Agronomic Management of Indigenous Mycorrhizas

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1 Introduction

Many benefits that accrue to plants from their association with arbuscular mycorrhizal (AM) fungi are a function of the increased volume of soil that can be explored by the extraradical mycelium. Sieverding (1991) estimates that for each centimetre of colonized root there is an increase of 15 cm^3 on the volume of soil explored, this value can increase to 200 cm^3 depending on the environmental conditions. The enhanced volume of soil explored, together with the ability of the extraradical mycelium to absorb and translocate nutrients to the plant, results in one of the most obvious and important advantage of mycorrhizal formation: the ability to take up more nutrients. The more important nutrients in this respect are those that have limited mobility in soil, such as phosphorus (P). In addition to nutrient acquisition many other benefits are associated with AM plants (Gupta et al. 2000): alleviation of water stress (Augé 2004, Cho et al. 2006), protection from root pathogens (Graham 2001), tolerance to toxic heavy metals (Audet and Charest 2006), tolerance to adverse temperature, salinity and pH (Sannazzaro et al. 2006, Yano and Takaki 2005) and better performance following transplantation shock (Subhan et al. 1998). The enhanced tolerance to toxic metals afforded by arbuscular mycorrhizas can be of benefit in phytoremediation (Göhre and Paszkowski, 2006). The extraradical hyphae also stabilize soil aggregates by both enmeshing soil particles (Jastrow and Miller 1991) and as a result of the production of substances that adhere soil particles together (Goss and Kay 2005).

Agricultural practices such as crop rotation, tillage, weed control and nutrient management all produce changes in the soil chemical, physical and biological properties, and can modify the ecological niches available for occupancy by the soil biota. All these changes can influence in various ways the performance of the symbiotic relationship between the higher plant and the AM fungi, the potential for the production of inoculum for new mycorrhizas, and consequently effecting changes in the balance of indigenous AM fungal communities. The molecular tools that have been developed in recent years have been very important in broadening our understanding of these changes, as well as building a greater awareness of the consequences, which the choice of management practice imposes on AM development. The interest in extensive farming systems, environmental sustainability and the economics of production focuses attention on the identification of agronomic management practices that may allow controlled manipulation of the fungal community and capitalization of mutualistic effects possible through mycorrhizal formation. In addition, they encourage evaluation of the use of local AM fungal inoculum as an option for mycorrhiza promotion and development in sustainable crop production.

In this Chapter we review the opportunities and limitations to the exploitation of recent research on arbuscular mycorrhizas in the development of sustainable crop production systems. Key aspects of agricultural land management that are considered include the choice of cropping sequences, the need for tillage, maintenance of soil structure, soil fertility and crop nutrition, weed and disease control. In addition, the issues around the use of AM fungal inoculum are presented.

2 Use of AM Fungal Inoculum

Despite the ubiquous distribution of mycorrhizal fungi (Smith and Read 1997), with only a relative specificity between host plants and fungal isolates (McGonigle and Fitter 1990), the obligate nature of the symbiosis implies the establishment of a plant propagation system, either under greenhouse conditions or in vitro laboratory propagation. These techniques result in high inoculum production costs, which still remains a serious problem since they are not competitive with production costs of phosphate fertilizers. Even though farmers understand the significance of sustainable agricultural systems, the reduction of phosphorus inputs by using AM fungal inocula alone cannot be justified except, perhaps, in the case of some high value crops (Saito and Marumoto 2002). Nurseries, large input horticultural enterprises and non-agricultural applications, such as restoration of degraded or devegetated landscapes, are examples of operations where the use of commercial inoculum is current.

A number of factors contribute to uncertainty in the minds of potential users. These include the quality of commercially available products, especially the guarantee that these are pathogen-free, the conditions required for storage before application, the most effective application methods and what is the appropriate inoculum for the application. Furthermore, information provided by suppliers about an inoculum can be deceiving, given that total counts of spores or propagules may be given, but only a fraction may be effective for a particular plant or under specific soil conditions. There is a clear need for registration procedures that can stimulate the development of the mycorrhizal industry (Gianinazzi and Vosátka 2004).

Advances in ecology during the past decade have led to a much more detailed understanding of potentially adverse consequences of introducing species into a new habitat, but there is little information available on the ecological consequences of inoculating with mycorrhizal fungi. Schwartz et al. (2006) recommend that a careful assessment should be made prior to inoculation that documents the need for inoculation and the likelihood of success, because the introduction of mycorrhizal fungi is not universally beneficial. In addition, there is inadequate knowledge of the basic biology and diversity of AM fungi (Abbott at al. 1995, Saito and Marumoto 2002).

Some on-farm inoculum production and application methods have been developed to allow farmers to produce locally adapted isolates and generate a taxonomically diverse inoculum (Mohandas et al. 2004, Douds et al. 2006). However, inocula produced this way are not readily processed for mechanical application in the field, and this is an obstacle to their utilization in large scale agriculture, especially for row crops. Moreover, it requires an additional mechanical operation, with the corresponding economic and soil compaction costs.

Although inoculation with AM fungi has potential significance for sustainable crop production, including environmental conservation, current knowledge and technologies limit the application for widespread use in many agricultural contexts.

3 Crop Rotation

Crop rotation is an agronomic practice with a long history that is still performed and retains its general beneficial aspects associated with maintenance or improvement of soil fertility, reduction in erosion potential and in the build-up of pests, spreading of workload, lowering the risks from inclement weather damage, and a lesser reliance on agricultural chemicals, and a need for increased net profits.

Although most crops support the formation of arbuscular mycorrhizas, roots of crops belonging to the Chenopodiaceae and Brassicaceae do not form these symbiotic relationships. Furthermore, the use of these crops in rotations tends to lead to a reduction in mycorrhizal propagules. In contrast, the cultivation of mycorrhizal host crops increases AM fungi populations and maintains mycorrhizal activity in soil (Vestberg et al. 2005). As a result there tends to be much greater spore densities present (Black and Tinker 1977, Karasawa et al. 2000) leading to improved colonization of the succeeding crop, which may be in the following season (Gavito and Miller 1998a, Miller 2000).

