Schönbeck and Dehne, 1989), and (3) cultural (Johnson and Pfleger, 1992; Kurle and Pfleger, 1994; Miller and Jastrow, 1992a) and environmental (Sylvia and Williams 1992; Wright and Millner 1994) plant stress. Recently, perhaps inspired by the impact of sustainability, the AMF have also come to life in the review literature as soil symbionts and agrosystem stabilizers (Bethlenfalvay and Svejcar, 1991; Finlay and Sönderström, 1992; Miller and Jastrow, 1992b; Tisdall, 1991). But no attempt had been made so far to integrate the information available on the interactions between specific AMF isolates and specific groups of soil biota with agrosystem stability.

The purpose of this contribution is to discuss the current concept of mycorrhizal effectiveness and to refocus it by making it applicable not only to the host plant but to the entire agrosystem, within the context of sustainability in agriculture.

Mycorrhizal efficiency and benefits to the agrosystem: changing views

The contributions of AMF in natural or disturbed ecosystems and in experimentation under controlled conditions have been traditionally measured by plant response (Asai, 1943; Gerdeman, 1968; Jeffries, 1987; Pfleger and Linderman, 1994; Schlicht, 1889; Stahl, 1900). The more an AMF was able to improve plant growth relative to other isolates under a given set of conditions, the more 'effective' it was said to be. In turn, the better an arbuscular mycorrhizal plant could approximate growth by an optimally fertilized non-arbuscular-mycorrhizal plant (Abbot and Robson, 1991), the more 'benefits' it was said to derive from its symbiotic status. These benefits (mycotrophy, or mycorrhizal dependence) were evaluated in terms of gains derived from mycotrophic P import against the price paid in reduced carbon by the plant to support its obligatorily biotrophic endophyte (Fitter, 1991; Koide, 1991).

Such an analysis of cost–benefit relationships from the plant's point of view continues to be of interest to agriculture and above–ground ecology, and is particularly applicable to a demonstration of host–endophyte relationships under the conditions of two–component agrosystems that consist only of the mycorrhiza and the sterilized soil used in most mycorrhiza experiments. In the field, however, the relationship between host plants and AMF is altered by the other biotic components of the agrosystem (Fitter, 1985; Hetrick et al., 1988; Safir, 1994), which permit measurable benefits to accrue to the plant only under particular conditions of growth (Fitter, 1986).

The extent to which the concept of mycorrhizal benefit is influenced by phytocentric thinking is illustrated by two important recent studies. Hetrick et al. (1992) found that a decline in dry weight was related to a loss of mycorrhizal dependence in modern wheat (*Triticum aestivum* L.) cultivars. These authors suggested that mycorrhizal dependency should be considered in breeding programs (Hetrick et al., 1993). In doing so, they equated mycorrhizal benefit with mycorrhizal dependence of the host plant, as if mycorrhizal contributions to the soil in which that plant grows were irrelevant. In the second study, Johnson (1993) suggested that an understanding of the mechanisms that let AMF enhance or inhibit plant growth is necessary for managing ecosystems. This view was based on findings that cultural practices select AMF that are inferior mutualists (Johnson et al., 1992). Johnson (1993) recommended a manipulation of AMF communities favouring proliferation of the most beneficial isolates with regard to plant yield instead of the inferior ones that contribute to yield decline. Again, the suggestion does not consider that yield, in the long run, depends on the quality of the soil.

We fully agree with these authors that plant growth response to AMF is important in agriculture, but wish to emphasize that there is more to mycorrhizal benefit than just the yield increase derived from mycotrophy. Stribley's verdict (1989): "mycorrhizal inoculants have failed to fulfil their promise because currently there is little promise to fulfil" was apparently based on the assumption that plant growth enhancement is all that AMF affect in the agrosystem. However, the full range of the promise is far from being elucidated, for many of the benefits are hidden below–ground. It is our hope that our discussion here will contribute to a better understanding of both the promise and the benefits, since the latter clearly fill a current conceptual as well as a practical niche in sustainable agriculture. These extra benefits may be summed up as 'agrosystem stability'. They accrue to plant and soil alike and cannot be weighed at harvest on a scale of dry weights. They result from the inseparable, complex processes that unite all components of the agrosystem, and represent a new agenda for agriculture (Board on Agriculture, 1993).

