The role of arbuscular mycorrhizal fungi in agro- and natural ecosystems

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Biography

Dr John C. Dodd is Director of the Biotechnology MIRCEN at the International Institute of Biotechnology (wwwbio.ukc.ac.uk/iibmircen) based on the campus of the University of Kent at Canterbury (UKC), UK and Honorary Senior Research Fellow in Biosciences at UKC. He is also co-ordinator of the European Bank for the Glomales (BEG) which runs an online ecological database and genetic archive (wwwbio.ukc.ac.uk/beg) for arbuscular mycorrhizal fungi. He has published extensively on mycorrhizal fungi including applied and fundamental research in diverse temperate and tropical ecosystems as well as in plant pathology and agronomy. His overall goal has been to study how these beneficial symbionts can be managed within plant production e.g. agrosystems, reforestation or ecological restoration of degraded sites. This aim fits in with an Institute aim of utilising the natural biodiversity of micro-organisms for biotechnological processes as an alternative option to genetic manipulation. Recently he has fostered the application of mycorrhizal fungi in the UK, helping a company (PlantWorks, PlantWksUK@aol.com) produce "tuned" products for the market.

Abstract

Symbionts called "mycorrhizal fungi" occur in most biomes on earth and are a fundamental reason for plant growth and development on the planet. The most common group of mycorrhizal fungi are the arbuscular mycorrhizal fungi (AMF) which colonise the roots of over 80% of land plant families but they cannot be cultured, as yet, away from the host plant. AMF are primarily responsible for nutrient transfer from soil to plant but have other roles such as soil aggregation, protection of plant against drought stress and soil pathogens and increasing plant diversity. This is achieved by the growth of their fungal mycelium within a host root and out into the soil beyond. There is an urgent need to study the below-ground microbiology of soils in agro- and natural ecosystems as AMF are pivotal in closing nutrient cycles and have a proven multi-functional role in soil-plant interactions. More information is also needed on the biodiversity and functional diversity of these microbes and their interactions with crops and plants.

Introduction

The arbuscular mycorrhizal fungi (AMF) are placed in the taxonomic order called the Glomales which currently comprises 6 genera (Fig. 1) with species from the genus *Glomus* the most researched (see Smith and Read, 1997[1] for general overview). *Glomus*-like fungi are believed to have originated around 400-500 million years ago based on fossil evidence[2] and DNA sequence analysis of ribosomal genes[3].Recognition of the presence of these symbioses occurred in the last century but subsequent investigation of their function only began in earnest in more recent times. Studies on the role of the fungus in association with the plant root system has been limited by the obligate nature of the symbiosis for the fungi. AMF form specialised structures inside root cells called *arbuscules* which are believed to be the main site for nutrient transfer between plant and fungus (Fig. 2).