Arihara and Karasawa (2000) studied the effects of fallow and prior cultivation of sunflower, maize, soybean, potato, sugar beet and canola (rapeseed) on the AM colonization of a subsequent maize crop. They found that shoot weight and grain yield of maize were much greater in the plots following sunflower, maize, soybean and potato than those after canola, sugar beet or a fallow. The cultivation of a non-AM host such as sugar beet or canola, reduces the mycorrhizal propagules and consequent AM colonization, P uptake and shoot dry weight (Arihara and Karasawa 2000, Gollner et al. 2004) even with no alteration of the availability of P in the soil induced by the previous crop (Karasawa et al. 2001). These results establish that cultivation of a mycorrhizal crop in the previous season promoted AM formation on roots of the following maize crop, which in turn enhanced its P uptake and growth, and finally increased the grain yield. The positive effect of having an AM host as the preceding crop for the maize was partly due to differences in AM fungal inoculum density (Karasawa et al. 2002).

Reduction of AM fungal propagules can also be a significant consequence of bare-fallowing. Because AM fungi are strictly biotrophic, their survival depends on the presence of host plants. During a bare-fallow the absence of host plants may cause the viability of AM fungi to decline and this decline may be further exacerbated by freezing conditions (Kabir et al. 1997b). Harinikumar and Bagyraj (1988) reported a 40% and 13% decrease in AM fungi propagules after fallow and a non-mycorrhizal crop, respectively. The extent to which AM fungi communities can be restored is inversely proportional to the duration of a fallow and the extent to which the land is grazed at the time (Duponnois et al. 2001).

Despite the ability of the extraradical mycelia to remain infective, even if the soil is frozen over winter (Addy et al. 1997), it is important to maintain the level of AM fungal inoculum to maximize the benefits of AM fungi on the following crop. Maintaining plant cover is very important, whether with cover crops or with cold tolerant crops, such as winter wheat. The choice of cover crops should be guided by the same principles as used to select the crop species to be adopted in a rotation. Preference should be given to mycotrophic cover crops capable of surviving in less favourable conditions while maintaining the AM inoculum potential in soil. Kabir and Koid (2000) demonstrated that using wheat or dandelion as mycotrophic winter cover crops increased subsequent sweet corn yield. Kabir and Koide (2002) reported that, relative to fallow, oats and rye were equally effective as cover crops in increasing mycorrhizal colonization in a succeeding sweet corn crop, as determined by the density of mycorrhizal hyphae and soil aggregate stability. Their results also underlined the importance of host crop diversity as they found that the combination of two cover crops (rye and oats) was significantly better than sowing a single species for the colonization of AM fungi, P uptake and yield of the following sweet corn crop.

Even though there is no obvious specificity between a host plant and colonizing AM fungal species, there are preferential associations (McGonigle and Fitter 1990, Vandenkoornhuyse et al. 2002, Gollotte et al. 2004). Furthermore, the cultivated host species can influence the abundance of the different AM fungi species present (Troech and Loynachan 2003). This explains how crop rotations can cause changes in a mycorrhizal fungal community (Johnson et al. 1991, Hendrix et al. 1995) and the stability of complex soil biotic communities (Cavagnaro et al. 2006), and increase biodiversity (Miranda et al. 2005). In contrast, monocultures tend to select specific AM fungi, which tend to be inferior mutualists (Johnson et al. 1992), making AM fungi a possible cause for the yield decline often observed when such cultures are grown over long periods of time.

Different host species and cultivars of the same species vary in the degree to which they form mycorrhizas (Azcón and Ocampo 1981). The level of AM colonization of a cultivar, and its associated benefits, is a heritable trait that can be selected through plant breeding (Kesava et al. 1990). Breeding programs are commonly conducted on experimental stations where mineral nutrients are not limiting factors. However, as increasing soil fertility can impair mycorrhizal development, this can result in the selection of host-crop varieties that form mycorrhizas less readily. For example, Hetrick et al. (1993) reported that the wheat cultivars released prior to 1950 were consistently greater in their level of dependence on mycorrhizal formation for production relative to more recent releases. Zhu et al. (2001) showed that modern wheat cultivars were less responsive to mycorrhizal colonization than were historical lines. The breeding of maize for resistance to fungal pathogens has produced lines that are less mycotrophic than previous varieties (Toth et al. 1990).

4 Soil Aggregation and Tillage Regime

Arbuscular mycorrhizas make direct contributions to soil aggregation and aggregate stability (Tisdall and Oades 1982), especially in no-till systems where hyphal networks remain intact. The direct effect of AM hyphae on soil aggregate formation was shown by Thomas et al. (1993), to be significant and at least equivalent to that of roots alone. Important aggregate cementing agents produced by soil fungi and bacteria have been characterized as extracelular polysaccharides (Tisdall 1991), although Wright and Upadhyaya (1996) reported the presence of copious amounts of glomalin, a glycoprotein, associated with AM fungi, later found to be located on the surface of active AM hyphae (Rillig et al. 2001), and that could be important for soil aggregate stability (Miller and Jastrow 1990). In a three-year study, Wright et al. (1999) measured an annual increase in both aggregate stability and weight of glomalin in the top 5 cm of the soil in no-till plots compared with ploughed plots. They also found that when soil was collected from the grassland adjacent to the tillage experiment, the structure of the top 0-10 cm of the grassland soil was more stable than of the cultivated soil after several years under no-tillage and 4 years under conventional tillage. Although there was not a full biochemical characterization of glomalin, in their study, Driver et al. (2005) showed that the material was tightly bound within the hyphal wall of AM fungi rather then being a primary release or secretion into the growth medium. They argued that glomalin has a role in the living fungus and any functionality in the soil was only secondary arising, possibly due to its relative slow turnover rate in the environment (Steinberg and Rillig 2003, Driver et al. 2005, Goss and Kay 2005, Rillig and Mummey 2006).

Soil tillage serves many purposes, including weed control, preparation of the seed bed, and improved water capture and storage in the soil profile (Cook, 1992). It is also used to incorporate fertilizer, manure and pesticides and to reduce the incidence of disease and pests. Unfortunately, through the gradual loss of organic matter from near the soil surface, tillage can reduce aggregate stability and make soil more vulnerable to wind and water erosion. The environmental impacts of soil erosion became very evident in the 1930s in the USA, and since the 1950s, there has throughout the world been a gradual transition from the mouldboard plough to various forms of conservation tillage, including no-till, with minimum soil disturbance. The basic principles of no-till agriculture include sowing directly into soil using the special planting equipment that cuts through or displaces the covering of crop residues. Retaining residues on the soil surface reduces erosion, evaporation and limits weed growth. It also improves water infiltration through the enhanced activity of the soil biota and the maintenance of macro-porosity, even if there is some increase in bulk density (Lal et al. 2007). The transition to no-till has implications for environmental quality, particularly because of its effectiveness in reducing soil erosion and surface runoff, enhancing soil organic matter concentration near the soil surface, increasing soil biological activity and reducing the energy required for crop production.