AMF and soil structure

Shifting the focus from the plant to the agrosystem A message to agriculture fifty years ago advised that "the presence of an effective mycorrhizal symbiosis is essential to plant health" (Howard, 1943). Now, looking back on hundreds of research reports and an extensive collection of mycorrhiza books, it seems that the time to fully appreciate this message has come, if only because the challenge posed by the complexity of interacting, interdependent factors that have a bearing on rhizosphere research is now more clearly delineated (Linderman and Paulitz, 1990; Schroth and Weinhold, 1986). Plant health and productivity are rooted in the soil, and the quality of soil depends on the diversity and viability of its biota (Doran and Linn, 1994; Visser, 1985) which shape the structures that support a stable and healthy agrosystem.

The interest shown by increasing numbers of mycorrhiza workers in the interactions of AMF with the soil and its biota is therefore not so much a sign of masochist's delight in grappling with unmanageably complex systems (Schroth and Weinhold, 1986), but stems from the needs and priorities of the agriculture of our times. In this sense, that the inclusion of soil structure into mycorrhiza research is a necessity whose time has finally arrived. Since Tisdall and Oades (1979) first reported that aggregate stability and AMF status are related in agricultural soils, work has advanced at three levels: (1) collection of evidence for the relationship, (2) elucidation of its mechanisms, and (3) the integration of its process into agricultural concepts. What is largely lacking is a realization of theory in practice.

Impact of mycorrhizas on soil aggregation The roster of reports of AMF effects on agricultural soils is still minuscule compared to the wealth of information available on plant responses. It starts with the pioneering work of Tisdall and Oades (1979, 1980a) on the relationships between crop rotation, fallowing and soil stability, showing a connection between the extent of the soil mycelium and macroaggregate formation and stabilization by arbuscular mycorrhizal roots (Tisdall and Oades 1980b). It moves on to Miller's extensive field studies (1984, 1987) on prairie reconstruction. Miller, in collaboration with Jastrow, reported in a series of important papers how the affinity between mycorrhizas and soil aggregates varies with root characteristics, with the intensity of root colonization, and with the amount of soil mycelium associated with the roots. They further elucidated, or contributed to the understanding of, the mechanisms of the formation of water–stable aggregates (Jastrow, 1987; Miller and Jastrow, 1990; Miller and Jastrow, 1992a and b; Miller and Jastrow, 1994). Thomas et al. (1986, 1993) experimented on effects of AMF on soil in pot cultures. They found that root and fungus effects are difficult to separate, but that the soil mycelium alone is capable to bring about soil effects equivalent to those of roots, while roots and fungi together affect soil aggregation synergistically.

Mycorrhizas and the mechanism of aggregate formation Articles discussing the concept of mycorrhiza contributions to soil structure are as numerous as those offering empirical data. The major recent reviews (Finlay and Sönderstöm, 1992; Miller and Jastrow, 1992a and b, 1994; Tisdall, 1991) agree that all of the biotic components of the agrosystem interact in the forming of its abiotic matrix from the parent materials (Robert and Berthelin, 1986; Emerson et al., 1986), but there are few findings, if any, that show interactions between specific groups of soil organisms and AMF isolates in the aggradative process (Jastrow and Miller, 1991). While each soil organism may have a necessary function in soil structure formation, fungi and filamentous actinomycetes had been shown to be most effective in binding soil particles into crumbs (Harris et al., 1966), even before Tisdall and Oades (1982) developed their concept of aggregate organization with its important niche for AMF.

