Chapter 7

Contributions of Arbuscular Mycorrhizas to Soil Biological Fertility

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1. INTRODUCTION

Mycorrhizas are ubiquitous plant-fungal associations that are important components of soil fertility (Table 1). Roots of most crops are normally inhabited by arbuscular mycorrhizal (AM) fungi. These Zygomycota in the order Glomales, function at the interface between plants and soils by greatly expanding the area from which plants can gather soil resources. Extensive networks of as much as 160 m of AM hyphae per g of soil (Degens *et al.* 1994) function as conduits for nutrient uptake. Crops with coarse root systems generally benefit greatly from AM associations, while mycorrhizal benefits in crops with more fibrous root systems tend to be determined by soil mineral availability (Baylis 1975, Hetrick *et al.* 1992). Only a few crops, such as lupines and members of the Brassicaceae and Chenopodiaceae, do not regularly form AM associations. In addition to their direct effects on nutrient uptake, AM fungi also contribute to soil fertility by enhancing soil structure and protecting crops from root pathogens.

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AM fungi form structures inside (intraradical) and outside (extraradical) the host root. After an infective soil borne hypha contacts a host root, it forms an appressorium, penetrates the epidermis, and grows in the space between the cells into the root cortex. Once in the cortex, the intraradical hyphae penetrate the cells and produce arbuscules. These highly branched structures are surrounded by the host cells' membranes and are thought to be where nutrients are exchanged between the partners: i.e. glucose from host to fungus and phosphorus (P) from fungus to host (Blee and Anderson 1998). Once the source of carbohydrate nourishment is secured, the extraradical hyphae can proliferate in the soil. New spores are produced typically on hyphae in the soil in response to achievement of a critical amount of root length colonised, senescence of the host, or other factors. There are clear differences in the effectiveness of AM fungal species to improve soil fertility (Abbott and Robson 1982, 1985, Graham and Abbott 2000), and these differences are likely to be related to differences in allocation to intraradical and extraradical structures (Abbott and Gazey 1994, Dodd *et al.* 2000).

Table 1 Arbuscular mycorrhizal functions that can ameliorate soil fertility*

Direct **positive** effects upon:	Lessen **negative** effects from:
• Uptake of immobile nutrients • Drought tolerance • Soil macroaggregate formation and stability • Soil organic matter	• Root pathogens • Leaching loss of nutrients • Microbial immobilisation of nutrients

*Combinations of crops, AM fungi, and soils differ greatly in their function. Most AM associations do not simultaneously enhance all of these components of soil fertility, and some may not enhance any of them.

The partnership between plants and AM fungi has a long history. Fossil and molecular evidence indicates that AM fungi were associated with the earliest land plants, and that the symbiosis evolved concurrently with the evolution of roots (Malloch *et al.* 1980, Stubblefield *et al.* 1987, Simon *et al.* 1993, Redecker *et al.* 2000). The intimacy of this association is reflected in the fact that Glomalean fungi are obligate biotrophs that have not yet been successfully cultured in the absence of root tissues. Although the Glomales are asexual and include fewer than 160 species (INVAM 2001), a surprising level of genetic diversity is maintained within populations of these fungi (Hijri *et al.* 1999, Hosny *et al.* 1999). Sanders (1999) suggested that, in genetic terms, an individual aseptate AM fungus is actually a population of discrete nuclei. This genetic variance within taxa corroborates physiological variance between geographic isolates of the same species. For example, Bethlenfalvay *et al.* (1989) found that *Glomus mosseae* isolated from an arid site improved the photosynthetic water use efficiency of soybean more than *G. mosseae* isolated from a mesic site. Other studies also have shown that different isolates of the same species can elicit different plant responses under identical conditions (e.g. Stahl and Smith 1984, Stahl and Christensen 1990, Sylvia *et al.* 1993-a).

Mycorrhizal function is strongly influenced by the soil environment, particularly those factors that control mineral fertility (Abbott and Robson 1982). Generally, mycorrhizal benefits are greater in phosphorus-poor soils than in phosphorus-rich ones (Koide 1991). Furthermore, crop species and even different cultivars of the same species interact with AM fungi differently (Hetrick *et al.* 1993, Hetrick *et al.* 1996). It is useful to envision mycorrhizas as dynamic systems controlled by interactions among plants, fungi, soil microbes, and soil properties. Bethlenfalvay and Schüepp (1994) suggested that sustainable agroecosystems require management to generate a stable community of soil biota that functions effectively with abiotic conditions to maximise crop productivity and minimise inputs and soil erosion.

Cultural practices have been shown to influence the species composition of AM fungal communities (see below). Certain taxa increase in abundance in agricultural systems relative to other taxa. Furthermore, species diversity of AM fungi is consistently lower in agricultural systems than in nearby natural areas (Sieverding 1990, Helgason *et al.* 1998-b). The consequences of this on crop production have not yet been carefully studied. Sieverding (1990) suggested that a few well selected AM fungi could increase yields if they are the best mutualists. Alternatively, if the proliferating fungi are simply the most aggressive colonists, and not the best at improving nutrient uptake, pathogen resistance, or soil structure, then this agriculture-induced reduction in diversity is cause for concern.

The potential for agricultural management of mycorrhizas to reduce reliance on inorganic fertilisers and develop more sustainable agricultural systems has long been recognised and has already been reviewed (e.g. Sanders *et al.* 1975, Azcon-Aguilar *et al.* 1979, Bethlenfalvay and Linderman 1992, Pfleger and Linderman 1994, Gianinazzi and Schüepp 1994). But, "promises of the applied value of AM fungi in agriculture, forestry and horticulture have been more rhetorical than deliverable" (Miller and Jastrow 1992). A much better understanding of the ecological and evolutionary mechanisms responsible for generating positive, neutral or negative mycorrhizal functioning in field environments is necessary before mycorrhizas can be effectively managed to maximise their contribution to soil fertility in sustainable systems.

This chapter has a twofold emphasis. First, it describes the fundamental ways in which AM fungi contribute to the biological fertility of the soil (Table 1). We discuss how AM fungi directly affect plant growth and soil structure and how their interactions with other soil organisms indirectly affect crop yields and nutrient cycling. We will see that these are not independent effects and that feedbacks between plants, fungi, and biotic and abiotic soil properties ultimately determine mycorrhizal effects on plant growth. Second, we discuss how agricultural management practices affect indigenous communities of these fungi. We show that management practices positively and negatively affect AM fungi, and that these have ramifications upon plant growth. Throughout we will point out key topics where further research is needed.

