dry aggregates	30.1	26.7	0.008	45.2	38.8	0.031
WSA* < 1 mm	6.9	5.4	0.043	5.8	4.4	0.028
WSA > 1 mm	13.0	2.6	<0.001	22.3	11.3	0.003
WSA ratio	1.9	0.5	<0.001	3.9	2.6	0.029
Root parameters						
Fresh mass (g)	5.4	4.5	0.001	4.7	3.2	<0.001
Length (m)	25.8	24.7	0.434	21.9	17.0	0.019
Colonized length (m)	4.7			13.9		

*WSA, water-stable soil aggregates in two size classes: 1 to 2 mm and 0.5 to 1 mm. **p-value refers to the statistical significance of the difference between +AM and -AM means by t-test.

Table 2. Soil aggregate characteristics as influenced by the vesicular-arbuscular mycorrhizal (AM) component in the treatment chamber (means of 10 replicates). Differences between the soil at the beginning of the experiment (initial soil) and the harvest soil were determined by t-test (Thomas et al., 1993).

Treatment	Soil parameters	Dry-sieved		Wet-sieved	
	1- to 2-mm particles	Coarse sand	Total aggregates+	Water-unstable aggregates	Water-stable aggregates
		% of total soil (W/W)			
Harvest soil					
AM root	18.2 b±	0.7a	17.5b	12.4c	5.1a
AM hyphae	21.5a	0.7a	20.7a	16.4a	4.3b
Non-AM root	18.5b	0.7a	17.8b	13.9b	3.9bc
Control	21.8a	0.7a	21.1a	17.7a	3.4c
Initial soil	14.9*	0.8NS	14.1*	6.8*	7.3*

*Initial soil was significantly different at p < 0.05 from each of the chamber soils at harvest; NS, not significantly different, + Sum of water unstable and water-stable aggregates, ± Means in each column followed by the same letter are not significantly different (p > 0.05) by Duncan's multiple range test.

Fertile soils have a high percentage of stable aggregates (Burns and Davies, 1986). AM fungi can bind and aggregate soil particles through the intensively growing mycelium. Sutton and Shephard (1976) showed that mycorrhizal plants grown in sand dunes aggregated five times more sand around the roots than plants of equal root biomass but without AM association. The formation of aggregates can be important to improve soil physical conditions. Additionally, binding the soil by AM fungi is a potential control mechanism of soil erosion. It is known that AMF mycelium not only binds soil particles loosely, but also that the hyphae are bound to them through amorphous polysaccharides (Burns and Davies, 1986). Tisdall et al. (1997) examined the aggregation of soil clay by mycorrhizal (*Hymenoscyphus ericae and Hebeloma* sp.) fungi, which significantly increased the percentage of aggregates of > 50 μm (Table 3), but did not change (p > 0.05) the percentage of aggregates of other sites compared with the uninoculated clay.

Table 3. Effect of growth of mycorrhizal fungi for 52 days on the mean diameter (±S.E.) of aggregates < 2 μm and hyphal length (mean ± S.E.) in Wiesenboden soil clay (Tisdall et al., 1997).

Treatment	Aggregate diameter (nm)	Hyphal length (m/g soil clay)
Mycorrhizal fungi:		
Hymenoscyphus ericae	1562 ± 84	2.1 ± 0.2
Hebeloma sp.	1545 ± 156	2.2 ± 0.2
Uninoculated control	1317 ± 112	—

In both field and pot experiments, AM hyphae stabilized sand dune soils or loams (Oades, 1984; Elliott and Coleman, 1988). The stability of macroaggregates of several soils was related to the length of these external hyphae in soil (Tisdall and Oades, 1980b; Miller and Jastrow, 1990), but not necessarily to the length of mycorrhizal roots (Reid and Goss, 1981; Stone and Bultery, 1989). This may be because the length of external AMF hyphae is not always related to the length of mycorrhizal roots (Sylvia, 1988). Thomas et al. (1986) found that mycorrhizal onion plants (*Allium cepa*) grown in pots for 230 days increased the percentage of water stable aggregates (> 2 mm diameter) of a silty clay loam by 72% when compared with non-mycorrhizal onion plants. The mass of roots and the length of external hyphae were each correlated with the percentage of water-stable aggregates (> 2 mm diameter). As the correlation was stronger with root length ($r^2 = 0.54$**) than with the hyphal length, Thomas et al., (1986) hypothesized that the AMF hyphae associated with the onion plants did not directly stabilize aggregates of the silty clay loam, but stimulated the growth of roots, which in turn stabilized aggregates. This hypothesis was not supported for C3 and C4 grasses, perennial composites

and other forbes growing in the field comprising of silt loams and silty clay loams for yet another decade (Miller and Jastrow, 1990).