The contribution of AMF hyphae to soil aggregation was summarized by Miller and Jastrow (1994) as consisting of three related steps. First, hyphal growth into the soil matrix creates the skeletal structure that holds the primary soil particles together through physical entanglement. Second, roots and hyphae together create the physical and chemical conditions and produce organic and amorphous materials (Gupta and Germida, 1988; Tisdall, 1991) for the binding of particles. Third, hyphae and roots enmesh microaggregates into macroaggregate structures. Once formed, the aggregates enhance carbon and nutrient storage (Elliott, 1986; Gupta and Germida, 1988; Cambardella and Elliott, 1993, 1994) and provide microhabitats for soil microorganisms (Foster, 1994; Tisdall, 1991). The quality and size distribution of the aggregates affects pore size distribution (Elliott and Coleman, 1988) and the pores offer improved access to the hyphae for grazing by soil invertebrates (Ingham, 1992). Although there is considerable evidence that interactions between the soil biota and AMF may have negative effects on plants (Hetrick et al., 1988; Ingham, 1988; Rabatin and Stinner, 1991; Ross, 1980), complementary effects of these interactions on the soil and its stability are little–known. One may speculate that these soil responses are largely positive, since they involve enhanced carbon input (Finlay and Sönderström, 1992; Hepper, 1975; Lynch and Whipps, 1991; Wright and Millner, 1994) from plant to soil. Ultimately, however, this loss of carbon by the plant not only improves soil quality, but also benefits plant growth (Burns and Davies, 1986).

Mycorrhizal effectiveness measured by soil responses Because of its importance to both plant and soil, aggregate stability has been suggested as a measure of AMF effectiveness in agroecology (Bethlenfalvay et al., 1988; Bethlenfalvay and Newton, 1991). This idea was expanded by Tisdall (1991), who described the characteristics of effective AM fungal soil stabilizers as (1) the production of greater quantities of more persistent and sticky mucilage, (2) bonding by hyrophobic bonds and polyvalent cations to clay platelets, (3) preferential interactions with plants, microorganisms and animals, (4) effective orientation of clay particles, (5) vigorous soil penetration, and (6) the production of a profuse soil mycelium. Tisdall's list supplements the selection guide for AMF effective in promoting plant growth (Abbott and Robson, 1984a, 1991) and refocuses priorities of mycorrhiza research in sustainable agriculture.

AMF and the soil biota

Different effects on plant and soil? Much effort has gone during the past ten years into the integration of the combined effects of specific plant–fungus combinations and specific groups of soil biota with basic and applied aspects of plant science (Azcón–Aguilar and Barea, 1992; Bagyaraj, 1984; Hendrix et al., 1990; Ingham, 1992; Miller, 1990; Paulitz and Linderman, 1991; Reid, 1990; Tinker, 1984). At the same time, soil biota effects on mycorrhiza formation have also received attention (Azcón et al., 1990; Linderman, 1992; Rabatin and Stinner, 1991). Much less is known, however, about the interactions between specific AMF isolates and distinct groups of soil organisms as it relates to soil structure, even though these interactions had been conceptualized thoroughly in general terms (Burns and Davies, 1986; Newman, 1985; Oades, 1984; Tisdall, 1991). We feel therefore confident in predicting that many experimental designs of future mycorrhiza research will include evaluations of soil responses as routinely as they now report determinations of root colonization. If stimulation of the rhizosphere biota and the resulting improvement of soil structure is in fact an evolutionary mechanism that imparts competitive advantages to plants (Burns and Davies, 1986), then a holistic approach to the joint study of arbuscular mycorrhizal plant and soil responses is indeed an absolute necessity.