2. GENERAL IMPACTS OF ARBUSCULAR MYCORRHIZAS

2.1 Plant Growth

Arbuscular mycorrhizal fungi long have been known to have a positive effect upon growth of their host plant (Mosse 1973), most notably in low nutrient soils. This is due to enhanced nutrient uptake, water relations, and disease resistance. These benefits are often contingent on environmental conditions, and when nutrients and water are in unlimited supply and pathogens are absent, then the costs of AM symbioses may sometimes outweigh their benefits and AM fungi may actually depress plant growth (Fitter 1991, Johnson *et al.* 1997).

2.1.1 Nutrient uptake

The extraradical phase of the mycorrhiza acts in effect as an extension of the root system for the uptake of nutrients, particularly those which are relatively immobile in the soil solution, i.e. phosphate, zinc (Zn), and copper (Cu). The zone of P uptake from the soil for a nonmycorrhizal root extends only just beyond the length of a root hair, 1-2 mm in most instances (Jungk and Claassen 1986). Hyphae of AM fungi can extend upwards of 14 cm beyond the root (Mozafar *et al.* 2001), effectively exploring a greater volume of soil for nutrients. This phenomenon was demonstrated clearly in experiments utilising compartmented pots (Li *et al.* 1991). Plants were grown in pots separated into root and hyphal compartments by a screen with mesh size small enough to restrict passage of roots yet allow penetration by hyphae. These experiments have shown a zone of uptake of soil P extending through the entire hyphal compartment for mycorrhizal plants and no uptake from this compartment by nonmycorrhizal plants.

There was some debate about whether AM fungi make available to the plant, or solubilise, unavailable forms of P such as rock phosphate. Much of the belief that AM fungi could solubilize unavailable forms of P came from the observation that mycorrhizal plants were more efficient at obtaining P than nonmycorrhizal plants in the presence of insoluble rock phosphate fertiliser (Powell and Daniel 1978). However, experiments with ^{32}P labelled fertilisers (Hayman and Mosse 1972), and others (Bolan 1991, Nurlaeney *et al.* 1996), indicated uptake of P only from the available pool. AM fungi may enhance plant uptake of rock P by a Le Chatelier's Principle type of mechanism. As P is taken up from the soil solution by the hyphae, more P enters the soil solution from sparsely-soluble forms of P (Ness and Vlek 2000).

AM fungi may allow plants to better utilise organic forms of P in the soil. The extraradical hyphae of mycorrhizas have phosphatase activity associated with their cell walls (Joner and Johansen 2000). Hydrolysis of organic P by extraradical hyphae and transport of that P to host roots recently was demonstrated *in vitro* (Joner *et al.* 2000).

Plants may limit colonisation of their roots in soils of high P availability (Menge *et al.* 1978). This serves to limit the carbon cost of supplying the metabolic needs of the fungus, which may be substantial, ranging from 4 to 20 % of plant photosynthate in the absence of enhanced nutrient uptake (Graham 2000, Douds *et al.* 2000).

2.1.2 Water balance

Another way in which AM fungi affect the growth of their host plant is through enhanced water balance by altering the behaviour of their stomata. Increased stomatal conductance, and hence transpiration, has been noted in mycorrhizal compared to nonmycorrhizal plants under both well-watered and drought conditions (see review; Augé 2000). P-supplemented nonmycorrhizal plants often function as do mycorrhizal plants under these conditions but transpiration and/or stomatal conductances have been measured to be greater in mycorrhizal than nonmycorrhizal plants when both groups were of similar size (Bryla and Duniway 1998, Allen 1982, Augé 2000) and when leaf water potentials were similar (Allen *et al.* 1981, Augé *et al.* 1986).

The mechanisms whereby arbuscular mycorrhizas enhance the water balance of their hosts is a matter of debate. When cultural conditions lead to a growth or P nutritional response to mycorrhizas (i.e. larger plants or increased P status relative to controls), reasons for enhanced stomatal conductance of mycorrhizal plants may be more apparent. Larger root systems access water from a greater volume of soil. Increased P in leaves allows for more rapid export of photosynthates so stomates remain open longer (Jarvis and Davies 1998). However, other factors must be operating when plants of similar size and P status are compared. Actual water uptake and its movement to the root by hyphae of AM fungi may (Ruiz-Lozano and Azcon 1995) or may not (George *et al.* 1992) occur. The enhanced water relations of mycorrhizal plants may be due to the effect of hyphae upon soil structure (see below) and the resulting influence upon water holding properties. Another way mycorrhizas may influence stomatal conductance is alteration of non-hydraulic root-to-shoot signalling of soil drying (Ebel *et al.* 1996, Augé and Duan 1991), keeping stomata open longer as portions of a root system are exposed to dry soil.

2.1.3 Resistance to plant diseases and pests

Mycorrhizas also confer upon their hosts a measure of resistance to a variety of soil borne diseases and pests (Table 2). As was found with water relations, some of these instances of disease resistance were due to enhanced nutrition of the mycorrhizal plant. Increased nutrition of nonmycorrhizal plants and the enhanced vigour it causes can lead to disease resistance (Graham and Egel 1988). Other root-pathogen interactions affected by the mycorrhiza require pre-colonisation of the roots by AM fungi prior to challenge by the pathogen (Afek *et al.* 1990). This suggests that AM fungi and the pathogen may compete for host derived carbon and/or infection sites, or that pre-colonisation of the root system potentiates the host defence system (Benhamou *et al.* 1994).