The direct effects of the various tillage practices on fungi, particularly conventional tillage (CT) and no-tillage (NT) systems, are related to physical disruption of the hyphal network and to the mixing of surface residues within the soil profile, affecting the effectiveness of AM symbiosis in many ways (Kabir, 2005).

When host plants are present and the soil is not disturbed, hyphae from colonized roots and mycelia network are the main source of inoculum, they colonize roots more rapidly and efficiently compared with spores (Martins and Read 1997). The latter are considered as “long-term” propagules (Kabir 2005), mainly because it would take longer for spores to germinate and make contact with roots compared with colonization by runner hyphae from a well developed extraradical mycelium (Klironomos and Hart 2002).

Since the 1980’s many studies, under field conditions or in pots have been developed, most of them using maize as host plant, to evaluate the effect of soil disturbance on AM colonization and its consequences, particularly for P uptake. In one of the first reports on the subject, Evans and Miller (1988) described a significant adverse effect of soil disturbance on AM colonisation of both maize and wheat roots (both mycorrhizal), and also upon the P absorption by these species but no effects were found with respect to spinach and canola comparisons (non-mycorrhizal). Moreover, the injection of benomyl, a potent inhibitor of mycorrhizal fungi, into the soil surface significantly reduced the influence of soil disturbance on P absorption. These results indicate that the negative effect of disturbance on P uptake is likely due to impaired AM associations. Later, Evans and Miller (1990) demonstrate that disruption of the hyphal network was directly responsible for much of the effect of soil disturbance on mycorrhizal colonization. Besides, deep ploughing (to more than 15 cm) hinders subsequent mycorrhiza formation by reducing propagule density in the rooting zone (Kabir et al., 1998b). Abbott and Robson (1991) found that under no-till there were more spores in the top 8 cm of soil whereas tilled soils had more spores in the 8-15 cm depth.

Under field conditions Brito et al. (2006b) found greater AM root colonization of wheat and triticale cultivated under NT compared to CT plots. Goss and de Varennes (2002), Antunes et al. (2006b) and Brito et al. (2006b) used the same technique for disturbing the soil in pot experiments, and, consistently found greater AM colonization of soybean or wheat, growing in pots of undisturbed soil.

The faster AM colonization observed in undisturbed or no- tillage systems supports earlier uptake of P (Vivekanandan and Fixen 1991, McGonigle and Miller 1996b, McGonigle et al. 1999), conferring a comparative advantage to the crop in the initial growth period, independently of soil P content (Fairchild and Miller 1990, McGonigle and Miller 1996b) although not always (Vivekanandan and Fixen 1991).

The number of spores, length of extraradical mycelium and hyphal density, particularly in the row zone (Kabir et al. 1998a), have been found to be enhanced when soil disturbance is reduced (McGonigle and Miller 1996a, Boddington and Dodd 2000a, Galvez et al. 2001, Borie et al. 2006). In addition to the enhanced concentration of P in the plant there are similar effects on Zn and Cu concentrations (Kabir et al. 1998a), which is not surprising considering the metabolic activity of hyphae in this system is greater (Kabir et al. 1997a). However, plant concentrations of other more mobile elements, such as K, Ca or Mg did not change with tillage regime (Kabir et al. 1998a).

The ability of an AM fungus to promote growth in undisturbed soil is related to the spread of mycelium in the soil and the capacity of nutrient transfer to the roots and, in addition, a capacity for persistence and retention of functional capacity of the extraradical mycelium from one plant generation to the next (McGonigle et al., 2003) and this is why the survival of AM extra-radical mycelium survival is particularly important, over winter in cold climates or over summer in Mediterranean climates, where field crop production is restricted to a few months. In Canada, Kabir et al. (1997b) evaluated the timing of tillage on the survival of AM fungal hyphae, either connected to or detached from corn roots and whether the extraradical mycelium was intact or disrupted. They verified that fall tillage severely reduced AM hyphae viability, whereas spring tillage had little effect. They also found that attachment or proximity to roots favoured over winter survival, but disruption of the extraradical hyphae far outweighed the benefits of host root presence on survival.

Given that there is no such thing as a fungal effect or a plant effect, but a cross effect of both symbionts, the extent of colonization in soil under different levels of soil disturbance is also influenced by the host plant. Under the same experimental conditions Mozafar et al. (2000) found an increase in AM colonization of maize under no-till, although there were no differences in colonization between tillage treatments in AM wheat.

Some exceptions to the promoting effects of no-tillage systems on AM colonization have also been reported. On one hand Gavito and Miller (1998a) did not find any effect of tillage practices or fertilizer application, on the AM fungal colonization of maize under field conditions. On the other hand even though Mozafar et al. (2000) observed greater AM colonization in maize under NT system then under CT, they did not see differences between tillage systems when wheat was the host crop. In other cases, despite the greater AM colonization and P content of plants cultivated under no-till than in conventional cultivation systems, it did not translate into enhanced growth yield (McGonigle and Miller 1996b, Galvez et al. 2001) suggesting an interaction of soil P and a yield depressing factor, possibly soil temperature, in no-till soils. In contrast to much previous research in mesic temperate climates, Y. Lekberg (personal communication, August 2006) found that in the semi-arid tropics, P fertilizer, long fallow periods, and tillage did not significantly decrease the AM fungi inoculum potential. McGonigle and Miller, (2000) verified that the high inoculum density of particular ecosystems, such as the pastures studied in Australia, likely overrides any soil disturbance effect and ensures that roots of all plants became colonized by AM fungi.

An increased presence of AM fungi in roots from less disturbed systems has been reported to be accompanied by greater colonization by pathogenic fungi (McGonigle and Miller 1996a, Mozafar et al. 2000). The latter probably take advantage of the same mechanisms as AM fungi in terms of preserved integrity of the mycelium under these conditions. Mozafar et al. (2000) suggested that changes in nutrient concentration in the leaves of the plants tested in their study (wheat and maize) were likely due to the combined effects of colonization of the roots by various mycorrhizal and non-mycorrhizal fungi and not to changes in the chemical or physical properties of the soil. The authors stress the need to take into account non-mycorrhizal roots parasites and especially non-filamentous obligate fungi in studies conducted under field conditions.