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                        │    Order    │
                        │  Glomales   │
                        └─────────────┘
              ┌────────────────┼────────────────┐
      ┌───────────────┐ ┌────────────────┐ ┌────────────────┐
      │  Glomaceae    │ │ Acaulosporaceae│ │ Gigasporaceae  │
      └───────────────┘ └────────────────┘ └────────────────┘
              │                 │                  │
 Genera       │                 │                  │
      ┌───────────────┐ ┌────────────────┐ ┌────────────────┐
      │    Glomus     │ │  Acaulospora   │ │   Gigaspora    │
      └───────────────┘ └────────────────┘ └────────────────┘
      ┌───────────────┐ ┌────────────────┐ ┌────────────────┐
      │  Sclerocystis │ │ Entrophospora  │ │ Scutellospora  │
      └───────────────┘ └────────────────┘ └────────────────┘
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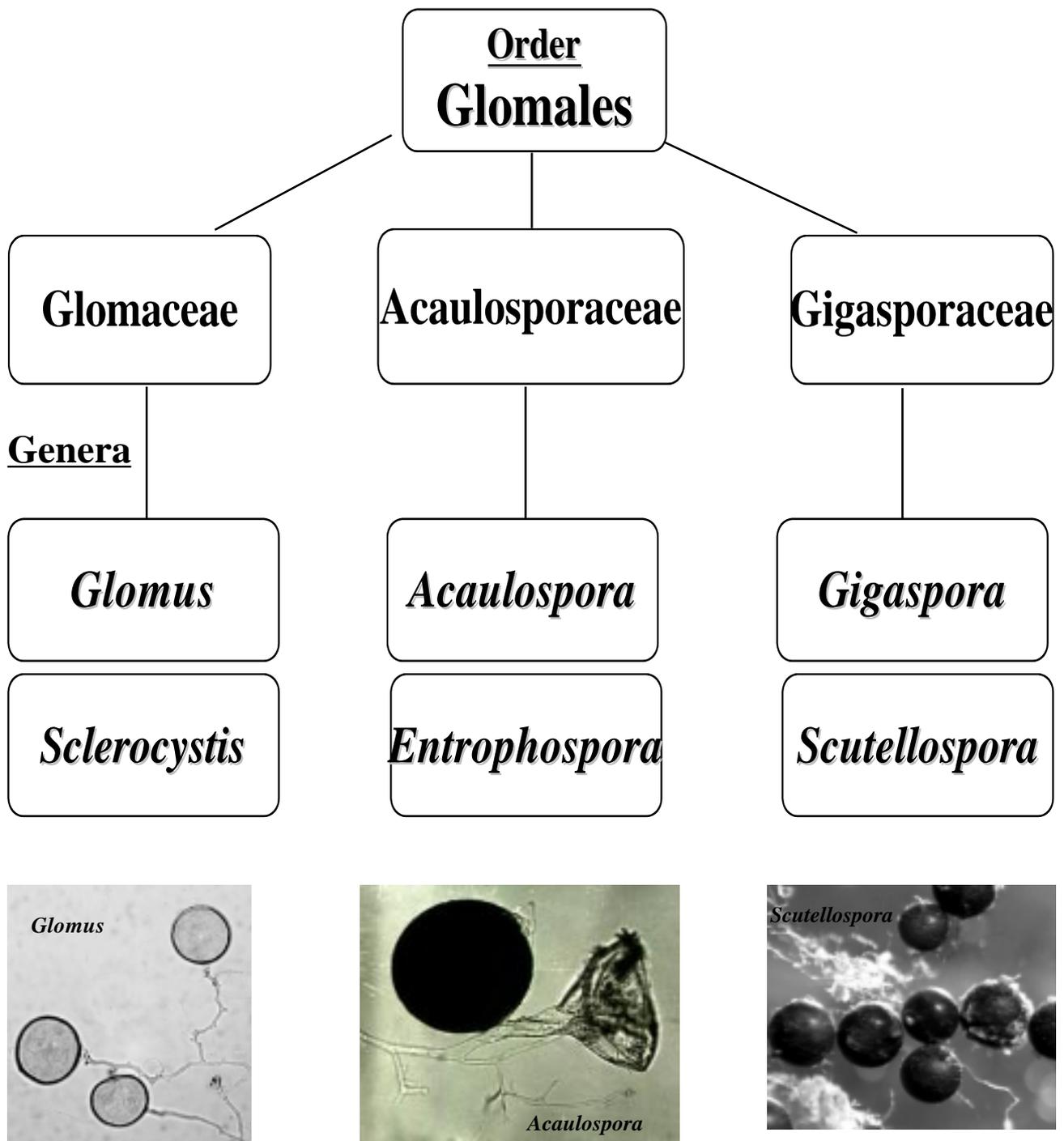
Figure 1. - The current taxonomy of AMF with examples of the large spores produced by different genera in soils.

Nutrients are captured by the network of mycelium (fungal hyphae) ramifying throughout the upper soil horizons and linking plants in natural ecosystems (Fig. 2) and transferred to the host plant. AMF gain all their carbon for growth from the plant photosynthate in exchange for a supply of mineral elements from the soil. The extraradical (soil-based) mycelium (ERM), produced by the fungus in the soil, is highly adapted to an efficient uptake and transfer of nutrients to the plants. To work with these fungi scientists need to isolate the spores from trap cultures and use these to colonise roots of suitable host plants growing in sterile or semi-sterile substrata (Fig. 3). Inoculum is generally produced by inoculating susceptible plant roots with spores of the selected AM fungus (frequently species of *Glomus* as they are easier to maintain).