Another mechanism, not usually considered in these studies, has been proposed by Linderman (2000). In addition to the rhizosphere, the volume of soil directly influenced by the root, one may also consider a "mycorrhizosphere," the volume of soil influenced by the extraradical phase of the mycorrhiza. Just as roots influence the rhizosphere microflora through exudation, sloughing of cells, and root turnover, mycorrhizal hyphae influence the microflora of the mycorrhizosphere (see above). In addition, their influence is amplified through mycorrhiza-mediated changes in root exudation (Norman and Hooker 2000). These changes in root exudation, or exudation and other influences on soil chemistry by the hyphae themselves, may directly affect pathogens or other soil microbes (Filion *et al.* 1999). These other soil fungi and bacteria, influenced by the mycorrhiza, can be antagonistic to pathogens. Linderman (2000) has measured the "antagonistic potential" of bacteria isolated from the rhizosphere and mycorrhizosphere of nonmycorrhizal and mycorrhizal plants against a variety of plant pathogens. Antagonistic potential is a measure of the zones of inhibition around bacteria colonies isolated from these "spheres," when challenged by pathogenic fungi. Bacterial isolates from mycorrhizosphere soils were more antagonistic to plant pathogenic fungi than those from the rhizospheres of nonmycorrhizal roots (Linderman, 2000).

Table 2 Demonstrated resistance to fungal diseases conferred to the host plant by AM fungi

Pathogen	**Host plant**	**AM fungus**	**Reference**
Fusarium oxysporum	*Lycopersicon esculentum*	*Glomus Intraradices*	Caron *et al.* 1986
	Asparagus officinale	*Glomus fasciculatum*	Wacker *et al.* 1990
	Daucus carota	*G. intraradices*	Benhamou *et al.* 1994
	Vulpia ciliata	*Glomus sp.*	Newsham *et al.* 1995
Thielaviopsis brasicola	*Nicotiana tobaccum*	*Glomus monosporum*	Giovannetti *et al.* 1991
Pythium ultimum	*Tagetes patula*	*G. intraradices*	St-Arnaud *et al.* 1994
Verticillium dahliae	*Solanum melongena*	*Glomus etunicatum*	Matsubara *et al.* 1995.
		Gigaspora margarita	Matsubara *et al.* 1995.
	Gossypium hirsutum	*Glomus versiforme*	Liu 1995
Cylindrocarpon destructans	*Prunus persica*	*Glomus aggregatum*	Traquair 1995
Phytophthora nicotianae	*L. esculentum*	*Glomus mosseae*	Cordier *et al.* 1996 Trotta *et al.* 1996
P. parasitica	*L. esculentum*	*G. mosseae*	Cordier *et al.* 1996 Vigo *et al.* 2000
P. fragariae	*Fragaria X ananassa*	*G. etunicatum* *G. monosporum*	Norman and Hooker 2000
Sclerotium cepivorum	*A. cepa*	*Glomus sp.*	Torres-Barragan *et al.* 1996
Aphanomyces eutreiches	*Pisum sativum*	*G. mosseae*	Slezack *et al.* 2000
Fusarium solani	*Phaseolus vulgarus*	*G. mosseae*	Dar *et al.* 1997

Other situations in which field functioning of AM fungi has been demonstrated bear discussion. Large scale flooding occurred along the Mississippi River in 1993. When floodwaters finally receded, maize grown in these areas the following year was stunted and exhibited P deficiency despite adequate soil test P levels (Wetterauer and Killorn 1996, Ellis 1998). Assays showed low levels of AM fungus colonisation of roots, and supplemental P fertilisation eliminated the P deficiency. The reduced levels of inoculum of AM fungi was due more to the extended fallow rather than the flooding *per se* (Ellis 1998), reminiscent of long fallow disorder (Thompson 1987, Thompson 1991, see below).

2.2 Effect of AM Fungi on Soil Structure

The organisation of soil particles into macroaggregates is important for soil aeration, water infiltration, resistance to erosion, and hence, is also important for plant growth. Tisdall and Oades (1982) proposed a hierarchical theory for the formation of soil macroaggregates. According to this theory, microaggregates (0.02- 0.25 mm in diameter) are formed from electrostatic interactions of primary clay particles and organic matter. These structures are highly stable in soil (Tisdall 1991). Macroaggregates form from microaggregates by processes that are not fully understood (Degens *et al.* 1994).

AM fungi are believed to play a role in the stabilisation of microaggregates into macroaggregates (Miller and Jastrow 2000). A number of studies have correlated the presence of mycorrhizas with increased water stable macroaggregates (Schreiner *et al.* 1997, Thomas *et al.* 1986, Miller and Jastrow 1990) though the effects of the fungus are difficult to dissociate from those of the root. Thomas *et al.* (1993) used split-root plants growing in four-chambered pots in a silty clay loam soil and compared water stable soil aggregates in soils containing all combinations (presence/absence) of roots and extraradical AM fungus hyphae. Though aggregation was greatest in the mycorrhizal root chamber, there were similar percentages of water stable aggregates in the nonmycorrhizal root *vs* the hyphae-only chamber. They concluded that the root and hyphae have similar effects on the stability of soil aggregates. Miller and Jastrow (1990) studied mycorrhizas in a chronosequence of tallgrass prairie restoration on a silt loam soil in Illinois, USA. They have used path analysis to quantify the relative contributions of extraradical hyphae, fine and very fine roots, and various soil organic matter pools to the formation of stable soil macroaggregates (Miller and Jastrow 1990, Jastrow *et al.* 1998). This analysis showed that the hyphae had a greater direct role in stabilising the aggregates than did fine or very fine roots, but the indirect effect of very fine roots, through their symbiosis with AM fungi, was substantial.

These studies support the view of the hyphae stabilising soil particles through a mechanism of physical entanglement. Indeed, the amount of hyphae calculated to be present in soil aggregates is impressive. Each gram of stable macroaggregates can contain 50-160 m of hyphae (Tisdall and Oades 1979, Degens *et al.* 1994). Microscopic examination also has allowed the visualisation of this phenomenon (see refs in Degens *et al.* 1994).

A key mechanism of AM fungus stabilisation of soil aggregates appears to be an iron containing glycoprotein termed "glomalin" (Wright *et al.* 1996, Wright and Upadhyaya 1998). Aggregate stability and glomalin content of soils have been positively correlated (Wright and Upadhyaya 1998, Wright *et al.* 1999, Wright and Anderson 2000). Soils may contain 4.4 to 14.8 mg glomalin per g. This hydrophobic molecule is produced by all AM fungi examined and is deposited on the walls of extraradical hyphae. Evidence suggests that *Gigaspora* spp produce more glomalin per mg hyphae than do *Glomus* spp (Wright and Upadhyaya 1996). This supports findings by Miller and Jastrow (1992) who found that one species in particular, *Gigaspora gigantea*, was most associated with macroaggregation of soil in the tallgrass prairie restoration chronosequence. Immuno-fluorescent assays have demonstrated its appearance on roots and root hairs of mycorrhizal plants, AM fungal spores (Wright and Upadhyaya 1996) and soil aggregates (Wright and Upadhyaya 1998). Further, glomalin and water stable soil aggregates are linked with agricultural management practices. The transition in tillage from ploughing to no-till increased both water stable aggregates and soil glomalin (Wright *et al.* 1999). Aggregate stability varies with glomalin in soils under various crop rotations (Wright and Anderson 2000).