Miller and Jastrow (1990) determined the path analysis of the relative effects of roots and AM hyphae on the geometric mean diameter, a measure of the stability of wet-sieved macroaggregates (Fig. 2). In path analysis, the larger the path coefficient between two factors, the larger
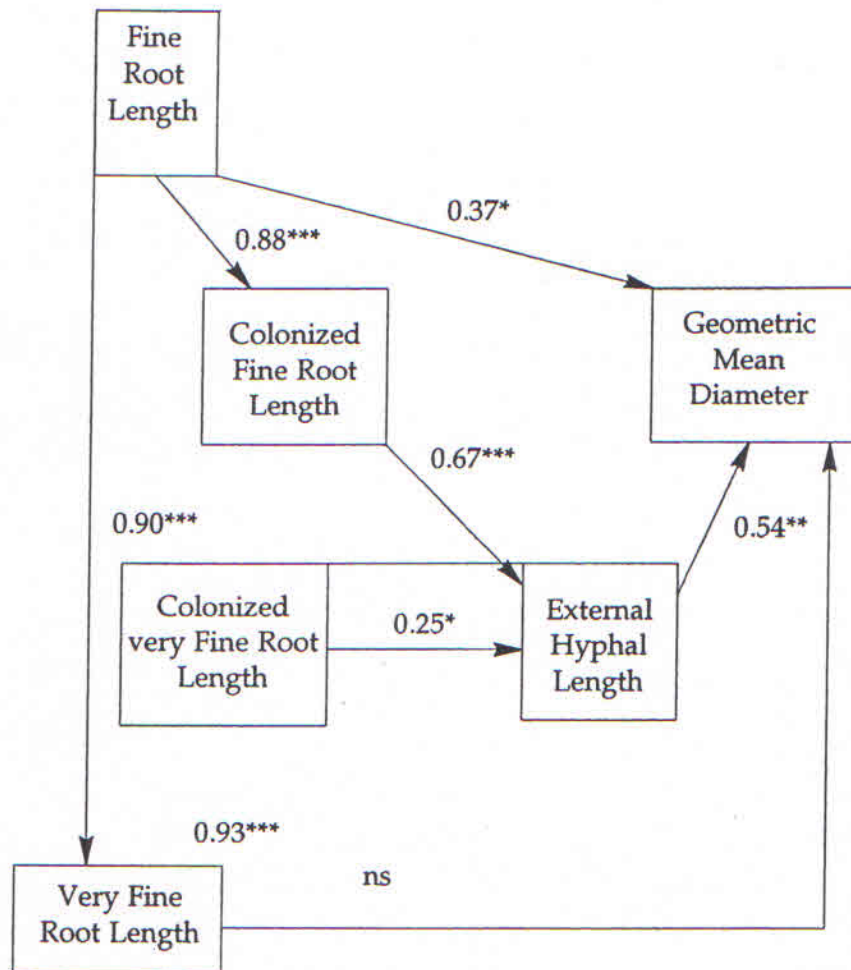

Fig. 2: Path model relating the lengths of root and fungal structures to geometric mean diameter in surveyed soils under pasture. Fine roots are 0.2-1 mm diameter; and very fine roots are < 0.2 mm diameter. Arrows show casual paths; numbers are path coefficients, showing the relative strength of each path leading to a given response: *p < 0.05; ** p < 0.01; *** p < 0.001; ns, non significant at p > 0.60 (Miller and Jastrow, 1990).