(a)   (b)
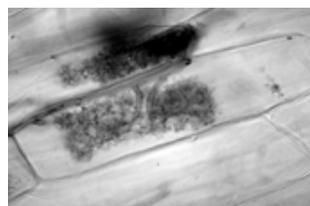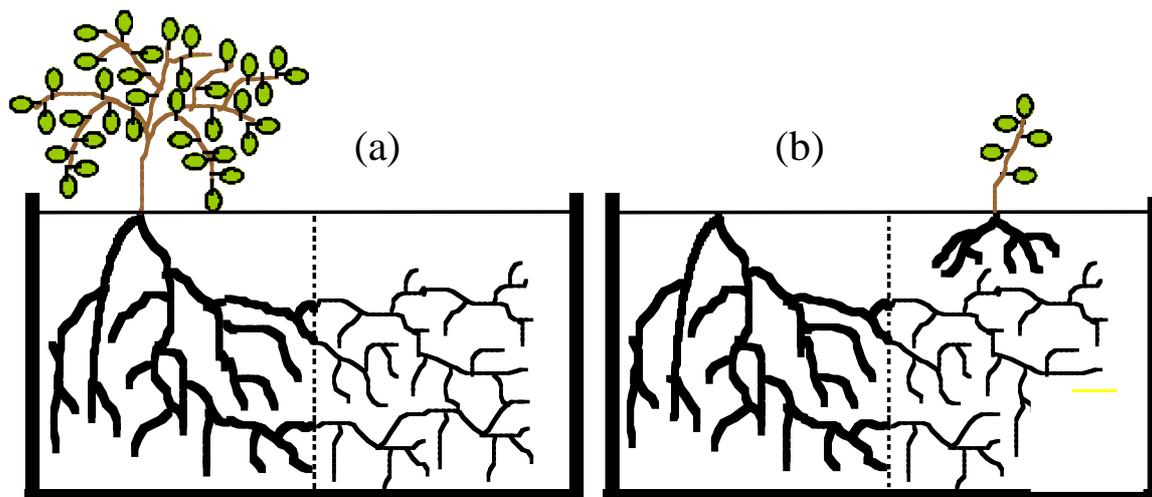
Arbuscule in an onion root cell
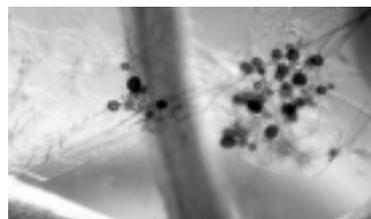
Hyphae of AM fungus connecting mycorrhizal roots with soil and producing spores.

Extensive soil based mycelium of fungus around roots can help soil aggregation processes

Figure 2 – The use of Rhizobox systems (where plant roots and hyphae produced by AMF can be separated during development by using a fibre mesh barrier) has allowed analysis of both the architecture of the extraradical mycelium and studies on how disturbance (or not) of this effects subsequent plant growth.

The resulting inoculant comprises a mixture of growth substrate, colonised roots and fungal propagules in the substrate. It is worth noting that spores of AMF are the largest fungal spores to be found in the soil and have a genome size comparable with that of humans (spores in the Gigasporaceae can contain several thousand nuclei). Estimates for the extent of their soil-based mycelium ranges between 10 and 100 m cm^{-1} (or g^{-1}) of soil[4] in agricultural and natural ecosystems. This is a large carbon sink and research on the effects of elevated CO_2 on AMF is being undertaken to see if there is potential to lock-up extra C in these soil-based fungi given the predictions on global climate change in the next century.

Figure 3 – The large collection of AMF held at IIB on different hosts (onion, leek, clover, sorghum) under controlled greenhouse conditions contrasts with the culturable fungal collections held in other repositories in the UK.