The goal of improving or restoring disturbed agrosystems may be approached by studying the conditions that provide stability in natural systems and use it as a model to reconstruct (Linderman, 1986) the disturbed system. Alternatively, a manipulation of the disturbed system may be tried to achieve specific, limited ends. These ends have been production–oriented in the past (Cooke, 1982; Hatfield and Karlen, 1994). Soil microbes have been tried, with or without AMF, to suppress plant pathogens, to control plant pests, to enhance plant nutrition, to promote plant growth, or to relieve environmental stress to plants. Now, regardless of its promise for enhancing plant production, a new agenda for agriculture advises and prescribes that each new biotechnique to be employed in agriculture be also scrutinized as to its effects on agrosystem stability (Board on Agriculture, 1993). This will take some rethinking of the premises, for the use of beneficial soil microorganisms as tools for the control of deleterious ones is evaluated by plant effects (Schippers et al., 1987). Let us speculate here, if only to stimulate controversy, that favorable plant responses to rhizosphere manipulation may not always be accompanied by beneficial soil responses, and that conversely, conditions may exist where processes favorable to soil stability may be unfavorable to plant growth, at least initially.

What are some of these processes in agrosystem biology that may affect plant production and soil stability differently? Among many, we will single out three examples: (1) microbe–mediated nutrient uptake and soil pH, (2) stimulatory or antagonistic relationships between AMF and soil microbes, and (3) soil fauna effects on the mycorrhiza and its microbial associates.

Nutrient uptake and soil pH Long–known as enhancers of symbiotic N_2 fixation in P–deficient soils (Asai, 1948; Mosse et al., 1976; Barea and Azcón–Aguilar, 1982), AMF have also been shown to affect N uptake from soil (Ames et al., 1983; Azcón et al., 1991; Johansen et al., 1992), although a preference for the form of N has not yet been conclusively demonstrated (Barea et al., 1987; Azcón et al., 1992; Vaast and Zasoski, 1992). Frey and Schüepp (1993a) showed, in a cuvette system with root-free soil compartments, separated from the confined rhizosphere of maize plants, that ^{15}N was taken up by the soil mycelium of AMF after addition of $(^{15}NH_4)_2SO_4$ to the soil to be transported in considerable amounts to plant roots being several centimetres apart from the site of application. Similarly N also can be transported via mycorrhizal hyphae from plant to plant (Frey and Schüepp, 1993b). The soil mycelium of AMF also provide channels for transfer of fixed N from legume to non-legume plants (Frey and Schüepp, 1992). This could be demonstrated in a cuvette system separating the nodulated roots of *Trifolium alexandrinum* from the rhizosphere of maize. Further studies are needed to elucidate the impact of AMF in N cycling in relation to N fixation. The function of AMF concerning the N cycle should not be reduced to the N nutrition of the plant by hyphal N uptake or N transport. AMF must be regarded in the dynamic processes resulting in the temporary immobilization of N within its biomass and the N mineralisation at phases of decomposition of arbuscular mycorrhizal mycelium. N losses from the root system and from the soil to the ground water may be reduced or enhanced by mycorrhizal activity.

While soil biologists are said to be more preoccupied with the tripartite legume association than with any other biological process (Lynch, 1987), an increasing number of bacteria with N_2–fixing capabilities are also being discovered. This provides the challenge of supplying, perhaps by means of AMF hyphae (Barea et al., 1992), nonlegumes with biologically–derived N (Döbereiner, 1989; Zuberer, 1990). In addition, an increase in associative diazotroph populations in the presence of AMF (Bagyaraj, 1984) may also improve soil quality, since aggregate stability can be proportional to the biomass of cells present (Lynch, 1987).

Biologically–fixed N always improves productivity, since N availability is one of the major limiting factors in agriculture. However, when N input is in the form of NH_4–N, as is the case with N_2 fixation, extrusion of H^+ and of organic acids is prevalent and results in an acidification of the growth medium not only in the rhizosphere (Marschner and Römheld, 1983; Marschner et al., 1987) but also in the entire mycorrhizosphere (Li et al., 1991). Soil pH effects on AMF have long been known (Wang et al., 1993), but it is little known to what extent mycorrhizas and their associated microflora may create, control, and maintain the pH of their environment through exudation (Schwab et al., 1991) and CO_2 levels (Knight et al., 1989) in the absence of soil disturbance. Elevated soil pH, however, affects the stability of aggregates (Oades, 1984; Reid and Goss, 1981) as well as the composition of the soil microflora (Harris et al., 1966). In fact, negative effects on soil aggregation by legume cropping have been documented (Alberts et al., 1985; Laflen and Moldenhauer, 1979). Soil loss, however is determined by many aggregating and disaggregating forces (Gisch and Browning, 1948; Strickling, 1950), is influenced by climatic, edaphic, cropping and tillage factors, and each of these affect the processes of soil biology. It is therefore not surprising that the connection between soil loss and legume cropping is unresolved (Alberts and Wendt, 1985), but the phenomenon serves as an example how mycorrhiza–microbe relationships may affect cost–benefit ratios in production and conservation.

