Chapter 1
Use of Mycorrhiza in Sustainable Agriculture and Land Restoration

Zakaria M. Solaiman and Bede Mickan

1.1 Introduction

Arbuscular mycorrhizal (AM) fungi form symbiotic relationships with over 80 % of terrestrial plant species (Brundrett 2002). Arbuscular mycorrhizas are ancient and ubiquitous symbioses formed between a relatively small group of soil fungi and higher plant roots which has been traced back 460 million years (Redecker 2002). The symbiosis is primarily characterised by its association with phosphorus (P) uptake by host plants and the enhancement of water uptake through the extraradical fungal hyphal networks. This symbiosis can also trigger physiological and molecular signals at subcellular levels, alter plant community structure and increase plant tolerance to various abiotic and biotic stresses. Mycorrhizal hyphal networks link plants of the same and different species below ground and are able to transfer resources between plants and release signal molecule defence-related proteins, lipochitooligosaccharides and strigolactones. There have been significant recent advances in the understanding of physiological processes and taxonomy of these fungi (Kohout et al. 2014; Saito 2000). They are obligate symbionts belonging to the phylum Glomeromycota (Redecker et al. 2000). Their activity in agricultural ecosystems is well documented (Abbott and Gazey 1994; Bedini et al. 2013; Pellegrino and Bedini 2014) as is their presence during rehabilitation of forest ecosystems (Brundrett and Nanjappa 2013; Solaiman and Abbott 2003, 2008). The distribution of ectomycorrhizal (ECM) fungi is also widespread, but they form associations with only 3 % of terrestrial plant families (Smith and Read 2008). ECM fungi are members of the phyla Ascomycota and Basidiomycota (Hibbett et al. 2000; Siddiqui et al. 2008). Unlike the ECM fungi, AM fungi are dependent

Z.M. Solaiman (✉) • B. Mickan
Soil Biology and Molecular Ecology Group, School of Earth and Environment (M087), Institute of Agriculture, The University of Western Australia, Crawley, WA 6009, Australia
e-mail: zakaria.solaiman@uwa.edu.au

Z.M. Solaiman et al. (eds.), *Mycorrhizal Fungi: Use in Sustainable Agriculture and Land Restoration*, Soil Biology 41, DOI 10.1007/978-3-662-45370-4_1

on plants for their carbon (C) and when a symbiosis is formed, both ECM and AM fungi can demand 20–40 % of photosynthetically fixed plant C (McNear 2013).

1.2 Molecular Identification and New Taxonomic Classification of AM Fungi

Molecular techniques are applied to the identification of AM fungi under both greenhouse and field conditions, but there are many limitations in relation to the detection methods used as these are multinuclear organisms (Kohout et al. 2014; Schüßler et al. 2001). The diversity of AM fungi identified using molecular techniques has been studied at an ecosystem level (Sanders et al. 1995), for particular plant species (Jansa et al. 2003; Kjøller and Rosendah 2001), during seasonal variation in colonisation of roots of arable crops (Daniell et al. 2001), for coexisting species (Gollotte et al. 2004; Vandenkoornhuyse et al. 2003), and in relation to the influence of agricultural practices (Brito et al. 2013).

Despite rapid advances in methodologies, molecular techniques are still considered difficult to use for the identification of AM fungi because DNA extraction from soils typically yields low quantity and quality compared to plant roots (Renker et al. 2003; Olsson et al. 2010). There are also methodological and biological challenges to accurately assess AM fungi community composition which arises from the vast differences in DNA quantity from spores and hyphae in soil used for template DNA (Schüßler et al. 2001). Moreover, the higher quantity of DNA in multi-nucleic AM fungal spores compared to hyphae which contain significantly fewer nuclei which can skew community composition data (Gamper et al. 2008). This leads to potential bias in estimates of relative abundance where AM fungal morphotypes during sporulation will have a greater relative abundance than other morphotypes (Saks et al. 2013). The recent progress of next-generation sequencing techniques will open up a detail examination of fungal communities, and the reduction of cost of analyses will lead to greater accessibility, but there will be challenges.