4.1 Impact of Soil Disturbance on AM Fungal Communities

Colonizing strategies of AM fungi differ considerably and the variation is taxonomically based at the family level (Hart and Read 2002). Consequently different survival strategies for soil disturbance or tillage regime can affect the population of AM fungi of a particular site (Brito et al. 2006b).

Douds et al. (1995) found that *Glumus occultum* group was more numerous under NT, while the *Glomus* spp. and *Glomus etunicatum* groups were more numerous in soils under cultivation, even though spore characterization and quantification have been done directly from field material. In the same study field soil from the low input field plots produced greater colonization in a greenhouse assay than did soil from conventionally farmed plots. However, the host plant used, *Paspalum notatum* Flugge, differed from ones in the field rotation (maize- soybean-wheat).

Other greenhouse experiments using inert attapulgite clay as a growth substrate, and AM fungi from genera that differed in their sensivity to soil disturbance, demonstrated that disturbance of pre-established extraradical mycelium reduced the formation of mycorrhizas by *Gigaspora rosea* but increased that by *Golmus manihotis* on *Desmodium ovalifolium* plants (Boddington and Dodd 2000b). Jansa et al. (2002) found a similar trend in their observations, which were based on morphological and molecular identification. There was an increase in the incidence of certain AM fungi, especially those not belonging to the *Glomus* spp., in intensively managed agricultural soil after long-term (13 years) of reduced tillage. In these soils an apparent increase in the incidence of *Gigaspora*, *Scutellospora* and *Entrophospora* was noted. In conventionally tilled soils, almost all the AM fungi present belonged to the genus *Glomus*. Surprisingly the authors did not find significant differences in AM fungi diversity among different soil tillage treatments, even though the community structure was profoundly affected by the tillage treatment. Similar results were obtained by Franke-Snyder et al. (2001), who concluded that 15 consecutive years of farming with conventional or low-input agricultural management practices did not cause many differences among the fungal communities. The majority of the 15 fungal species found throughout the site were present in all treatments. The sporulation of a particular fungal species differed between farming systems or host plants but the general structure of AM fungal community was similar. These results contrast with those of Boddington and Dodd (2000a) and Oehl et al. (2003) who concluded that species richness can be reduced by soil disturbance.

Glomus spp. tend to survive perturbation and hence they prevail in highly disturbed agricultural systems, leading to the idea of a possible adaptation of different AM fungi species to different levels of soil disturbance. Oehl et al. (2003) also support the view that the result of this preferential selection favours the species that colonize roots slowly but form spores rapidly. AM fungi isolates from low input farming systems seem to be more efficient in promoting plant growth (Scullion et al. 1998, Oehl et al. 2004).

Jansa et al. (2003) made further progress using a nested PCR approach, and produced the first report on community composition of AM fungi in the roots of a field-grown crop plant (maize) as affected by soil tillage. Their results showed that the presence of the genus *Scutellospora* was strongly reduced in maize roots from ploughed and chiselled soils. Fungi from the suborder *Glomineae* were prevalent in roots from ploughed soils, but were also present in the roots from other tillage treatments. Jansa et al. (2003) attributed these changes in community of AM fungi colonizing maize roots to differences in tolerance to the tillage-induced disruption of the hyphae between AM fungi species, together with changes in the nutrient content of the soil, microbial activity and changes in weed populations in response to tillage.

5 Weeds and AM Fungi

AM fungi colonize the roots not only of most agricultural crops but also of the weeds present (Yamato, 2004). In most of the cases AM fungi and weeds have co-evolved for longer time then AM fungi and crops.

Agro-ecological functioning of weed communities may be affected by AM fungi through facilitative effects mediated by the mycelial network. Mycelial interconnections among host species in a weed-crop mixture may cause patterns of resource uptake and distribution among host species that differ qualitatively from those occurring in plant communities where AM fungi are absent (Moyer-Henry et al. 2006) as dying host species may release nutrients into the AM fungal mycelium (Smith and Read 1997) which may then be redistributed among other host species, enabling facilitative effects in crop-weed mixtures. For example, after selective weed control, nutrients acquired by host weeds may be transferred to host crop or cover crop via the mycelium. Such processes may result in greater nutrient cycling and reduce competitive effects from non-host weeds. If such phenomena occur and are qualitatively important, then AM fungi may be capable of significantly altering the agro-ecological functioning of weeds. Properly timed control operations, such as sub-lethal post-emergence herbicide applications might be used to transfer nutrients from weeds to crops. In this scenario, the weeds might function as a temporary nutrient sink, restricting the competition for nutrients from non-host weeds and reducing leaching and other mechanisms of nutrient loss.

Facilitative functions may also occur in which one host species supports populations of mycorrhizal fungi that are beneficial to another plant species. Host species may provide carbon to the mycelium which may support formation of arbuscular mycorrhizas with other species. In effect the first host plants provide energy that serves, directly or indirectly, to support formation of AM colonization on a second newly germinating host. This allows the seedlings of the second host to receive nutrients and other mycorrhizal benefits while minimizing the energetic costs of mycorrhizal establishment to seedlings. For example weed communities in several cropping systems have been shown to enhance mycorrhizal colonization and growth of subsequent crops, providing an alternative host between AM dependent crops (Kabir and Koid 2000, Brito et al. 2006a) or to maintain infective propagules over winter (Schreiner et al. 2001). The negative impact of fallow periods or the cultivation of non host crops on the AM inoculum may be mitigated by the presence of weeds on the field. Jansa et al. (2002) considered that the higher spore counts in no-till soil after the non-mycorrhizal plant (canola), was due to the increased presence of mycorrhizal weed plants in the no-till plots. These weeds may have supported AM fungi development in their roots and also allowed some spore formation under the canola. In the tilled plots, ploughing eliminated the majority of weeds and, therefore, AM fungi development during the growing of canola would be negligible. In Dehérain plots Plenchette (1989) also reported that when weeds were not controlled mycorrhizal infectivity was maintained. However this effect would be beneficial only if the species that received the additional resources was desirable, and would have economic importance under the prevailing conditions. For example, under a Mediterranean climate, where the long, very dry summer might compromise the ability of extraradical mycelium to survive between the harvesting of one crop, in early summer and the seeding of the next crop in the rotation, in autumn. Feldmann and Boyle (1999) studied the interaction of weed competition and AM fungi in maize monoculture. They found decreased richness of AM fungal species and effectiveness in weed–free versus plots with weeds. Maize grew better in the presence of weeds and the authors concluded that the effective AM fungi over-compensate for any weed-mediated decrease in crop biomass. However, the benefit of enhanced AM fungi colonization of maize observed by Galvez et al. (2001) in the absence of effective weed control did not translate into enhanced growth or yield.