the direct effect of one factor on another. The direct effect of external hyphae on the geometric mean diameter (path coefficient = 0.54**) was larger than that of the length of fine roots on geometric mean diameter (0.37*). The length of roots mainly affected the geometric mean diameter indirectly through their effect on arbuscular mycorrhizal hyphae. That is, the external hyphal length depended on the length of fine roots colonized by AM fungi (0.76*), which in turn depended directly on the length of

fine root (0.88**). The length of very fine roots only affected the geometric mean diameter indirectly. The results of Miller and Jastrow (1990) support the conceptual model of an aggregate of Tisdall and Oades (1982). External hyphae of AM can extend up to 30 mm from the surface of the roots, with upto 50-m hyphae per g of stable aggregates (Tisdall and Oades, 1979; Miller, 1986). Even within one species of the fungus, the morphology of external hyphae varies considerably (Bonfante-Fasolo, 1984). The hyphae range over 2-27 *u*m diameter, have thick or thin walls, are septate or non-septate, are straight or fan-like, or have angular projections with irregular orientation. The amount of external hyphae of some species of AM fungi are affected by other micro-organisms, root exudates, pests, clay content, soil pH, organic matter, fungicide and pesticide content of the soil, and phosphorus content of the plants (Abbott and Robson, 1985; Finlay, 1985; Wang et al., 1985). Some selection in natural soils may be related to the surface changes in the external hyphae or in their polysaccharide and in clay, as reported for some bacteria (Bushby, 1990).

Mycorrhizal roots translocate carbon to the external hyphae at the expense of root exudates and may change the microbial biomass in the soil (Schwab et al., 1983; Meyer and Linderman, 1986). This may, in turn, stimulate or inhibit the growth and activities of the roots or the fungus (Bowen, 1979), and possibly the subsequent stabilization of aggregates. Increased photosynthesis, with or without increased growth of the plant, usually compensates for the drain on carbon from the roots (Abbott and Robson, 1984). Also, roots of the same or different species can exchange carbon through connecting AM hyphae and could possibly change the amount and kind of materials exuded by roots (Miller, 1986). The factors which affect the amount of carbon translocated to the hyphae or between connected plants include temperature, light intensity, day length, grazed or cut shoots, nutrient status, growth stage of the plant and water content of the soil.

Much of the past interpretation of the role of roots and mycorrhizal fungi in the soil aggregation process has been independent of their interactive nature. Although Tisdall and Oades (1979, 1980b, 1982) recognized the importance of roots, colonized roots and mycorrhizal hyphae in aggregation, their data were interpreted on the basis of simple regressions between the lengths of roots or hyphae and the proportion of the soil found in selected aggregate-site classes. Miller and Jastrow (1990) observed similar correlations between these variables and aggregate-size distribution in their data. From path analysis, however, they found that because of the interrelationships among the biotic variables, a large portion of the effect of roots on aggregation was due to indirect effects of root associations with mycorrhizal fungi. Furthermore, the strength of this associa-

tion and its relationship to aggregate-size distribution appeared to vary depending upon root morphology. Because of the effect of lifeform on root morphology, it also appeared that some lifeforms might be more effective than others in promoting aggregate formation.

MECHANISM INVOLVED IN STRUCTURAL DEVELOPMENT

Tisdall and Oades (1982) stressed on the mechanisms of aggregate stabilization. It is necessary to consider the scale at which the various associations take place and to visualize aggregate stabilization at several different levels where particles of < 0.2 μm are built up into larger aggregates (< 0.2 μm → 0.2-2 μm → 2-20 μm → 20-250 μm → 250-2000 μm → > 2000 μm) with different agents being responsible for stabilization at each level. For example, these workers have suggested that 2 to 20 μm aggregates are bound together by persistent organic bonds, while aggregates > 2000 μm are held together mainly by a network of roots and hyphae. The following mechanisms explain the effectivity of aggregation stabilization.

A. Binding by Polysaccharides

Polysaccharides synthesized by soil micro-organisms can be divided into two groups: homo-polysaccharides, which include levans and dextran and are uncharged; and hetero-polysaccharides, generally composed of repeating sugar units, often with uronic acid groups. These polysaccharides can be linear or branched with a variety of functional groups such as hydroxyls and carboxyls. At the pH that exists in soils, many would be expected to be negatively charged, owing to dissociation of their functional groups. Similarly, clay surfaces have a negative charge arising from isomorphous substitution within the clay lattice, but some positive charge can develop at the edges of clay platelets; some clay minerals also have a pH-dependent negative charge.