There is a definite need for the involvement of other disciplines in the study of glomalin and its role in soil aggregation. Soil chemists and physicists should study how this glycoprotein interacts with soil particles and why it is so recalcitrant. Since this compound can be 1% of the weight of upper layers of soil, it represents a significant portion of total soil organic matter and as such deserves further study. Very little is known about its structure, and nothing is known about its biosynthesis and secretion outside the hyphal wall. Also, the impact of plant and soil P status on the production of glomalin is not known. This is important with the increasing application of P-rich animal manures on many soils.

Most studies linking AM fungi and other biological processes to soil aggregation have been conducted in fine textured soils. There is some doubt as to whether AM fungi play a role in soil aggregation in sandy soils however (Degens *et al.* 1994). Stabilisation of aggregates in these soils may be limited by the inhibitory effect of large particle sizes upon aggregation.

Lengths of hyphae well in excess of 50 m per g of aggregates may be needed for AM fungus hyphae to contribute to water stability of aggregates (Degens *et al.* 1994). In addition, the effect of an AM fungus upon aggregation may differ for different soil types. An isolate of *Glomus mosseae* improved soil aggregation by 400% in a gray silt-loam high in organic matter and P, but in a yellow clay-loam low in organic matter and P the same fungus had a much smaller (50%) affect on aggregate stability (Bethlenfalvay and Barea 1994).

2.3 Interactions among AM Fungi and Other Soil Organisms

Increasing attention is being paid to the complex interactions among AM fungi and other soil organisms because these relationships can potentially enhance or eliminate mycorrhizal benefits for crop production and soil stabilisation (Bethlenfalvay and Schüepp 1994, Hodge 2000). As mentioned previously, AM fungal colonisation changes the chemistry of roots and exudates and generates a 'mycorrhizosphere community' of microorganisms that is distinct from that of the rhizosphere of nonmycorrhizal roots (Linderman 2000). Furthermore, because AM fungal species, and even isolates of the same species, differ in their influence on roots and exudates, microbial assemblages differ in the mycorrhizospheres of different AM fungal isolates (Meyer and Linderman 1986, Schreiner *et al.* 1997, Andrade *et al.* 1997). The activities of soil bacteria, actinomycetes, fungi, mites, collembolan and nematodes can influence the formation and functioning of mycorrhizal associations through a variety of mechanisms (Table 3). This finding opens the possibility that mycorrhizal function may result from a consortium of soil organisms that are associated with AM fungi and not from the fungi alone (Bethlenfalvay and Schüepp 1994, Gryndler 2000).

Table 3 Mechanisms by which biotic interactions can mediate mycorrhizal function

Biotic interactions mediate mycorrhizal function through:
● Changing the availability of essential resources/substrates
● Producing stimulatory or inhibitory compounds
● Modifying rhizosphere chemistry
● Grazing extraradical hyphal networks
● Modifying soil structure
● Dispersing or destroying propagules

Soil organisms can be either beneficial or antagonistic to AM fungi. Nearly forty years ago certain bacteria were shown to enhance germination of AM fungus spores (Mosse 1962), and since that time, many other beneficial interactions between AM fungi and bacteria have been observed. Garbaye (1994) reviewed the scope of these associations and defined 'Mycorrhization Helper Bacteria' (MHB) as "bacteria associated with mycorrhizal roots and mycorrhizal fungi which selectively promote the establishment of mycorrhizal symbiosis." Beneficial associations can also be mediated through the host plant. For example, by reciprocally supplying P and nitrogen (N) to a common plant host, AM fungi and N-fixing bacteria generate a synergistic tripartite symbiosis which is superior to a dual symbiosis, with either the AM fungus or diazotroph individually (Barea *et al.* 1992, Biro *et al.* 2000). Antagonists of AM fungi include mycoparasites, spore and hyphal grazers, and competitors. Detrimental effects of antagonistic soil organisms on AM fungi and their hosts have been recognised for over twenty years (e.g. Ross and Ruttencutter 1977, Ross 1980, Wilson *et al.* 1988), but much work remains before the mechanisms of these interactions are understood. As the natural history of associations between AM fungi and other soil organisms becomes better elucidated, it will be possible to design management strategies that deter organisms that are antagonists of mutualistic AM fungi and stimulate organisms that are beneficial to them.

Although field-based research is necessary to develop management strategies that maximise the beneficial AM fungus-microbe interactions and minimise the detrimental ones, to date, studies of AM fungus interactions with soil microbes have largely been confined to pots in glasshouses or growth chambers. This is because the staggering diversity and rapid growth rates of most soil organisms in the field often makes field studies of these interactions too complicated for human comprehension. One way microbial ecologists study tremendously diverse microbial communities is to make generalisations from 'functional groups' of microbes. Functional groups have been defined in various ways, usually according to tropic status or specific physiological requirements. Nutritional profiles of components of communities of soil microbes are now routine using standardised carbon sources, such as in Biolog (Biolog Inc. Hayward, CA) microplates (Garland and Mills 1991). Future mycorrhizal research may make significant advances using Biolog microplates designed to reflect the availability of carbon substrates in mycorrhizospheres vs uncolonized soil. For example, one of the few carbon substrates known to be taken up by extraradical hyphae of AM fungi is acetate (Bago *et al.* 2000). One would therefore expect limited availability of acetate in the soil of the mycorrhizosphere *vs* the bulk soil. This may affect the microbial community. Enzyme assays are another technique that could be used in field-based research of AM-soil microbe interactions (Sinsabaugh 1994). This technique quantifies extracellular enzymes and reflects the actual physiological activity of microbes and could be used to describe the differences in enzymatic activities of soil microbial communities as affected by AM fungi or various management practices which affect AM fungi. Both of these methods have great value in community level exploration. Once interactions among functional groups of organisms are identified, PCR, DNA probes, and other molecular or immunological tools can be applied to track the organisms involved and better understand the mechanisms of the interactions (Table 3). The following discussion briefly summarises the range of feedbacks that exist between soil organisms and begins to identify the kinds of interactions that will most likely lead to sustainable mycorrhizal benefits.