Although it is possible that AM fungi may have negative effects on agro-ecological functioning of weed communities, simply by increasing abundance of problematic weeds (Jordan et al. 2000) management of the existing weed population might provide an important tool to guarantee a more rapid colonization of a winter crop with the consequent advantages of an early adequate phosphorus nutrition. Abbott and Robson (1981) suggested that the many factors associated with the differences in effectiveness of different AM fungi in stimulating plant growth are due to their influence in the rapidity of infection rather than the ability of infected roots to take up phosphorus. Given that colonization from spores is relatively slow because it needs to begin with a successful biochemical dialogue between plant roots and the AM fungal spores, the existence of weeds roots to initiate this process may be important so that fast colonization of the sown crop can take place from a well established mycelium network as soon as germination occurs. In natural ecosystems or reduced-tillage agricultural systems, young seedlings can germinate and "plug" into an already established AM fungi hyphal network which permeates the soil and links different plant species. The lack of specificity confers a great advantage for the success of AM fungi in mixed plant communities. Another benefit to the plant of interest is that photosynthate is needed only for maintenance of the AM fungi following colonization, and not for the development of the extraradicle mycelium since it was pre-established (Dodd et al. 2000).

Excessive tillage to control weeds, associated with frequent cultivation of non-mycorrhizal crops, could also hamper development of a diverse AM community (Gosling et al. 2006). In fact Abbott and Robson (1991) reported a positive impact of weeds as host plants on the increase of AM fungi diversity. The multiplicity of roles that could be played by weeds of an agro-ecosystem in relation to arbuscular mycorrhiza formation requires careful planning of the timing and method for their control if the benefits are to captured in terms of crop production.

6 Nutrient management

The appropriate provision of macro and micro nutrients is a critical part of crop husbandry, to ensure both production potential and environmental safeguards are achieved. Investigation over the last two decades has indicated significant potential for the use of arbuscular mycorrhizas in enhanced nutrient management practices.

6.1 Phosphorus

In most agricultural systems the application of P to the soil is necessary to ensure plant productivity. Phosphorus is largely taken up by plants from soil solution as inorganic PO_4^- ions. The recover of P applied as fertilizer or organic amendment by crop plants over a growing season is very small, as in the soil more then 80% of the P becomes immobilized and unavailable for plant uptake because of adsorption of ions on soil surfaces, precipitation of mineral phosphates or conversion to the organic form (Holford, 1997). Between 20 and 80% of soil P is present in organic form (Richardson, 1994). The conversion of organic P into inorganic forms and the consequent availability to plants depends on hydrolysis either by microorganisms or by enzymes originated in the organisms themselves (autolysis). The remaining P is found in the inorganic (Pi) fraction, which may contain up to 170 mineral forms (Holford, 1997). Pi may be held very firmly in crystal lattices of sparingly soluble forms, such as various Ca, Fe and Al phosphates, and may also be chemically bounded to the surface of clay minerals. This Pi exchanges very slowly with ions in the soil solution and constitutes a non-labile pool, which is regarded as unavailable to plants. A small but less tightly bound P fraction exchanges relatively rapidly with the soil solution and constitutes a labile pool regarded as being available to plants.

Under conventional management practices, the role of the soil biota, including both saprophytic and mycorrhizal fungi, in nutrient cycling has been largely marginalized by the use of agrochemicals, particularly fertilizers but including fungicides, herbicides, and pesticides that counter disease and pests but can adversely affect other biota. Accumulation of P in the soil from applications of animal manure or fertilizer in excess of that taken up by the crop can increase the risk of P movement to surface and groundwaters, with serious consequences for the aquatic environments. However, with increased societal pressures to reduce the use of agrochemicals and fertilizers, a greater reliance on processes influenced by soil biota, and specially AM fungi are assuming greater relevance. According to Grant et al. (2005) management of the cropping system to improve the availability of P to the crop early in the growing season may improve P nutrition while reducing the potential for excess accumulation of P in the soil and the risk of its transport into water systems. This requires a detailed understanding of the process governing soil P cycling and availability in which AM symbiosis may play a significant role.

Provision of adequate P early in crop development is usually directly related to an improved final grain yield (Gavito and Miller 1998b). For example, in maize, early P nutrition increased the number of kernels per plant, and similar increases in number or biomass of reproductive structures are reported for other crops (Gavito and Miller 1998b). The corollary is that deprivation of early P leads to a reduction in shoot growth accompanied by an initial stimulation of root growth (Mollier and Pellerin 1999).

An increase in the absorption of P by mycorrhizal plants can result by both the increased physical exploration of the soil and by increased transport into mycorrhizal fungus hyphae. Modifications of the rooting environment can enhance the transfer of P to plant roots and changes in the efficiency with which plants utilise P can all contribute to more effective crop nutrition (Bolan 1991).

Arbuscular mycorrhizal and non-AM plants show markedly different kinetics for P absorption, indicating that AM fungi hyphae have greater affinity for phosphate ions and a smaller threshold concentration for absorption than do plant roots (Smith and Read 1997). P is translocate in hyphae in the form of polyphosphates and translocation rates could be affected by concentration gradients and cytoplasmic streaming (Jakobsen 1992). Sanders and Tinker (1973) observed that the rate of inflow of P into AM roots was much greater than that of non-AM plants. By assuming that the difference in the rate of inflow was all due to the AM fungi, they calculated that transport via mycorrhizal hyphae was six times that through a root hair.