Mycorrhiza–microbe interactions and their effects on plant and soil An important function of the arbuscular mycorrhizal soil mycelium is the transport of carbon to microbial communities (Jakobsen and Rosendahl, 1990). This is especially significant when root density is low (Abbott and Robson, 1984b), since the hyphae can penetrate several centimeters of soil (Camel et al., 1991) and reach the microfauna of the bulk soil outside the influence of the rhizosphere (Finlay and Sönderström, 1992). In view of their role as mediators of carbon flow

(Whipps, 1990), one would expect the influence of AMF on soil microbes to be positive. This is not always the case, however. Many studies have shown that AMF may alter the soil microflora (Ames, et al., 1984; Bagyaraj and Menge, 1978; Christensen and Jakobsen, 1993; Meyer and Linderman, 1986; Secilia and Bagyaraj, 1987) by stimulating as well as inhibiting total bacterial counts or selected bacterial groups. Soil microbes, in turn, may promote (Ames, 1989; Azcón, 1989, Azcón et al., 1990; Azcón–Aguilar et al., 1986; Staley et al., 1992; Vejsadová et al., 1993) or antagonize (Azcón et al., 1990; Bethlenfalvay et al., 1985; Dhillon, 1992; Krishna et al., 1982) mycorrhiza development.

How do these complex interactions affect plant production and soil stability? A stimulation of plant growth may be achieved by manipulating specific groups of organisms, such as phosphate solubilizing (Azcón–Aguilar et al., 1986) or diazotrophic (Paula et al., 1992) bacteria, or rhizobacteria that promote plant growth by various mechanisms (Burr and Caesar, 1984). However, when the arbuscular mycorrhizal plant is grown in the field, subject to many influences at the same time, growth stimulation by AMF becomes elusive (Fitter, 1991; Hetrick et al., 1988, Ross, 1980). This led some workers to conclude that it is the soil microflora that regulates mycorrhiza formation and plant growth response, regardless of the AMF isolates present (Hetrick and Wilson, 1991). One must keep in mind, however, that the 'growth response' is only one of the ways to evaluate the AMF effect on plants (Koide and Schreiner, 1992), let alone the agrosystem, of which the plant is but one component.

The absence of a plant growth response to AMF, or a negative one, was interpreted as a loss of carbon by the plant, which outweighs the mutualistic advantage of enhanced P uptake by the endophyte (Fitter, 1991). This form of parasitism has been viewed traditionally as a lack of arbuscular mycorrhizal efficiency, and in a wider sense, as a lack of application potential for AMF in agriculture (Stribley, 1989). From the point of view of agrosystem stability, on the other hand, the gain of carbon by the soil represents an increase in substrate availability, resulting in greater microbial activity (Kirchner et al., 1993) and increased organic matter content and soil stability.

Seen in this context, one may even ascribe useful (agrosystem–stabilizing) functions to mycoparasites: although the parasites may limit AMF populations and thereby reduce plant growth (Paulitz and Menge, 1986; Ross and Ruttencutter, 1977), they may also stimulate hyphal regrowth, thus further increasing carbon flux and microbial activity in the soil. Seen from this angle, the utility of chemical control of mycoparasites (Sylvia and Schenck, 1983), may be revised, using soil aggregation measurements as an alternate tool for the evaluation of mycoparasite effects. Microbial biomass and activity (Dinel et al., 1992) play an important role in the formation and stability of soil aggregates, and promise a wide range of applications for AMF and their associated microflora.