2.3.1 Resource availability

Transfer of essential resources is a strong mediator of species interactions. A resource can be defined as any substance that is consumed by an organism and can lead to increased growth rates as its availability in the environment increases (Tilman 1988). According to this definition, the copious extraradical hyphae produced by AM fungi provide substrates for soil microbes. Because extraradical AM hyphae can transport significant quantities of carbon substrate into the soil (Jakobsen and Rosendahl 1990), one might expect that total populations of soil organisms should consistently be elevated in mycorrhizosphere soils compared to rhizosphere soils of nonmycorrhizal plants. However, this is not the case, total microbial populations are often lower in the mycorrhizosphere (Ames *et al.* 1984, Christenson and Jakobsen 1993, Andrade *et al.* 1997, 1998). This suggests that AM fungi and certain soil microbes compete for the same rhizosphere substrates. As mentioned above, this is likely to be an important mechanism by which AM fungi protect their hosts from some root pathogens and is a desirable goal of mycorrhizal management.

2.3.2 Stimulatory or inhibitory compounds

Soil organisms are known to produce an arsenal of biochemically active compounds like antibiotics, vitamins, and growth regulators, and these compounds can impact mycorrhizal function (Vancura 1986). A recent review (Gryndler 2000) illustrates the diversity of interactions between AM fungi and other soil organisms involving both stimulatory and inhibitory compounds. For example, an isolate of *Aspergillus niger* that produced substances similar to indole-3-acetic acid and gibberellic acid was shown to increase the fitness of both *Glomus fasciculatum* and the host plant

(Manjunath *et al.* 1981). In contrast, unidentified compounds produced by another isolate of *A. niger* were shown to inhibit spore germination and hyphal growth of *Glomus mosseae* (McAllister *et al.* 1995).

2.3.3 Modification of rhizosphere chemistry

Soil bacteria and fungi also impact mycorrhizal function by modifying soil chemistry. For example, synergistic relationships have been observed between AM fungi and P-solubilising bacteria (Barea *et al.* 1975, Piccini and Azcon 1987). These bacteria are thought to increase the solubility of calcium phosphate through acidification of the rhizosphere with organic acids (Kim *et al.* 1998). Enzymatic activities of rhizosphere organisms also generate synergistic relationships with AM fungi (Camprubi *et al.* 1995). For example, Tarafdar and Marschner (1995) found that extracellular phosphatase produced by *Aspergillus fumigans* increased P uptake and growth of wheat inoculated with *G. mosseae.*

2.3.4 Grazing extraradical hyphal networks

Microarthropod grazers may also be important mediators of mycorrhizal function. Most subterranean species of collembola feed heavily, if not exclusively on soil fungi. Some studies suggest that collembola could be important regulators of AM function because grazing on extraradical hyphal networks could seriously reduce the nutrient uptake capacity of AM fungi and potential benefit to plants (Warnock *et al.* 1982, Finlay 1985, Thimm and Larink 1995). However, other studies indicate that when given the choice, collembola avoid eating AM hyphae and much prefer to feed on nonmycorrhizal fungi (Klironomos *et al.* 1999). A recent review (Gange 2000) explores the complexity of collembola-AM fungal interactions and suggests that the grazing of collembola on nonmycorrhizal fungi may indirectly benefit AM fungi and host plants and stimulate nutrient cycling. This review also cautions against generalising too much from the current pool of literature because, to date, nearly all of the studies of AM-collembola interactions have used a single, easily cultureable collembola species: *Folsomia candida.* Many more studies need to be conducted that incorporate a wider diversity of collembola as well as other fungal grazers, such as fungivorous nematodes and mites, before the full impact of AM-grazer interactions on mycorrhizal function can be understood.

2.3.5 Modification of soil structure

Large, earthmoving soil organisms such as ants, earthworms, and gophers modify soil structure and impact propagule densities of AM fungi

(Allen 1991, Friese and Allen 1993). Mycorrhizal effects on soil structure also impact other soil organisms. As discussed previously, AM fungal hyphae facilitate the formation and stabilisation of soil aggregates. Andrade *et al.* (1998) used a split-pot design to show that soil populations of bacteria, actinomycetes and fungi all responded positively to the structural modifications caused by AM fungal hyphae. Total microbial populations were not correlated with AM root colonisation directly, but were strongly correlated with the increased aggregation caused by the AM fungi. Highly aggregated soil will be more aerobic and have a higher moisture holding capacity than soil with few stable aggregates. Both of these factors are likely to strongly influence soil microbial populations and indirectly feedback on mycorrhizal function.

2.3.6 Dispersal or destruction of propagules

Ants, grasshoppers, earthworms, millipedes, mites, and other soil animals are known to be important dispersal agents of AM fungi (Allen 1991). For example, Klironomos and Moutoglis (1999) showed that the collembola *Folsomia candida* increased the dispersal range of *Glomus etunicatum* by at least 30 cm. On the other hand, AM fungi can also be vectors for other soil organisms (Gryndler 2000). For example, Bianciotto *et al.* (1996) found that several strains of rhizobia and pseudomonads adhere to the surface of AM fungal spores, hyphae, and auxiliary cells and thus, AM fungi may transport these soil microbes throughout the soil.

From a negative perspective, interactions can also destroy propagules. Soil animals such as mites, collembola and worms can destroy AM fungal propagules through direct ingestion or piercing and sucking out the spore contents (Hetrick 1984). Also, bacteria, actinomycetes, and fungi are known to degrade spore walls and reduce their viability (Ross and Ruttencutter 1977, Ames *et al.* 1989).