Diffusion, rather then mass flow is the most important delivery system of P to plants, and movement through the soil is much slower than the rate of uptake into the roots. This results in a depletion zone around the roots (Smith and Read 1997). The size of the soil P depletion zone is significantly larger in AM plants then in non-AM plants. Li et al. (1991) found differences over 10 mm in some cases but in others this difference was greater than 110 mm, depending on the plant host colonised and the fungal isolate involved. In addition they estimated that 80% of plant P could be supplied by AM fungi hyphae from as far as 100 mm distance beyond the zone of direct root exploitation. Bucher (2007) concluded from analysis of physiology, molecular and cell biology, and genetics of P uptake in vascular plants that soil P availability and the formation of P depletion zones around roots and their mycorrhizas are the major physical parameters determining plant P acquisition efficiency.

A wide range of biological events, and consequent environmental changes, occur in the rhizosphere and particularly in the mycorrhizosphere, leading to direct or indirect effects on the availability of sparingly soluble forms of P. The exudation of organic substances by roots and their formation and excretion by AM fungal hyphae might be important in facilitating host plant accessibility to available P or making P more available (Bolan 1991, George et al. 1995). Koide and Kabir (2000) showed that extraradical hyphae of *Glomus intraradices* can hydrolyse organic P and can transport the resultant inorganic P to host roots. However direct evidence that organic acids such as oxalic and citric acid, which can make sparingly soluble P sources available, have only recently been reported for AM fungi. Tawaraya et al. (2006) developed a system that allowed them to collect exudates specifically from hyphae. Their results showed that hyphal exudates can actually contribute to increased P uptake into colonized roots. They found no oxalic acid production, and suggested that the type of organic acid produced might be related to the specific mycorrhiza and soil in which the fungi grew. They also stressed the importance of soil pH in relation to the ability of hyphal exudates to solubilize P.

Other examples of mycorrhizosphere environmental modifications include the presence of P solubilizing companion microorganisms and changes in pH following AM colonization of roots. P is more readily available at pH 6.5, but for pH values above this the amount of sparingly soluble Ca-phosphates tend to increase, and for pH values less than 6.5 the levels of Al and Fe-phosphates increase.

In the rhizosphere, alkaline phosphatase activity is commonly greater than in the bulk soil, which contributes to increased availability of sparingly soluble P compounds. However mycorrhizal hyphae do not appear to influence soil phosphatase activity, even where hyphal length density is considerable (Joner et al. 1995), but can influence alkaline phosphatase secretion by other microorganisms, probably through competition for nutrients (Joner and Jakobson 1995). In fact the quantitative importance of extracellular phosphatases for P nutrition in AM plants, which has frequently been used to indicate promotion of P uptake by mycorrhizas, is considered to be insignificant relative to the total phosphatase activity in soil (Joner et al. 2000).

Jayachandran et al. (1989) suggested that siderophore production by AM fungi or other soil microbes could significantly increase P availability in low-pH soils, and that is a feasible mechanism by which AM plants could acquire P sources unavailable to non-AM plants.

P acquisition by AM plants varies not only with plant species and cultivar but also with the AM fungus colonizing the roots (Munkvold et al. 2004). The influence of the AM fungi species or isolate is effective at different levels: the size of the depletion zone, on the speed and rate of soil exploration by hyphae, phosphatase activity, the effectiveness of the symbiosis (as measured by the proportional AM benefit compared with the benefit from added P), P uptake by hyphae, shoot P content, growth performance at a given pH and accumulation of polyphosphates in the extraradical mycelium.

Fertilizer application, particularly P fertilizer and the associated increase in soil P level, decreases AM fungal infectivity and effectiveness (Dickson et al. 1999, Kahiluoto et al. 2000, Sorensen et al. 2005) and spore density (Chandrashekara et al. 1995). Irrespective of high levels of P in the soil, it is the concentration of P in the root system that determines whether AM fungi colonize roots (Menge et al. 1978). This suggests that the effect of P level in the soil on AM formation appears to be indirect, effected through the influence on P concentration in plant tissue, rather than directly on the fungus in the soil. This may explain why fertilizer application does not always reduce mycorrhizal associations. Fairchild and Miller, (1988) observed extensive colonization at very high rates of fertilizer addition. Paradoxically, if the available P in the soil is very low, AM and spore production may be restricted and AM may increase by P application (Grant et al. 2005). For example, sunflower grown in a sand medium that was almost P-free showed only poor mycorrhizal development and the infection increased as P was added (Koide and Li 1990).

Less soluble forms of P fertilizer, such as rock phosphate, have a very slow effect on P availability and mycorrhizal colonization of the host plant is favoured. The slow release of P likely prevents the P concentration in root tissue from reaching a level that can inhibit the formation of a mycorrhiza.

Also the moderate application of farmyard manure seems to be less detrimental to root colonization by AM fungi than is the application of the same amount of nutrients in the form of inorganic NPK fertilizer (Joner et al. 2000). Gryndler et al. (2006) reported reduced growth of AM fungi (assessed by hyphal length and the signature fatty acid 16:1ω5) following mineral fertilizer application, but a manure application increased the growth of AM fungi. Colonization of roots followed the same pattern as the growth of AM fungi hyphae. In contrast, Allen et al. (2001) reported a greater AM colonisation of dry bean and sweet corn in unamended than in manured soils.

Although no changes in AM fungi species composition were observed (Kahiluoto et al., 2001, 2004), cumulative P in soil decreased the size of the AM fungi communities, but did not affected the hyphal P transport capacity of hyphae (Kahiluoto, 2004). Fertilizer application also seems to select for inferior AM mutualists (Johnson, 1993).

Each combination of AM fungus, plant species or cultivar, and soil environmental condition is unique with several possibilities in terms of outcome for beneficial effects on the plant and in terms of the uptake of P and other nutrients (Kahiluoto 2004, Jansa et al. 2005). However, the evidence for other nutrients is limited as they have been studied less. Pandey et al. (2005) found P uptake by wheat, rye and triticale was 10%, 64% and 35%, respectively, greater in the presence of mycorrhizas than in their absence. The authors argued that the differences in the enhancement of P uptake induced by mycorrhizal formation in triticale seem to be inherited from wheat rather then from rye. Different species of the same genera of the AM fungal symbionts, *Glomus mosseae* and G*lomus intraradices*, also exhibit a degree of functional complementary in terms of spatial P acquisition (Drew et al. 2003).