The benefits of optimisation (via inoculation or management) of AMF in production systems with low indigenous inoculum or efficacy have included:

♦ Increased plant nutrient uptake via the AM fungus e.g. P
♦ Increased tolerance of root pathogens by the plant system
♦ Increased tolerance of water stress and adverse environmental conditions (e.g. heavy metal pollutants)
♦ Increased efficacy of N-fixation by *Rhizobium* (Plant nodulating bacteria which fix atmospheric N for legumes)
♦ Increased plant biodiversity in restored ecosystems
♦ Increased stability of soils (erosion control)

Plant nutrient uptake by AMF

The nutrient most commonly associated with mycorrhizal benefit has been phosphorus (P) which is highly immobile in most soils and limiting to plant growth and reproduction. The main areas where the benefits of introducing inoculant AMF into a plant growth system will accrue are where they are lacking indigenous inoculum of AMF (e.g. sterilised soils, *post-vitro* plant micropropagation). The effect is subsequently to increase early growth and nutrient uptake by phosphate (Fig. 4). This uptake and transfer of mineral elements is done by the ERM, once established in agro-systems, as it provides an increase in exploited soil volume beyond that of the plant root system (Fig. 2). It is widely accepted that plants with highly branched root systems (Graminae) are less mycotrophic (less dependent on the fungus for normal growth) than those with coarser roots [e.g. cassava, onion], and that this determines the dependence of the plant on the symbiosis. Over 10% of plants (including complete plant families e.g. Chenopodiaciae and Brassicaceae) are non-mycorrhizal and these plants compensate by developing extensively branching root system architectures. They include many of the crops used in Europe today e.g. oil seed rape (canola).

Figure 4 - The classic 'big plant versus small plant' response of a responsive host plant (*Paraserianthes falcataria* – a fast growing tree legume used for reforestation in SE Asia) to inoculation with an effective isolate of AMF (on right) in sterile soils with reduced P availability.

In containerised plant production, however, the balance of nutrition and other environmental factors such as light levels will impact on the efficacy of the symbiosis and may explain some of the lack of success of using AMF under commercial conditions. Under unfavourable conditions apparent early growth depressions can occur as the fungus drains extra carbon from the plant to establish its mycelium (a critical balance between C and P supply)[5]. This is also relevant to varieties of crops bred for high inputs rather than those able to form compatible relationships with AMF (see later).

It is well-documented that high inputs of chemical fertilizers (especially phosphates and high nitrates) along with certain fungicides (e.g. benomyl) and soil sterilants have negative effects on AMF. This is primarily observed as reductions in colonisation levels in plant roots over time but also in P-uptake.

Increased resistance to root pathogens by AMF

AMF have been shown to increase resistance to root-infecting pathogenic fungi e.g. *Phytophthora parasitica* or *Fusarium* spp. and root invading nematodes. This topic has been extensively reviewed in recent times but mechanisms involved are not well understood[6]. Cordier et al.[7], however, provided evidence for the benefits of pre-inoculation of tomato plants with an AM fungus when subsequently challenged by *Phytophthora parasitica* showing that seedlings had less root damage. Using immunogold labelling techniques they showed that the number of hyphae of the pathogen was greatly reduced in mycorrhizal root systems and in mycorrhizal tissue infected by the pathogen. The same authors[8] showed that the AM fungus tested (an isolate of *Glomus mosseae*) was able to confer bioprotection against *P. parasitica* via localised and induced systemic resistance in mycorrhizal and non mycorrhizal roots respectively. This is an intriguing area of research and bioprotection maybe the primary role for AMF in some natural ecosystems rather than nutrient acquisition. There are other observations showing how the ERM provides a surface for soil bacteria to use as a niche, the so-called 'mycorhizosphere'. The production of these 'natural biofilms' on the surface of hyphae may also play an indirect role in influencing pathogen levels and in aiding nutrient acquisition and soil stabilisation (Fig. 5).

Figure 5 - Biofilm of bacteria (fluorescing bodies) on the surface of a soil-based hypha of AMF showing close synergy between soil bacteria and AMF.

Alleviation of Environmental Stress by AMF

The role played by AMF in alleviating water stress of plants has been investigated and it appears that drought resistance is enhanced. The precise mechanisms underpinning this are still in doubt but it could be an indirect effect of the ERM improving nutrient absorption. The alleviation of water stress is not only limited to arid or semi-arid zones of the planet but also where short-term droughts occur (e.g. east of England) an increased reliance on AMF for nutrient uptake[9] can frequently be detected.