2.4 Impacts of Arbuscular Mycorrhizas on Nutrient Cycling

Sustainable natural and managed systems efficiently recycle essential nutrients and minimise losses through erosion, leaching, or volatilisation. All of the functions of mycorrhizas (Table 1) may influence nutrient flux within ecosystems. Because AM fungi are often among the largest consumers of net primary production, they immobilise a tremendous quantity of nutrients, and the rate at which their tissues decompose will impact nutrient availability (Allen 1991). Also, intact networks of AM mycelia act as conduits for nutrient transfer within plant communities and may be important in reducing leaching losses (Read *et al.* 1985). The role of

AM fungi in direct acquisition of nutrients from organic matter is controversial (Hodge *et al.* 2000), but their indirect roles through plant nutrition and microbial communities can be substantial and need to be considered in ecosystem-level management.

3. INFLUENCE OF MANAGEMENT PRACTICES UPON FUNCTION OF AM FUNGI

3.1 Effects of Tillage and Soil Disturbance upon AM Fungi

Given that extraradical hyphae are both the inorganic nutrient absorbing organ of the mycorrhiza and an important component of the inoculum of AM fungi in the soil, soil disturbance can affect both the inoculum potential of the soil and the ability of the mycorrhiza to take up nutrients. In addition, tillage can affect the distribution of AM fungi through the soil profile.

First, severe soil disturbance, such as moldboard ploughing, can greatly affect the distribution of AM fungi within the plough layer of soil. Inoculum of AM fungi in undisturbed soil or at the end of a growing season in agricultural soil is found primarily in the top 8-15 cm of soil (Smith 1978, An *et al.* 1990, Abbott and Robson 1991). Moldboard ploughing would transport this inoculum to greater depths due to inversion of the soil (Smith 1978).

The rapid colonisation of a newly germinated seedling can depend to a large extent upon the intact network of extraradical mycelium already present in the soil. This hyphal network is built and destroyed with each tillage and planting cycle in an agricultural soil under conventional tillage. This affects the rate of colonisation of young seedlings by AM fungi. A common observation is greater colonisation of roots of seedlings in no-till soils early in the growing season relative to those in paired, tilled plots (Galvez *et al.* 1995, Kabir *et al.* 1997, McGonigle and Miller 1993) (Table 4), though this may not always happen (Miller *et al.* 1995). Two situations in which soil disturbance may not affect colonisation of roots by AM fungi are when the majority of the inoculum is in the form of spores, which remain viable after disturbance (Jasper *et al.* 1991) and when inoculum levels in the soil are low (McGonigle and Miller 2000). Characteristics of both the host crop and fungal symbionts should be considered in future studies of this phenomenon (McGonigle and Miller 2000). For example, genera of AM fungi differ in both the hyphal growth possible from a germinated spore and in the ability of infected root pieces or extraradical hyphae to act as inoculum (Biermann and Linderman 1983). The relative proportions of these groups within the AM fungus community would influence the response to tillage.

Soil disturbance or tillage more consistently affects the mycorrhiza-mediated P uptake of plants whether or not a concomitant decrease in colonisation occurred. This has been demonstrated in greenhouse (Evans and Miller 1990, Miller 2000) and field experiments (McGonigle *et al.* 1990, McGonigle and Miller 1996). There is a general consensus on the mechanism behind this phenomenon. The plant sown into the undisturbed, pre-existing network of extraradical mycelium becomes colonised and is then 'plugged into' an already extensive nutrient absorbing organ of the mycorrhiza. There may not need to be great levels of inoculum for this to occur. The plant in the undisturbed soil will exhibit increased P status early in the growing season (Table 4). However, the hyphal network in the disturbed soil eventually redevelops allowing these plants to 'catch up' as early as the 6-leaf stage in maize (McGonigle and Miller 1993). Indeed, the early season enhancement in P uptake for no-till *vs* conventionally tilled maize does not translate into increased growth and yield (Miller *et al.* 1995), possibly due to reduced soil temperatures in no-tilled soils (Miller 2000). Also, tillage is likely to select for different AM fungal species (Johnson unpublished observation, Jansa *et al.* 2001), with different symbiotic function. More research is needed to increase the yield of no-till crops so as to encourage this management practice with a wide range of environmental benefits.

Table 4 Effect of moldboard plough (MP) and no-till (NT) upon maize shoot P concentration and colonisation of roots by AM fungi in the field.*

Days after Planting	**Shoot P (mg kg^{-1})**		**Root length with arbuscules (%)**	
	MP	**NT**	**MP**	**NT**
25	0.642 b	0.752 a	11 b	27 a
32	0.344 b	0.480 a	27 b	45 a
48	0.442 a	0.441 a	44 a	55 a

*Numbers in a row, for a given pairwise comparison, followed by the same number are not significantly different (p=0.05). Adapted from McGonigle and Miller 1993.

Tillage should also be expected to interact with the soil aggregation function of AM fungi. A three year transition from tillage to no-till was studied in a silt loam soil (Wright *et al.* 1999). Both soil aggregate stability and glomalin levels in the soil were greater for no-till than tillage treatments, and the effect was greater with successive years of no-till (Table 5).

Table 5 Aggregate stability (0-5 cm depth) and glomalin content for a silt loam soil in transition from tillage to no-till.*

Treatment	**Aggregate stability (%)**	**Total glomalin (mg g^{-1} aggregates)**
No-till 3 yrs	37.7 a	1.567 a
No-till 2 yrs	30.8 ab	1.389 ab
No-till 1 yr	25.0 b	1.323 bc
Plough tillage	16.7 c	1.195 c

*Numbers in the same column followed by the same letter are not significantly different ($p=0.05$). Adapted from Wright *et al.* 1999.

3.2 Effects of Crop Management upon AM Fungi

The community of AM fungi in agricultural soil is also influenced by the choice of crop host and crop rotation history. In addition, the presence and length of fallow periods, or the presence of over-wintering or fallow cover crops, have significant effects on the composition of AM fungal communities, which in turn affects the productivity of the soil.

Greenhouse studies showed that AM fungi proliferate more in the presence of one host than another, and that preferred hosts differ among AM fungal species (Hetrick and Bloom 1986). This also occurs in the field where the abundance of spores of certain AM fungal species will rise and fall according to the cycle of the crop rotation (Hayman *et al.* 1975, An *et al.* 1993, Hendrix *et al.* 1995). For example, *Gigaspora gigantea* spores were more numerous in the autumn following maize (3.5 spores 50 cm^{-3}) than following small grains or a vegetable crop (0.5 spores 50 cm^{-3}) (Douds *et al.* 1997). However, this species was more prevalent following soybean at another site (An *et al.* 1993), underscoring the important interaction with soil characteristics, which has been noted elsewhere (Johnson *et al.* 1991).