Burleigh et al. (2002) investigated whether functional diversity between AM fungi species is limited to the level of mycorrhizal formation, plant nutrient uptake and plant growth. Their study advanced current understanding of functional diversity and showed that plants can respond differently to AM fungi at the morphological and physiological levels and also at the level of gene expression. Functional diversity in mycorrhizal Pi uptake in different plant-AM fungi combinations and the control mechanisms involved are likely to be dependent on the molecular cross-talk between plant and fungal symbionts. Bucher (2007) suggested that to improve our knowledge of the role of fungal and plant metabolic status, elucidation of the chemical signals that orchestrate P transporter gene expression will possibly be the critical step towards a systems view of P uptake dynamics.

6.2 Nitrogen

In addition to the commonly reported enhanced P acquisition by AM plants, enhanced N acquisition is also often reported (George et al. 1995). Although it is thought that AM fungi have little ability to increase plant uptake of more mobile ions such as NO_3^-, as these move rapidly through the soil to roots, they do transport the less mobile NH_4^+ (Smith and Read 1997).

Corkidi et al. (2002) observed that enrichment with N consistently decreased root colonization by AM fungi in grasses grown in soils with high P availability, but not when they were grown under conditions of limited P availability. Such results point to the conclusion that when mycorrhizal costs exceed the benefits AM colonization is severely reduced, and is consistent with the hypothesis that N fertilizer application alters the balance between costs and benefits in mycorrhizal symbiosis. The authors also observed that AM fungal communities from N fertilized soils are less mutualistic than those from unfertilized soils.

Whether AM can take up or transform organic forms of N has long been a subject of debate, but recently Hodge et al. (2001) found that AM can enhance decomposition and increase N capture from complex organic material (grass leaves) in soil, independently of the host plant.

Considerable research has been conducted on the benefits conferred by the simultaneous AM colonization and nodulation of legumes with N_2 fixing bacteria. A synergistic effect between both microsymbionts and the host leguminous plant lead to the idea of a tripartite symbiosis (El-Hassanin and Lynd 1985, Niemi and Eklund 1988) and has been explained on the basis of a high P demand in the N_2 fixation process, which is offset by the AM symbiosis (Stribley 1987, Smith and Read 1997). However, there is now evidence that P uptake is not the main driver for the development of the tripartite symbiosis. In fact both symbioses share transduction pathways and effects of the tripartite symbiosis (e.g., increased nodulation) can be observed within 10 days after plant emergence, when the seedling still relies on P contained in the cotyledons (Goss and de Varennes 2000, Antunes et al. 2006a).

Variation in the enhancement of N acquisition by AM plants may also occur with different AM fungal isolates (Azcón-Aguilar et al. 1980). Antunes et al. (2006b) found no difference in N_2 fixation of soybean plants colonized with *Glomus clarum* or *Gigaspora Margarita*, however Chalk et al. (2006) highlighted the current paucity of quantitative data and lack of understanding of the interactions of legume genotype with AM fungal species in respect of the potential of AM to enhance legume yield and symbiotic dependence, particularly under field conditions.

Common mycorrhizal networks (He at al. 2003) can interconnect component intercropped species or cultivars by extending AM mycelia from one plant roots to another. The direct transfer of N from soybean to maize mediated through AM fungi has been shown by van Kessel et al. (1985) and between berseem and maize by Frey and

Schüepp (1992). He et al. (2003) review not only one-way transfer of legume-N to a non N_2-fixing mycorrhizal plant but also a few studies showing transfer from non-fixing mycorrhizal plants to N_2-fixing mycorrhizal plants as a kind of bidirectional transfer. Hauggaard-Nielsen and Jensen (2005) believe that a better understanding of the mechanisms behind facilitative interactions may allow a greater benefit from these phenomena in agriculture and environmental management.

6.3 Other Nutrients

Clark and Zeto, (2000) reviewed a number of studies where improved acquisition of sulphur (S) was observed in AM plants relative to uncolonized plants. Even though hyphae have not been shown to be highly active in S transport, the uptake of sulphur in AM plants appears to be very dependent on host plant, AM fungal symbiont, temperature and soil pH.

Hight boron (B) soil concentration may have negative effects on root AM colonization (Ortas and Akpinar 2006) and B acquisition in AM plants seems to be relatively inconsistent. It has been reported as enhanced (Kothari et al. 1990), reduced (Clark et al. 1999) and not affected (Lu and Miller 1989) in shoots of AM plants and it is also reported that AM fungi differed extensively for B acquisition/restriction (Clark et al. 1999). The same kind of variation in nutrient acquisition, including the response to biotic and edaphic factors has been noted for potassium, calcium, magnesium and sodium (Clark and Zeto 2000).

Uptake of both zinc (Zn) (Ryan and Angus 2003) and cooper (Cu) are enhanced in AM plants but to a lesser extent than reported for P. These nutrients may not be as readily translocated from roots to shoots as is P, but the amount is probably adequate given that plants have a smaller requirement for these micronutrients. Its distribution in roots and shoots depends on soil P level. Zn, like P, is diffusion limited and its mobility in the soil is very small. AM involvement in Zn nutrition has been implicated from the negative effects of both tillage (Evans and Miller 1988) and long fallow (Wellings et al.1991) on crop growth. Beneficial responses to AM fungal colonization vary according to the different environmental conditions impacting the plants, especially soil pH.

AM plants generally acquire less manganese (Mn) than non-AM plants (Arines and Vilariño 1989, Bethlenfalvay and Franson 1989) although in acid soils, where Mn is more soluble, enhancement of Mn has been reported. Alleviation of Mn toxicity has also been reported frequently, it seems to be due to a more favourable equilibrium of

Mn oxidising and reducing microorganisms in the mycorrrhizosphere of AM plants (Nogueira et al. 2004).

Acquisition of iron (Fe) by AM plants is strongly affected by soil pH and the fungal symbiont. Amounts are reported to be enhanced or reduced depending on the conditions (Al-Karaki and Clark 1998, Nogueira and Cardoso 2002).

The presence of some elements also affects the way others are taken up in the presence of AM fungi. Liu et al. (2000) reported that, in the experimental conditions tested, the effect of AM fungi on Zn, Cu, Mn, and Fe uptake varied with micronutrient and P levels added to the soil.