Several workers have described the isolation and composition of soil polysaccharides (Finch et. al., 1971; Cheshire, 1979). Newman et al., (1980) have used nuclear magnetic resonance to characterise humic substances. Extraction and fractionation of soil polysaccharides has revealed a complex mixture of sugar units, perhaps because the soil contains very complex molecules (Martin, 1971). During degradation, microbial polysaccharides could be built up to form new polymers, perhaps through the action of free enzymes. Burns (1983) has suggested that extracellular enzymes, or materials from lysed cells, may survive for a long time in soil, possibly because of their interactions with organic and inorganic soil components. Emerson (1959) reported that the quartz-clay bonds were

strengthened by organic polymers linking the quartz surface and the edge or basal surfaces of the clay. Cationic polymers may participate in normal ion-exchange reactions, but the interaction is more complex for negatively charged polymers, which would be expected to be repelled by the negatively charged clay surfaces. Martin (1971) summarized the binding activity of polysaccharides as under:

1. their length and linear structure, allows them to bridge spaces between particles;
2. their flexibility allows many points of contact so that van der Waals forces can be more effective;
3. the number of hydroxyl groups present helps hydrogen bond formation; and
4. the number of acid groups present allows ionic bonding through di- and trivalent ions.

Tisdall and Oades (1982) suggest that polysaccharides are transitory binding agents. It is possible that polysaccharides may be protected from degradation by other chemical means. When humic substances were adsorbed to soil before glucose was added and the soil incubated, persistently stable aggregates were produced (Swift and Cheney, 1979), suggesting that the humic materials were able to confer long-term stability. Griffiths and Burns (1972) found that phenolic substances (tannic acid) prolonged aggregate stabilization by a polysaccharide if this material interacted with the aggregate after it had been formed, suggesting a physical as well as chemical function. Phenolic units present in humic acids may originate from fungal decomposition of lignin (Martin and Haider, 1971). In general, microbial polysaccharides, while being effective in aggregation, are often easily decomposed in soil although some appear to be protected either chemically or physically.

B. Adsorption of Cells to Soil Surfaces

Marshall (1971, 1980) defined the following interactions between micro-organisms and soil particles:

1. Sorption between micro-organisms and surfaces of large soil particles;
2. Sorptive interaction between cells and soil particles of like size; and
3. Sorption of very small particles to surface of micro-organisms.

Electrophoretic mobility measurements have indicated that clay particles can adsorb to cells and vice versa. Clay particles have a higher electrophoretic mobility than cells, so when they are mixed, changes in the mobility of the components reflect an interaction between cells and

particles. One mechanism of adsorption is through functional groups on the surface of cells. Marshall (1969a, 1969b) suggested that clay adsorption onto cells that had carboxyl-type surfaces was through positive charge on the clay edges. Limited clay adsorption to cells occurred with more complex amino-carboxyl surfaces, suggesting that positively charged amino groups may interact with negatively charged clay surface.

The adhesion of soil particles to fungal hyphae may have important consequences for aggregate stabilisation. Fungi tend to produce lower molecular weight polymers than bacteria. These low molecular weight polymers are less effective soil binding agents than those of bacteria. However, adherence of soil particles to hyphae, indicating the presence of binding agents, has been noted by Clough and Sutton (1978) and Tisdall and Oades (1979). The inoculation of aggregates with media in which fungi had been grown showed that stability was a function of substances closely associated with the cells, rather than something that diffused away from the hyphae (Clough and Sutton, 1978).

Fungi may be effective aggregate stabilisers because the spread of hyphae between aggregates and into large pores distributes their associated binding agents throughout the soil. Dead hyphae retain their strength and remain firmly attached to soil particles (Bond and Harris, 1964), so that even after the hyphae die and break up, they may still form the center of small aggregates.

C. Interaction between Groups of Micro-organisms or with Roots

Mixed cultures of fungi or actinomycetes gave better aggregation that soil inoculum (Swaby, 1949), perhaps because the presence of antagonistic bacteria in soil inoculum decreased the effectiveness of other organisms. Gel'tser (1940) suggested that the decomposition of fungal hyphae yielded products that were better aggregate stabilizers than most other sources. Low and Stuart (1974) suggested that although neither roots nor fungal hyphae persist for long in soil, they may act as a scaffolding from which the products of bacterial action could form transient binding agents. McHenry and Russell (1944) attributed increase in aggregate stability to the decomposition of microbial wastes and dead cells. They found that there were two maxima in aggregate stability and suggested that the first came from the decomposition of readily available organic material and the second from the decomposition of cells and wastes.