The species composition of the AM fungal community can have important ramifications for the biological fertility of soils. Certain species, notably those from the genus *Gigaspora*, are more often associated with well aggregated soils (Miller and Jastrow 1992), and therefore may play a stronger role in stabilising macroaggregates than other genera. As abundance of AM fungal species changes within the rotation, so may the susceptibility of the soil to erosion. These conclusions are based upon spore populations. Researchers have not had the proper tools to allow them to consider the relative contribution of the high or low abundance sporulators to the length of extraradical hyphae in the soil (for discussion, see Douds and Millner 1999). There have been no field-based descriptions of AM fungal communities based upon extraradical hyphal networks, i.e. the structures that actually do the work of nutrient uptake and soil stabilisation. Some researchers have successfully discriminated among selected AM fungi based upon morphology of intraradical structures (Abbott 1982), and this was useful in greenhouse studies (Abbott and Robson 1984). Merryweather and Fitter (1998) described the arbuscular mycorrhizas of *Hyacinthoides non-scripta* and assigned genus and sometimes species designations based upon intraradical morphology, but later found discrepancies between morphology-based identifications and those based upon molecular techniques (Helgason *et al.* 1998-a). If this was due to phenotypic plasticity of the AM fungi, then molecular techniques hold the greater promise for future study. Although there have been recent successes in greenhouse pot experiments (Jacquot *et al.* 2000, Kjoller and Rosendahl 2000pa), there is need for field application of molecular techniques for the identification and quantification of the extraradical phase of mycorrhizas.

Another aspect of ‘functional biodiversity’ of AM fungi to be considered with changes in the community is in the exploration of the soil for nutrients. Smith *et al.* (2000) and the related commentary by Koide (2000) recently demonstrated this. *Scutellospora calospora* enhanced P uptake by *Medicago truncatula* from soil close to the root while *Glomus caledonium* enabled access to more distant soil. The whole subject of functional diversity of AM fungi requires further research. There are approximately 160 described AM fungus species, upwards of 26 at a site (Ellis *et al.* 1992), and beyond the work noted above, the prevailing view is that they more or less occupy the same niche in the soil (Dodd *et al.* 2000).

There is evidence that the efficacy of the entire community of AM fungi can change due to cropping sequence and that crop monocultures may generate fungal communities that do not enhance crop performance (Schenck *et al.* 1989). This phenomenon may partly explain the reduction of yield that occurs with continuous monocultures of maize, soybean (Johnson *et al.* 1992), and tobacco (Hendrix *et al.*1992). Feldmann *et al.* (1991) also reported that AM fungi from a monoculture of *Hevea* spp were ineffective at growth promotion of both *Hevea* seedlings and maize compared to those from a nearby natural area.

The presence of weed host plants in an agricultural field can serve to offset the negative effect of a monoculture upon the AM fungal community. Populations of spores of AM fungi were positively correlated to the presence of weeds in lettuce fields (Miller and Jackson 1998). Feldmann and Boyle (1999) found beneficial effects of weeds, not only upon diversity of AM fungi in the soil, but upon the efficacy in enhancing plant growth, overcompensating for any yield reduction of maize due to competition with the weeds. Other studies have noted no increased spore populations or diversity with increasing weed levels (Kurle and Pfleger 1996).

One of the crop management practices most harmful to AM fungi is a nonhost plant, such as *Brassica* or *Lupinus* in the crop rotation (Blaszkowski 1995, Harinikumar and Bagyaraj 1988). These crops resist colonisation by AM fungi, thereby restricting the carbon flow to these obligate symbionts. This results in lower levels of inoculum and less colonisation of the next mycotrophic crop in the rotation (Gavito and Miller 1998). The growth of some high value vegetable crops, with wide spacings and strict weed control, can also depress AM fungal populations due to restriction of available root biomass for the symbiosis. Less inoculum of AM fungi was present in soil following a crop of *Capsicum annuum* than following small grains or maize (Douds *et al.* 1997).

Long fallow periods without plant cover are detrimental to AM fungi. A striking example of this is long-fallow disorder in Australia (Thompson 1987, 1991). Long fallows of 11-14 months may be necessary in semi-arid climates to allow for replenishment of soil moisture for the next crop. A wide range of crop species, among which *Linum usitatissimum* is one of the most sensitive, can grow poorly after long fallows and exhibit P and Zn deficiency. Poor crop growth was correlated to reduced root colonisation by AM fungi due to the reduction in inoculum caused by long fallow in northern Australia (Thompson 1987), but this effect was not observed in southern Australia (Ryan and Angus 2001).

On the other hand, one of the most AM fungus-friendly crop management practices, besides reduced tillage, is inclusion of over wintering cover crops in a crop rotation. One of the primary differences between 'low-input, sustainable' agriculture and 'chemical-based, conventional' agriculture is that the proportion of the year with live plant cover is much greater in the low-input than conventional system (Douds *et al.* 1993). Soils of the low-input farming system studied at the Rodale Institute Experimental Farm are covered with live plants approximately 70% of an average year *vs* 40% for a conventional maize-soybean rotation. This is primarily due to over wintering cover crops. Spores in bare fallowed soils may be induced to germinate during mild late fall or early spring periods, after crop senescence and before the planting of the next crop. Several such germinations cause the spore to drain its carbohydrate and lipid reserves, limiting its ability to colonise roots of the next crop when they are finally available. The cover crop, in addition to retarding soil erosion and replenishing and retaining soil N, serves as an interim host plant for the AM fungi. This results in greater amounts of infective inoculum for the next cash crop (Galvez *et al.* 1995; Boswell *et al.* 1998).

The use of transgenic plants as a crop management technique to control insect pests is practiced widely in some parts of the world, particularly in the US (Stewart *et al.* 2000). Future application of this technology to modify the human nutritional value of crops is likely (Ye *et al.* 2000). Oger *et al.*

(2000) showed that *Lotus corniculatus* with transgenes for opine production were capable of altering the rhizosphere microflora. The future likelihood of the development of transgenic plants resistant to root diseases, encouraged due to future restrictions on the use of chemicals such as methyl bromide, underscores the need for studies of the effects of transgenic plants upon beneficial soil microbes such as AM fungi (Glandorf *et al.* 1997).