In more recent years the potential role of AMF in helping to increase a plant's tolerance of heavy metals and for the restoration of degraded natural ecosystems has been investigated. Work on heavy metal tolerant strains of AMF, isolated from polluted sites, has provided evidence for their rapid adaptation to contaminated soils. Joner and Leyval[10] found, using a Cadmium(Cd)-tolerant *Glomus mosseae* isolate, that the ERM was capable of uptake and transport of Cd. They also found that uptake was greater in mycorrhizal plants but that Cd was immobilised within the mycelium. Pioneer plant species which colonise contaminated or degraded soils earliest are frequently found to be weakly mycorrhizal (e.g. *Holcus lanatus* or ryegrass) or non-mycorrhizal. However, where these weakly mycotrophic plants can invade early, the succession process can be stimulated by increasing the inoculum potential of AMF around the plants and hence allow the obligately mycorrhizal plants into the habitat. Louis[11] found that where plant cover was greatest, the community was dominated by mycorrhizal species (>87 %) 5 years after reclaiming coastal land in Singapore. Cuenca and Lovera[12] found that perturbation reduced the propagule numbers of AMF compared with undisturbed savanna in areas around a DAM building project in Venezuela. The use, however, of mycorrhiza-dependent grasses and legumes to revegatate these areas reversed the latter process. Other work has shown that inoculation of a pioneer dune sand grass in Florida, USA, under commercial conditions, led to either better growth or increased hyphal densities in two sites[13]. The latter was important for dune stabilisation which occurred quicker than in non-inoculated sites.

Increased Nitrogen fixation

The tripartite interactions between nodulating legumes/AMF/nitrogen-fixing *Rhizobium* frequently result in increased nodulation and nitrogen fixation as the result of improved P nutrition in infertile or P-fixing soils in the tropics[14]. The ease of isolation and use of *Rhizobium* species has masked their crucial interactions with AMF. Recent work in our group has shown that specific AMF and *Rhizobium* can interact on the same plant to produce different growth and development of tropical tree legumes, like *Acacia mangium*, used for reforestation in South East Asia. Thus AMF interactions with *Rhizobium* and other soil micro-organisms (e.g. *Azospirillum* spp.) require further research to find optimal combinations of micro-organisms which could benefit plant production, rather than 'single-shot' options by one component of the soil microbiota.

Plant diversity and AMF

Van der Heijden et al.[15] have provided evidence that the community of AMF determine plant community structure by the response of individual plant species to colonisation by single or multiple species of AMF. This is certainly a point which also needs attention in agro-systems via better screening of plants and AMF for functional compatibility. In further work Van der Heijden et al.[16] showed that belowground diversity of AMF is a major factor in the maintenance of plant biodiversity and to ecosystem stability and function. AMF can enter the roots of many plant species in the same community resulting in simultaneous colonisation by several species of AMF. This results in interconnections of plants via the ERM of each. The conclusion being that increasing the species richness of AMF in grasslands leads to the increased spread of highly responsive herb species at the expense of relatively unresponsive grasses. A survey of the architectures of the ERM produced by species of AMF from different genera provide indications that each can exploit soil resources in different ways. This whole subject is at present a topic of great debate and new theories may evolve to fit these findings.

Soil Aggregation and AMF

Miller and Jastrow[17] have undertaken an intensive study of a prairie ecosystem in North America and showed that root and extraradical mycelium lengths were correlated with increased water stable macroaggregates and their geometric diameters.

The major component causing this was in fact the ERM of AMF. They also showed that a switch in dominance from *Glomus* spp. to *Gigaspora* spp. was also positively correlated with increased length of the ERM and macroaggregation. Mycorrhiza formation in soils results in an increased movement of C into roots and rhizosphere via better root growth and respiration. Increases into the bulk soil are via ERM production by AMF, respiration and breakdown. The ERM provides a physical structure which can entangle soil particles and lead to micro- then macro-aggregate production (Fig. 2). The recent finding that a glycoprotein called "Glomalin" is produced by AMF soil-based mycelium and is a major binding agent in soils adds further weight to the importance of AMF in stabilising soils and hence ecosystems.