Kohout et al. (2014) recently used different primers to compare four routinely used AM fungal-specific primer systems for nuclear ribosomal DNA such as (1) the partial small subunit (SSU), (2) the partial large subunit (LSU), (3) the partial SSU and internal transcribed spacer (ITS; “Redecker”) and (4) the partial SSU-ITS-partial LSU region (“Krüger”). They also included a new primer combination (5) the ITS2 region in the comparison. They concluded that “Krüger” primers tended to yield the highest AM fungal diversity and higher Shannon diversity index than did SSU primers. They confirmed a strong bias towards the Glomeraceae in the LSU and SSU primer systems and differences in the composition of AM fungal communities based on the “Redecker” primer system.

Willis et al. (2013) considered aspects of AM fungal ecology emphasising past and present importance of the phylum and concluded that it is essential to include

the AM symbiosis in studies of higher plants in order to provide a more holistic view of the ecosystems. Concomitant morphological and molecular analyses have led to major breakthroughs in the taxonomic organisation of the phylum Glomeromycota (Oehl et al. 2011). Fungi in this phylum are known to form arbuscular mycorrhizas, and so far the phylum has 3 classes, 5 orders, 14 families and 29 genera described. They present the current classification developed in several recent publications and provide a summary to facilitate the identification of taxa from genus to class level. The history and complexity of the taxonomy and systematics of these obligate biotrophs has been addressed by recognising four periods (Stürmer 2012). The initial discovery period (1845–1974) was categorised mainly by description of sporocarp-forming species and the proposal of a classification for these fungi. The following alpha taxonomy period (1975–1989) established a solid morphological basis for species identification and classification, resulting in report of many new species and the need to standardise the nomenclature of spore subcellular structures. The cladistics period (1990–2000) stated the first classification of AM fungi based only on phenotypic characters. At the end of this period, genetic characters played a role in defining taxa and elucidating evolutionary relationships within the group. The most recent phylogenetic fusion period (2001 to present) started with the proposal of a new classification based on genetic characters using sequences of the multicopy rRNA genes.

Opik et al. (2010) have offered a new database, MaarjAM, that summarises publicly available Glomeromycota DNA sequence and associated metadata. These data have been made accessible in an open-access database (http://maarjam.botany.ut.ee). Two hundred and eighty-two SSU rRNA gene virtual taxa were described based on a comprehensive phylogenetic analysis of all collated Glomeromycota sequences showing limited distribution ranges in most Glomeromycota taxa and a positive relationship between the width of a taxon's geographical range and its host taxonomic range.

Based on morphological and molecular characteristics, 19 genera, viz. *Acaulospora*, *Ambispora, Archaeospora, Cetraspora, Dentiscutata, Diversispora, Entrophospora, Fuscutata, Geosiphon, Gigaspora, Glomus, Intraspora, Kuklospora, Otospora, Pacispora, Paraglomus, Racocetra, Scutellospora* and *Quatunica*, comprising more than 200 species are documented in AM fungi (Manoharachary et al. 2010). Liu et al. (2009) stated that the AM fungal taxonomy position has moved forward to a phylum with 214 species belonging to 19 genera, 13 families, 4 orders and 1 class now reported. It was suggested that molecular techniques would be the key approaches in the future study of AM fungal species diversity. However, the intraspecific diversity of *Glomus mosseae* in a survey of 186 publications reporting the occurrence of *G. mosseae* from at least 474 different sites from 55 countries resulted in a geographical map of their distribution based on both morphological and molecular techniques (Liu et al. 2009).

While the taxonomy of AM fungi is based on morphological characters of the asexual resting spores, molecular approaches to community ecology have revealed a previously unknown diversity from colonised roots (Rosendahl 2008). The long asexual evolution of the fungi has resulted in considerable genetic diversity within

morphologically recognisable species which challenges concepts of individuals and populations. The fossil record and molecular data show that the evolutionary history of AM fungi goes back at least to the Ordovician (460 million years ago), coinciding with the colonisation of the terrestrial environment by the first land plants (Redecker 2002). The fast-growing number of available DNA sequences for molecular identification of the Glomales within roots has been designed and tested. These detection methods have opened up entirely new perspectives for studying the ecology of AM fungi.