3.3 Nutrient Management

Mycorrhizal fungi are generally very sensitive to phosphate enrichment. Their responses to fertilisation are mediated by their host plants and are strongly influenced by edaphic properties and chemical composition of the fertiliser. Fertilisation usually decreases AM fungus colonisation in agricultural soils but in extremely nutrient deficient soils, it sometimes increases colonisation (Hayman 1975). These contrasting responses suggest that plant nutrition mediates mycorrhizal responses to fertiliser. Severely nutrient deficient plants are stunted and can supply little photosynthate to AM fungi. Fertilisation of these systems will increase plant size and their ability to provide AM fungi with carbon compounds. Plants usually preferentially allocate photosynthate to the organs that maximise acquisition of the resources that are most limiting to growth (Chapin 1980, Tilman 1988). Thus, when plants are strongly limited by soil resources, relatively more photosynthate is allocated to their roots; and, when they are more strongly limited by light, relatively more is allocated to shoots. Fertilisation reduces limitation by soil nutrients and induces plants to allocate less carbon to roots, root exudates and AM fungi. Most agricultural soils have moderate to high nutrient contents and this is why fertilisation usually decreases AM colonisation in agricultural systems. Together, the chemistry of soils and fertiliser supplements will control the nutrient status of plant hosts and they will ultimately control mycorrhizal responses to fertilisation.

Studies show interactions in mycorrhizal responses to P, N, and potassium (K) enrichment, indicating that the relative availability of these essential nutrients is important to mycorrhizal function (Saif 1986, Gryndler *et al.* 1990). Although AM fungi are best known for their uptake of P and immobile micronutrients, mycorrhizal uptake of N, particularly as NH_4, is also well documented (Ames *et al.* 1983). Enrichment of P does not necessarily reduce AM fungal colonisation in N-limited plants, but it does reduce colonisation when N levels are adequate. This suggests that P:N ratio is an important factor governing AM responses to nutrient enrichment (Hepper 1983, Sylvia and Neal 1990).

In general, conventional agricultural systems enriched with high inputs of inorganic fertilisers have lower AM fungus activity than organically managed systems enriched with low inputs of farmyard manure or legume cover crops (Sattelmacher *et al.* 1991, Douds *et al.* 1993, Galvez *et al.* 1995). A study of 24 fields at 13 farms showed that fields enriched with inorganic fertilisers had significantly lower AM fungal colonisation and fewer spores than fields managed with no inputs or enriched with manure and slurry (Eason *et al.* 1999). This study took the important next step of assessing the symbiotic functioning of the AM associations in these fields. Spores were sieved from the 24 soils and approximately 1,000 spores from each soil were used to inoculate *Allium ameloprasum* and *Trifolium repens* grown in irradiated soil in a greenhouse. On average, these crops had significantly larger shoots when inoculated with spores from organic fields than from conventional fields (Table 6). These findings suggest that the AM fungi in the low-fertility organically managed soils were more beneficial to their hosts than those in the high-fertility conventionally managed soils. Analyses of spore populations in other systems indicate that fertilisation changes the species composition of AM fungal communities (Johnson 1993, Egerton-Warburton and Allen 2000). These results provide support for the hypothesis that fertilisation selects for less mutualistic AM fungi (Johnson 1993). Theoretically, nutritional mutualisms would be expected to be selected in nutrient deficient systems and fertilisation would be expected to eliminate the benefits conferred by such a relationship and set the stage for more parasitic interactions (Johnson *et al.* 1997, Hoekesema and Bruna 2000).

More studies are needed to link the composition of AM fungal communities with their symbiotic function. Because the benefits that plants gain from mycorrhizas are often unrelated to root colonisation and spore densities (McGonigle 1988), future field-based research needs to systematically examine fertiliser impacts on mycorrhizal functioning, across a range of crops and soil types, to provide the information that is necessary to effectively coordinate management of mycorrhizas and fertilisers in a sustainable manner.

Table 6 Responses of *Allium* and *Trifolium* to inoculation with AM fungal spores from grassland soil under conventional management (CM) or organic management (OM)*.

	Allium ameloprasum		***Trifolium repens***	
	CM	OM	CM	OM
Total shoot weight (mg)	0.39b	0.55a	9.44b	10.30a
AM infection (% root length)	56.9a	64.0a	54.5a	63.3a

*Numbers in a row, for a given pairwise comparison, followed by the same number are not significantly different (α=0.05). Adapted from Eason *et al.* 1999.

3.4 Effects of Synthetic Pesticides upon AM Fungi

Chemical pesticides applied to agricultural soils throughout the production cycle may have variable affects on AM function. Soils may be fumigated prior to planting. Most of these fumigants, including dazomet (Mark and Cassells 1999) and methyl bromide / chloropicrin (McGraw and Hendrix 1984) are also effective at killing indigenous AM fungi. Although enhanced growth of the following crop due to control of pathogens is the expected result of fumigation, stunted growth and P, Cu, or Zn deficiency may also occur. This has been linked to the destruction of AM fungi because inoculation with AM fungi relieves the stunting (see thorough review by Menge 1982).

Seeds sown into agronomic soils may also be coated with fungicides. These fungicides were shown to have no effect on the development of mycorrhizas on the seedlings (Spokes *et al.* 1989). Fungicides may also be applied to soils prior to or during plant growth. These affect AM fungi to varying degrees, and species of AM fungi differ in their susceptibility (Schreiner and Bethlenfalvay 1997). Further, the extraradical hyphae, i.e. the nutrient absorbing organ of the mycorrhiza, appears to be the most susceptible to fungicide application (Kjoller and Rosendahl 2000b, Larsen *et al.* 1996).

4. CONCLUSION

Mycorrhizal effects on plant production are mediated by complex interactions among soil properties, plant genotypes, AM fungal genotypes, and the physical and biotic environment. The result of these interactions over time is the selection of communities of soil organisms that may or may not maximise crop production. Thus, in the context of developing management strategies to maximise AM benefits, it is necessary to analyse these associations from an evolutionary perspective and consider them dynamic systems integrating interactions at molecular, population, community and ecosystem scales (Miller and Kling 2000).

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