Soil tillage in agricultural production may reduce the subsequent rate of colonisation of plants by AMF by breaking up the living ERM in the soil. The result of this disturbance will be a reduction in propagules of 'susceptible' AMF (Acaulosporaceae and Gigasporaceae) but may increase those of more resistant species of *Glomus*. This reduction in diversity is supported by recent molecular biology studies using PCR-based techniques to detect rDNA sequences in roots[18]. Some excellent work has been done over many years in Canada to investigate why tillage reduced plant P absorption in early season Maize (*Zea mays*). The overwinter survival of the extraradical mycelium and its non-disturbance seems to be a vital agronomic practice for the subsequent colonisation of spring crops and optimum functioning of the mycorrhizas[19]. It appears that the survival of the extraradical mycelium in tact, allows plants to be incorporated into functional mycorrhizal associations early in spring.

Strategies for the management of AMF for plant growth.

Two management options exist:

♦ Inoculation with selected AMF
♦ Management of indigenous AMF to produce effective communities

Inoculation - Much of the data gained on AMF have been obtained in greenhouse experimentation using single species inoculants in sterilised soils on responsive hosts plants (Fig. 4). Nevertheless field-based studies have shown increases in early growth and development of crops even in unsterilised soil when inoculated with effective AMF populations (Fig. 6), particularly in the tropics e.g. Latin America[14,20]. Sieverding[20] performed over 50 field trials inoculating responsive cassava varieties with effective AMF in acid soils of varying fertility and obtained an average of a 20-25% increase in tuber yields (3 tonnes per hectare) and a greater stability in production year-on-year. The usefulness of this approach was demonstrated for small farm holdings in Latin America which comprise the majority of farms in these countries if not the biggest agricultural area.

Figure 6 - The use of effective AMF populations to increase early growth and development of Sorghum in an oxisol in Colombian savanna system when fertilised with rock phosphate.

Other areas where inoculation would be the obvious management option include Horticulture where micropropagation is becoming more common to produce clonal outplanting material. *Post-vitro* inoculation of seedlings would be desirable prior to outplanting in field or greenhouse since the plants can easily be raised with an effective mycorrhiza with minimum inoculum input. The benefits of reducing fertiliser inputs to optimise conditions for the AMF has been noted for strawberry where different AMF stimulated either increased stolon production or earlier flowering[21]. This was done by using slow-release fertilizer sources. The expense, however, involved in inoculum production will only be justified, in today's economic climate, for high value agricultural or horticultural crops where there are extra benefits to better plant growth like improved plant fitness or tolerance of biotic or abiotic stresses.

Management of Indigenous AMF - The merits of maintaining high levels of both indigenous inoculum and biodiversity of AMF, by adopting appropriate soil management practices over inoculation, has been debated in many recent reviews[22]. Pre-cropping, as a cultural practice, with a tropical legume, cassava or *Sorghum* sp. in the previous growing season in the Colombian Llanos improved the subsequent growth of the forage and crop legumes *Stylosanthes capitata* and cowpea respectively compared with converted savanna. This was correlated with greater early colonisation due to increased levels of AMF inoculum surviving the dry season and by populations of AMF different to that found in the direct savanna sown plots[14,23].

There have been a few other novel approaches to the study and testing of methodologies to manipulate AMF in the field in recent times. The recent use of molecular probes, however, has enabled gene sequences of rDNA from root samples in natural and adjacent arable fields in the UK to be compared. This showed that there was a marked decrease in sequence diversity detected in roots of crops compared with roots of plants in the natural ecosystems[18]. As further screening of the sequence diversity of AMF colonising roots is correlated more precisely with those from specific species then it should become easier to identify those AMF functioning in different plants at any one time. The spin-off will be an ability to manipulate AMF for the production system once effective functional assemblages of AMF have been identified.