For potentially toxic elements (e.g. Cd, Pb, Ni, Ba, As) the ability of AM to growth in heavily contaminated sites has long been reported (Heggo et al. 1990, Ahmed 2006). Apparently the toxic elements are sequestered in the hyphae, in the polyphosphate granules, and not transferred to the plant (Smith and Read 1997, Rivera-Becerril et al. 2002). Even when transferred their negative influence on the plant metabolism is not critical because in AM plants the vegetative part is more developed allowing the dilution of trace elements. Different isolates have diverse tolerance to excess levels of many trace elements (Turnau et al. 2001). The size and diversity of AM fungi populations may be modified in metal-polluted soils (Del Val et al. 1999) and it appears that a prolonged exposure to this type of elements can result in the development of tolerance by the AM fungi (Oliveira et al. 2001).

7 Fungicides and AM Fungi

The use of pesticides, particularly fungicides, appears to impair mycorrhizal formation and development. In fact most of the time the effects of these chemicals are detrimental to AM fungi (Manjunath and Bagyaraj 1984, Salem et al. 2003) although the degree of toxicity varies with the active ingredient, the application rate (Habte and Manjunath 1992) and the AM fungus (Schreiner and Bethlenfalvay 1997). Systemic fungicides would be expected to be more detrimental to AM fungi then non-systemic ones. However, this distinction does not seem to be a key variable. For example, captan, a non-sytemic fungicide, can significantly reduce mycorrhizal formation while conversely triadimefon and pyrazophos, both systemic fungicides, actually promoted AM formation (von Alten et al. 1993). Kjøller and Rosendal (2000) concluded that external hyphae are more sensitive to the application of systemic fungicides, than are the internal hyphae.

An extensive review made by Menge (1982), on the effects of many fumigants and fungicides specifically on AM fungi, is highly recommended despite the passage of time since it was published. A general analysis, confirmed by Vyas and Vyas (2000), indicates that for AM development, soil-applied products should be avoided.

8 Evaluation of AM Fungal Diversity

According to Douds and Miller (1999), an understanding of the impacts of agronomic practices upon communities of AM fungi would help to ensure an opportunity for the utilization of the symbiosis and contribute to the success of sustainable practices. Plenchette et al. (2005) argue that we need to be able to characterize AM fungi and mycorrhizas as easily as soil chemical properties, such as exchangeable cations. This approach could allow AM fungal characterization to be integrated into an agronomic diagnostic approach, and would help us establish when mycorrhizal development leads to poorer productivity. However, for the purpose of assessing the impact of any biotic or abiotic stress factor, measurement or evaluation of diversity in AM fungi communities in field soils, at least at the species level, presents a variety of challenges.

Spore characters and their various states of expression, especially spore wall structure (e.g. number of layers, size, colour, refractivity, flexibility, histological reactivity, ornamentation) and developmental sequence with associated morphological features, have long been the basis for species-level taxonomy (Morton and Benny 1990). Identification and its appropriate application are further challenged by the obligate dependence of these fungi on plant host. Spores collected from the field loose or change the appearance of their structural characters in response to root pigments, soil chemistry, temperature, moisture and microbial activity. For the purpose of identification this necessitates the establishment of trap cultures to obtain healthy spores with clear structural characteristics. Depending on the set of plants chosen for the trap culture (Jansa et al. 2002), this technique may allow detection of non-sporulating members of the community. Mathimaran et al. (2005) have confirmed that the identity of plant species in trap pots significantly affected composition and diversity of associated AM fungi communities.

There is no clear relationship between functional diversity of organisms and the morphological diversity of spores used to delineate species (Douds and Millner 1999). Life-history traits that are important for the AM symbiosis (e.g. amount and architecture of external hyphae, proportional fungal biomass as arbuscules versus vesicles and absorptive and transport capacity of hyphae) are not linked to any apparent character trait used to distinguish species (Morton and Bentivenga 1994). It is known that each AM fungal spore may have hundreds or thousands of nuclei (Becard and Pfeffer 1993), and although the genetic diversity has not yet been proven, it is possible to speculate that each individual carries the genome necessary to adapt to a wide variety of environmental conditions and plant hosts.

The morphology of fungal structures that can be detected in roots is in general very similar and doesn't necessarily reflect the extent to which different fungal species colonize the root systems. For a long time the lack of reliable methods for the identification of fungal species that colonize a root greatly limited our ability to characterise changes in mycorrhizal populations (Miller et al. 1994). One of the most important objectives in AM research includes the need to find good and practical methods for describing communities. Serological (Hepper et al. 1988, Cordier et al. 1996), enzymatic (Hepper et al. 1986, Dodd et al. 1996), fatty acid profile (Graham et al. 1995) and many modern molecular tools have been developed and continuously improved in the last decade, and now constitute a powerful and promising approach to detect and evaluate this diversity, inclusively directly at soil level (van Tuinen et al. 2004).

9 Conclusion

Agricultural practices such as tillage, crop rotation, crop residue retention and fertilizer use all affect ecological niches available to the soil biota. Agro-ecosystems are managed biological systems that may involve the use of several practices that are detrimental to a mycorrhizal symbiosis. Furthermore, these systems also conform to the concept that organisms best adapted to the changing habitats and niches will gradually replace those individuals not so well adapted (Rovira 1994). Conventional practices of land management usually result in a loss of the spatial heterogeneity of soil and diversity of organisms. In addition, it is very apparent that highly disturbed and unbalanced systems can became almost sterile habitats (e.g. mining sites) or completely dominated by only some groups of organisms (e.g some weed species).

The goal of sustainable management is to create a more spatially heterogeneous habitat that offers the potential for more diverse and balanced systems to establish, in which natural occurring organisms, like AM fungi, can express their genetic potential, evolved over millions of years of co-existence with most terrestrial plants (Simon et al. 1993, Redecker et al. 2000). Management practices like no-till, controlled nutrient supply, and cautious control of weeds and pests, clearly have the possibility of encouraging arbuscular mycorrhizas.

Farmers have to be attentive and conscientious about the possible consequences of their management choices. There are no guaranteed “recipes” and each decision must take account of the multiplicity of economic and organizational aspects that pertain locally, including production goals, constraints on the farm and the resources available. This new context is much more demanding for producers, since they must adapt our generalized understanding to their particular reality and be able to use the information for responsible and wise management decisions.

Communication between researchers and farmers is an essential element for success in developing new opportunities for a more effective use of mycorrhizal symbioses. Importantly, it must be strengthened by the flow of useful and easily understandable information in one direction, and clear, pertinent questioning and challenging in the other.

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