Mycorrhizas and the soil fauna Invertebrates and AMF are ubiquitous and abundant coinhabitants of the soil environment. Together they fill important functions in processes which regulate nutrient availability and mineralization (Ingham, 1992). Interactions between the major groups of fungivorous soil invertebrates (nematodes, springtails, mites and microarthropods have been reviewed (Fitter and Sanders, 1992; Paulitz and Linderman, 1991; Rabatin and Stinner, 1991) and discussed in ecological (McGonigle and Fitter, 1988) and agricultural (Sylvia and Williams, 1992) settings. Grazing by invertebrates on the soil mycelium of AMF may limit its development or disconnect it from the root mycelium, but it may also stimulate its growth (Fitter and Sanders, 1992). Damage to the hyphal network would result in an impairment of nutrient uptake, a preponderance of root– over soil–mycelial biomass. Stimulation of hyphae and spore production, on the other hand, would be beneficial to the agrosystem and to plant growth. Such positive effects have been reported with springtails (Harris and Boerner, 1990) and nematodes (Ingham, 1988), and related to grazer density and grazing intensity (Moore, 1988). Plant growth may have been affected by the increased mineralization or mobilization of nutrients by the grazers (Finlay, 1985; Ingham et al., 1985; Harris and Boermer, 1990). Alternatively, the removal of senescing soil mycelia by the grazers may have resulted in the elimination of growth–inhibitory secondary metabolites (Moore, 1988).

The consequences of such trophic interactions between the soil fauna and AMF on soil aggregation specifically, are little–known. Generally, however, all biota found within the agrosystem were shown to contribute to the development of soil structure (Jastrow and Miller, 1991). In mycorrhiza research, it remains to be seen how the soil fauna affects the cost–benefit ratio of plant or soil development as they relate to agrosystem stability.

Summary and conclusions

An agrosystem is that part of the larger (natural or agricultural) agroecosystem that may be subject to experimental control, and where roots, the soil microflora and the soil fauna interact to support plant growth and to form a stable soil matrix. An agroecosystem is sustainable when the biotic components of the agrosystem are in balance. In disturbed ecosystems, this balance depends on the goals of land management: production or conservation. The two goals may be combined if the agricultural manager understands the biological complexity of the land under his stewardship.

Among the multitude of organisms that make up the agrosystem, AMF stands out because of its ability to form a bridge between plant and soil. These fungi penetrate and colonize the cells of host–plant roots, while their soil hyphae are in intimate contact with the microbiota that inhabit soil aggregates and contribute to soil structure formation. By mediating nutrient fluxes between plant and soil, the fungi influence both plant growth and health and the development of communities of soil organisms. In the course of experimental manipulation of the agrosystem, complex relationships between organisms manifest themselves that can be stimulatory, antagonistic, or both, depending on the circumstances. Such relationships may be real or artefacts of artificial environments, and their effects may be beneficial or deleterious to plant and soil in divergent ways, at least initially and in passing. It is one of the challenges of agricultural and ecological research to draw valid inferences from such transient effects achieved under controlled conditions to the reality of the field.

In the field of agriculture, sustainability has become the paradigm of our time, and in biological research sustainability means plant production without soil loss. For mycorrhiza research, this means a rethinking of the concept of mycorrhizal benefit. Synonymous with plant growth enhancement in the past, in the context of sustainability it may be redefined in terms of agrosystem stability, resting on soil biotic communities in harmony with roots and balance with each other within a strong, resilient, life–supporting soil matrix.

Thus, we see a closed chain of cause–effect relationships as the ultimate benefit of mycorrhizal fungi in the agrosystem. The fungi improve plant growth, health, and stress resistance; the plant so strengthened is a more abundant source of energy to the soil, encouraging the development of its biota; the organisms enhance soil aggregate formation; and the life–supporting soil structure so formed permits better plant growth, closing the chain.

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