Plant roots have been shown to increase the stability of surrounding aggregates (Tisdall and Oades, 1979; Reid and Goss, 1980). Sutton and Sheppard (1976) found that hyphae of *Glomus* sp. were a major factor in the aggregation of a Canadian dune soil by beans (*Phaseolus vulgaris*) and that aggregation was enhanced in the presence of other organisms, possi-

bly through stimulation of fungal growth. Tisdall and Oades (1979) concluded that the efficiency of rye grass (*Lolium perenne*) in aggregate stabilization was due to the large AM fungal population it supported; hyphal length was related to aggregate stability, and the organic materials responsible for aggregate stabilization were decomposing roots and fungal hyphae (Tisdall and Oades, 1980b).

Several interacting mechanisms may be responsible for aggregate stabilization around roots. The roots themselves can move particles together, or localized drying of the soil could stabilize aggregates to some extent. The presence of fungi, possibly AM, could mechanically bind soil particles together with stabilisation being enhanced by polymers produced either directly by the fungus or by bacteria associated with the hyphae.

Recently, Wright and Upadhyaya (1998) reported that AM fungi could produce glycoprotein, glomalin that helps in aggregate stability. Aggregate stability was linearly correlated (p < 0.001) with all measures of glomalin (mg g^{-1} of aggregates) in these soils. The best predictor of aggregate stability (AS) was immuno-reactive easily extractable glomalin (IREEG) according to the followinjg relationship: AS = 42.7 + 61.3 x log$_{10}$ IRREG (r^2 = 0.86; p < 0.001, n= 37). It is possible that glomalin simply contributes to hydrophobicity of soil particles to allow for air penetration and water drainage. It is also possible that the insoluble, glue-like, hydrophobic nature of a glomalin coating may initiate and protect nascent aggregating material-soil minerals, other microbes, and organic matter. Insoluble glomalin in its native state could trap and protect the microbes that contribute polysaccharides and other by-products to aggregates.

AGRICULTURAL MANAGEMENT

It should be possible to match specific AM fungi to each agricultural system (Hayman, 1986). However, the management of soil and plants which enables AMF hyphae to stabilize aggregates most efficiently and persistently is not known. Tillage breaks up the network of roots and hyphae, readily destabilizing the aggregates (Tisdall and Oades, 1980b). In direct-drilled soils, roots follow old root channels (Ehlers et al., 1983), where infective propagules of AM fungi are probably concentrated. Hence, the new season's roots in direct-drilled soils could become mycorrhizal and stabilize aggregates more quickly than those in tilled soils. Farmyard manure, but not mineral fertilizers, increase AM infection which may contribute indirectly to hyphal stabilization of aggregates (Hayman, 1986).

St. John et al., (1983) showed that, rather than growing randomly in soil, external AM hyphae were associated with decomposing organic matter, more of which would be present after pasture than after crops, or in

direct-drilled soils than in tilled soils (Tisdall and Oades, 1980b; Miller, 1986). If these hyphae grew preferentially among organic debris in most soils, it could partly explain why stable macroaggregates are associated with organic debris from roots, faecal pellets and worm casts (Oades, 1984). Also, the infection of the new season's roots may depend on infection and management of the previous crops. As the hyphae from the same fungus can connect roots of the same or different species of plants (Miller, 1986), roots of a young plant may be able to tap immediately into an estabilished network of an older plant. Therefore, mixed or relay crops may be more efficient stabilizers than sole crops.

Crops (specially non-mycorrhizal), long fallow, biocides and waterlogged soil can each significantly decrease the growth and infection of mycorrhizal fungi (Black and Tinker, 1977; Reid and Bowen, 1979; Menge, 1982; Thompson, 1987) and probably reduce the rate at which external hyphae can subsequently stabilize aggregates. Unless research can determine the management of soil which encourages the most efficient stabilization of aggregates by AM hyphae, it would be difficult to match specific fungi to each agricultural system.