Sustainable Production using AMF

In natural ecosystems or low-tillage agriculture young seedlings can germinate and effectively 'plug' into an already established 'motorway' of hyphae of AMF which permeates the soil and links different plant species (see Fig. 2a,b). The lack of host specificity is the secret to the success of AMF in mixed plant communities. The benefit to plants in natural plant communities is perhaps that less carbon from the plant photosynthate is needed by AMF following colonisation since it is plugged into a pre-established mycelium. In contrast, crops in agricultural systems are frequently sown into tilled soil where this mycelium has been completely disrupted. Agriculture would therefore allow only those AMF with aggressive colonisation strategies and able to produce a new ERM quickly (mainly species of *Glomus* in temperate climates) to survive. There is a case to answer as to whether such practices have selected for "inferior mutualists"[24] as a result. Graham and Eissenstat[25] have discussed such data in terms of a higher than normal carbon drain on the host for little return from the mycorrhizal fungus for certain *Citrus* cultivars. One could postulate that there would be more resources available to support a greater diversity of plants and AMF in natural systems as a result.

So why is there a problem in managing AMF for sustainable production? There is a conflict of interest in the idea of maximising plant production against an aim of maintaining a high biodiversity of AMF in soils. The latter maybe a necessity in natural ecosystems or restoration of degraded natural habitats but selection for efficient populations of AMF compatible with the aim of maximising yields of certain crops may require a different management approach in agro-systems.

Modern agricultural practices, such as high levels of fertiliser and pesticide inputs and long-term monocultures, have proven adverse effects on the diversity of soil microbiota which are at odds with the use of AMF. The answer may ultimately lie in the use of both intensive and extensive agro-systems alongside each other to provide both basic food requirements and supply an increasing market for sustainably-produced crops. It is becoming clear that sustainable production practices, e.g. crop rotations with legumes, would benefit the survival of inoculum of AMF from season to season and hence increase or maintain inoculum of AMF for subsequent mycorrhizal crops. One potential weakness is that both systems are using varieties (genotypes) of crops bred for high inputs. This is a selection process driven by conventional plant production, and the varieties may not be suitable for optimal production under organic or other sustainable systems. There are examples of where modern lines of plants in commercial production appear to be less susceptible to colonisation by AMF as a result of breeding programmes e.g. wheat[26]. Other work has shown that the inbred lines of *Zea mays* L. with resistance to fungal pathogens were less able to form mycorrhizas compared with disease susceptible lines[27]. The relationship, however, between reduced colonisation and nutrient uptake ability of AMF is uncertain and maybe uncoupled genetically. However, there is evidence for increased root fibrosity to compensate for the reduced role of AMF. These traits will operate fine under high input agricultural production but can the same varieties produce high yields under reduced input systems? This may need a change in emphasis in plant breeding in the future to screen for optimal functioning of AMF under normal nutrient and environmental stresses if sustainable production is to become more widespread.

Past and Future of AMF in Plant Production

Research on AMF in the 1970s and 1980s was dominated by the search for 'superstrains' capable of increasing plant biomass under any environmental and soil conditions. The desire to exploit AMF as a natural biofertilizers for the agricultural biotechnology industry was understandable, but it became clear that more knowledge was needed of the fungi themselves to allow commercial exploitation. Many inoculant companies have tried to commercialise the use of AMF with limited success. This has masked the importance of the symbiosis for normal plant growth and development in natural ecosystems where mycorrhizal plants dominate climax vegetation. Many mycorrhiza inoculants use the same fungal consortia for all environments. The philosophy of a new company, PlantWorks in the UK, is to "tune" consortia for the prevailing conditions (PlantWksUK@aol.com). The benefits of the symbiosis for nutrient uptake by plants in agro-systems is important but a more complete understanding of how to manage arbuscular mycorrhizas for optimum plant growth and development and general health is needed urgently, as high-input plant production practices are challenged by more sustainable approaches (biological production systems).

Conclusions

Huge changes in land use are predicted for Europe in the coming century resulting from technological, socio-economic, global environmental and political changes. These changes will always be governed by policy of individual governments and global entities like the EU and USA. The balance to be struck will be between maintaining food production for the increasing world population and the pressing need to conserve biodiversity (as well as supply for the markets for 'organic' or low-input products). The current trend is for intensive production using high yielding crops using classical plant breeding techniques and more recently transgenic breeding programmes. The potential therefore for incorporating beneficial micro-organisms within crop production is limited by the fact that no screening ever occurs in plant breeding to optimise the role of symbionts like AMF. There are scientific data which indicate that modern high input agriculture has actually selected for AMF which can survive perturbation and higher inputs but which appear to function sub-optimally under these conditions.