Tisdall and Oades (1980a) found a linear increase in percentage of water-stable aggregates (> 2000 μm dia) with time for which rye grass was grown without wilting. As the stabilization increased with time, the root length and the hyphal length per g stable particle (> 2000 μm dia) also increased (Table 4). Most of the hyphae in the stable aggregates >

Table 4. The effect of management of rye-grass on water-stable particles (Tisdall and Oades, 1980a).

Treatment	Time (Week)	Stable particles > 2000 μm (%)	Total oven dried leaves per pot 80°C (g)	Root length (mg^{-1}) stable particles > 2000 μm	Hyphal length (mg^{-1}) stable particles >2000 μm
Ryegrass control (sampled)	30	33.5 ± 1.4[A]	54.9 ± 3.1	2.1 ± 0.2	15.6 ± 0.6
Ryegrass control (sampled)	52	45.4 ± 3.2	75.7 ± 1.2	4.9 ± 0.6	22.4 ± 2.7
Clipped ryegrass (sampled)	30	42.0 ± 2.8	34.5 ± 0.9[B]	2.4 ± 0.3	18.0 ± 2.7
Killed ryegrass (sampled)	30	5.3 ± 0.4	14.9 ± 0.8	0.8 ± 0.1	6.9 ± 0.2
Killed ryegrass (sampled)	52	34.1 ± 2.3	64.7 ± 1.0	2.5 ± 9.3	12.7 ± 2.5

A-SE mean; B-Includes mass (oven-dried) of leaves removed at all clippings and at harvest.

2000 μ m diameter were of AM fungi. Clipping appeared to stimulate the growth of hyphae. Stressing the plants by allowing them to wilt reduced the stability of aggregates. The mycorrhizal hyphae persisted for at least several months after the plants had died. Although the hyphae may not have been viable, they continued to bind particles of soil in stable aggregates. Tisdall and Oades (1979) found a strong relationship between length of hyphae in total soil and the water stable particles > 2000 μm (Fig. 3). These results suggest that most of the increase in the percentage of water-stable particles > 2000 μm is due to the binding of small aggregates in the large aggregates by AM fungi.
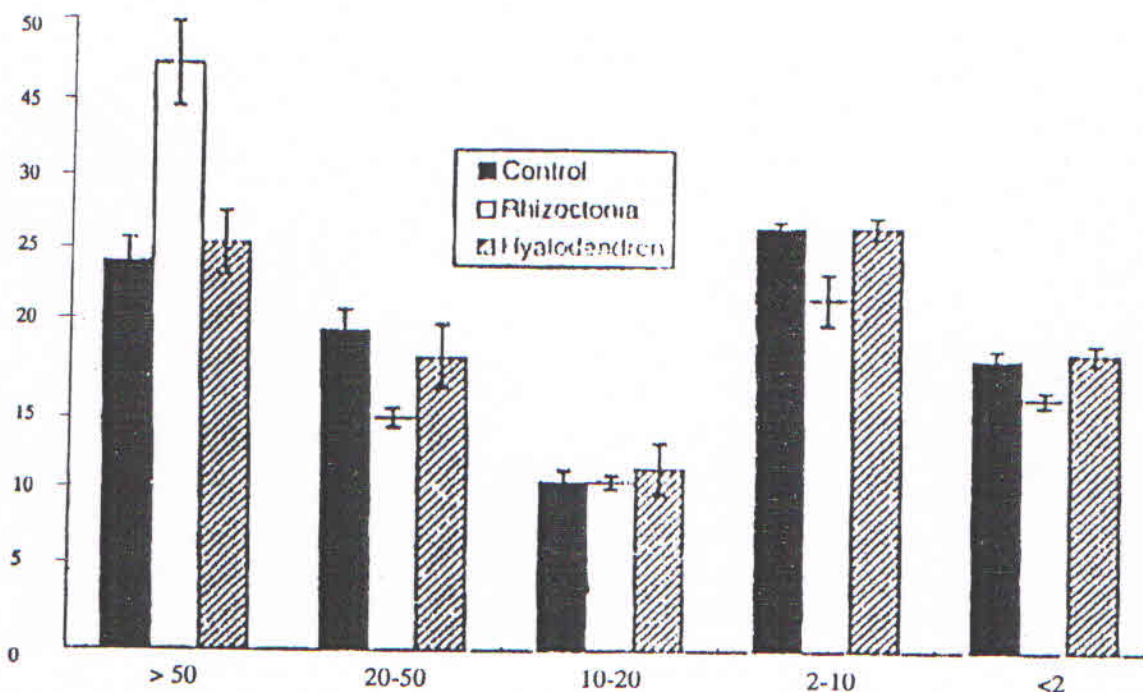

Fig. 3. Effect of the growth of saprophytic fungi for 15 days on the size distribution of water stable aggregates in Wiesenboden soil clay. Each error bar represents 2x aps.m. (Tisdall et al., 1997).

Reduced tillage and maintenance of surface residue helps to reduce the death rate of AMF propagules (Thompson, 1991). The best way to improve the mycorrhizal condition of the soil is through cropping with mycorrhizal host crops, which include cereals, legumes and oilseeds. To avoid subsequent problems, it is best not to sow mycorrhiza-dependent crops, which include chickpea and pigeonpea, in AM-depleted situations. Depletion of AM inoculum potential can arise from weed-free fallowing, growth of non-host crops such as mustard and rape seed, severe soil disturbance in tillage operations, waterlogging in paddy rice and flood fallowing, severe fires, and topsoil stripping. Therefore, intense cropping is beneficial for AMF. In semi-arid areas, the frequency of cropping will be dictated by available water, and avenues to improve this through

reduced tillage and residue retention should be pursued. Intensification of cropping also places demands on soil nitrate supply, and replacement through fertiliser or legumes is essential. Here the possibility of grain legumes such as chickpea and pigeonpea being self-sufficient for N allows economic intensification of cropping, and any prospects of improved N supply for the following cereal crop is a bonus. Not only will chickpea and pigeonpea benefit from the AM inoculum present from a previous host crop but they themselves are excellent providers of AM inoculum for the subsequent mycorrhiza-dependent crop species.

FUTURE THRUST

Very little is known concerning the development of soil structure by AM-fungi. Research is needed to determine whether the most effective stabilizers: (1) produce more mucilage; (2) produce more persistent or stickier mucilage; (3) are bonded by hydrophobic bonds or bridges of polyvalent cations or have greater electrostatic attraction to clay platelets; (4) persist longer in soil; (5) interact better with some species of plants, micro-organisms or animals than others; (6) orientate particles of clay so that they are strongly bound together; (7) invade the soil more readily, or (8) produce more external hyphae or more of one type of hypha than another.

Tillage, long fallow, biocides and compacted or waterlogged soil can each significantly decrease the growth and colonization of roots by mycorrhizal fungi. Research is needed to determine whether these factors slow the rate at which external hyphae can subsequently stabilize aggregates. Greater thrust is required to determine whether mixed or relay crops, or agroforests are more effective than sole crops. Research is also needed to determine whether crop rotation affects the stability of macroaggregates through its effect on AM fungi. It is important to determine whether some combinations of plant, fungus and other organisms lead to more external hyphae or more polysaccharide than others. For each soil, we need to determine the best combinations and management of plant and organisms, which will better stabilize aggregates.

More thrust is needed to determine the relative longevity of various types of fungi and their stabilization of aggregates. Many saprophytic fungi disappear from the soil once they have used their substrate, so that stabilization of aggregates by them lasts for a few weeks only (Molope et al., 1987). On the other hand, external hyphae of AM fungi and stabilization of aggregates by them persists in soils for at least several months after plants have died (Tisdall and Oades, 1980a).

Arbuscular mycorrhizal hyphae were still present in one patch of untilled soil several months after the plants were killed (Tisdall and Oades,

1980a), but it is not known for how long did these hyphae persist in soil once the host has died. More research is needed to determine the factors which control the distribution of AM fungi in soil, the growth and survival of external hyphae, the exudation of polysaccharides and the production of macroaggregates.

An inoculum of mixed species of AM fungi may adapt better to different environments than a single species and stabilize aggregates more consistently (Koomen et al., 1987). However, because the introduced fungus does not always compete successfully with indigenous AM fungi, management of the indigenous fungi and their stabilization of aggregates requires to be examined (Miller, 1986). We probably only need to introduce fungi deliberately into soils which have been greatly disturbed, e.g., fallows, drained, limed, mined, sterilized or eroded soil. However, development of suitable methods for inoculation on a large scale is still a research priority (Hayman, 1986).

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