The current requirement in agriculture for high yields as quickly as possible may be an ongoing necessity for the future of food production in Europe. The increasing consumer demands for 'organic' or sustainably-produced food, however, will require changes to incorporate cultural practices which increase AMF diversity. What is important is that the maximum pool of diversity of AMF is maintained at as high a level as possible for subsequent crops, if dependent on AMF for growth, under reduced inputs. What is often forgotten however is that large acreage's (in UK for example) are sown to non-mycorrhizal hosts e.g. oil seed rape, cabbage, cauliflower, sugar beet etc. and their effect on AMF can only be one of reducing infective propagules and hence diversity for subsequent mycorrhizal crops. Interestingly a phenomenon known as "Long Fallow Disorder" in vertisols in Northern Australia has been linked to a decline in viable propagules following periods of fallow longer than 12 months and also where non-hosts followed fallow.

Plant breeders may need to find newer more appropriate plant cultivars which can maximise the role of AMF and other beneficial micro-organisms in agriculture in the 21st century. A recent discussion of conventional versus "organic" production systems highlighted how the Green Revolution helped to meet the needs of an ever increasing world population but at the price of environmental pollution[28]. The aim is therefore for practices that can give high enough yields with fewer environmental costs. The success noted in the enhancement of soil fertility and stability by adding manure, reducing tillage etc. in "organic" systems may, indirectly, be the result of optimisation of the soil microbiota and specifically AMF. Multidisciplinary research is needed in these areas. Other commentators have noted the need for optimisation of the recovery of P using effective AMF in agriculture given the dwindling phosphate resources[29]. All this leads us to the conclusion that a fundamental knowledge of ecological processes is needed urgently to manage our plant production systems sustainably in the future[30].

In conclusion we hear much talk and little action in implementing sustainable strategies such as Integrated Pest Management, given that the 'bottom line' is always the perceived financial cost and likely profit. The harnessing of natural biodiversity such as AMF is a biotechnological approach which counterbalances the current negative image of genetically modified organisms in conventional production systems. It is one that needs support from legislators, politicians and society in general to achieve balanced and yet realistic plant production strategies in the coming century. The poor status and diminishing resources, however, of agriculture, agricultural science and scientists, in the UK specifically, at present does not bode well for the future.

Glossary of Terms

Arbuscular mycorrhizal fungi (AMF) – fungi forming arbuscules inside roots. Also known in older literature and by some groups as vesicular-arbuscular mycorrhizal fungi since vesicles (storage bodies formed in roots) are formed by some Glomalean fungi but not the Gigasporaceae (see Figure 1).

Arbuscules - named by because of their resemblance to small trees, these are intricately branched structures formed within root cortex cells. The branching is dichotomous and the hyphal branches gradually decrease in size from 5-10μm in the trunk hypha (see Figure 2) to <1μm. They are considered to be the major site of symbiotic exchange of nutrients (C from host to fungus and P from fungus to host) with the host plant.

Ectomycorrhizal fungi – a group of fungi forming a mantle around roots of tree species and a structure inside the root called a Hartig Net between root cells. They appear to have more host specificity than AMF.

Extraradical mycelium – individual hyphae which extend out from the roots of the plant into the soil. These initiate new infection in susceptible roots, acquire nutrients and help soil aggregation processes.

Intercellular hyphae – hyphae of the fungus which grow between the walls of root cells.

Intracellular hyphae – hyphae of the fungus which grow within the wall of root cells.

Pathogenic fungi – invade living tissues of plant roots for example causing disease.

Spores – Form as swellings on hyphae alone or in groups (see Figure 1). They form thick walls and act as propagules for spreading the fungus. These are used identify species of AMF.

Symbiotic fungi – involved in mutually beneficial relationships e.g. AMF with plants.

Trap cultures – Soil or plants from the field are placed into sterile substrata in pots to encourage the colonisation of a susceptible host root systems e.g. red clover or onion. This process will lead to spore production by the fungus and allow identification to species.

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