The AM fungal phylogeny of the genus *Glomus* of the family Glomaceae has been analysed based on full-length SSU rRNA gene sequences and shows that *Glomus* is not monophyletic (Schwarzott et al. 2001). The separation of *Archaeospora* and *Paraglomus* from *Glomus* was reported. Two ancestral families of AM fungal species such as Archaeosporaceae and Paraglomaceae were discovered from deeply divergent ribosomal DNA sequences in the past (Morton and Redecker 2001). Each family is phylogenetically distant from each other and from other glomalean families despite similarities in mycorrhizal morphology. Morphological characters once considered unique clearly are distributed in phylogenetically distant groups. The spores of some species in *Glomus* have considerable divergence at the molecular level. It is the combination of DNA sequences and mycorrhizal morphology which provides the basis for recognising *Archaeospora* and *Paraglomus*. These investigations reinforce the value of molecular data sets in providing a clearer understanding of phylogeny which in turn can lead to a more robust taxonomy.

1.3 Mechanisms of Nutrient Exchange in Arbuscular Mycorrhizas

In AM associations, nutrient exchange between fungi and host is one of the most important functions. Recent advances in biochemical and molecular biological techniques have revealed a great amount of new information on this topic (Smith and Read 2008; Harrison 1999; Saito 2000; Smith and Smith 2012). This has largely reinforced the ideas concerning symbiotic C and P transfer proposed by classical works in the 1970s and 1980s (Tinker 1975). However, the biochemical mechanisms of nutrient exchange in this symbiosis are still unclear. The following view of phosphorus transfer from fungus to host plant has been widely accepted (Smith and Read 2008). Phosphate in the soil solution is absorbed in the extraradical hyphae via a P transporter (Harrison and van Buuren 1995). The absorbed P is condensed into polyphosphate (poly-P) in the extraradical hyphae and translocated by protoplasmic streaming into the intraradical hyphae (Cox et al. 1975; Cooper and Tinker 1981; Solaiman et al. 1999). At the end, the poly-P may be hydrolysed and released as P across the fungal membrane, probably at the arbuscule. Solaiman and Saito (2001) observed that a substantial proportion of P in

mycorrhizal roots was of fungal origin, while the proportion of fungal biomass to root biomass was <2 %. Phosphate efflux and the decrease in poly-P content in the hyphae were both improved by the addition of glucose and 2-deoxyglucose, an analogue of glucose. The rates of enhancement for P efflux and poly-P decrease were analogous, suggesting that P efflux from intraradical hyphae was coupled with poly-P hydrolysis. Based on these findings, the translocation of P from fungus to host was estimated in relation to the distribution of hyphal P in extraradical and intraradical parts of the AM fungus (Solaiman and Saito 2001). By applying the technique of separating intraradical hyphae from host roots, they were able to clarify the translocation and transfer of P in AM symbiosis in a quantitative manner. Further investigation of P efflux using the present experimental system will shed light on the mechanisms of nutrient exchange.

AM fungi rely on the photosynthetic C supplied by their host plants to complete their life cycle. In return, the fungi supply nutrients to the plant especially P, N and Zn. The site of nutrients exchange is primarily the arbuscule (Solaiman and Saito 1997; Harrison 1999; Balestrini and Bonfante 2005). The molecular and structural organisations of arbuscules facilitate and regulate the processes of nutrient exchange. Plant N and P transporter proteins have been reported (Ellerbeck et al. 2013; Javot et al. 2007b). Gene expression studies also showed that specific members of these protein families are expressed in the roots of colonised plants (Harrison et al. 2002; Javot et al. 2007a). Phosphate acquisition via the mycorrhizal pathway begins with the uptake of available P from soil by fungal extraradical hyphae (Bucher 2007). These hyphae extend beyond the host root zone, allowing a greater soil volume to be exploited for P uptake. Uptake at the soil hypha interface is mediated by fungal high-affinity P transporters (Harrison and van Buuren 1995). Following fungal uptake, phosphate is transferred to the fungal vacuole where it is polymerised to form polyphosphate chains and translocated through the vacuolar compartment to the intraradical hyphae (Solaiman et al. 1999). The poly-P is then hydrolysed and phosphate released to the interfacial apoplast from where plant mycorrhizal Pht1 transporters guide the phosphate across the periarbuscular membrane for delivery to other parts of the plant. The extraradical hyphae of AM fungi also absorb ammonium, nitrate and amino acids (Hodge et al. 2001), and the role of mycorrhiza on N delivery is becoming better understood (Chalot et al. 2006; Ellerbeck et al. 2013). The majority of N is thought to be taken up in the form of ammonia via the fungal-encoded AMT1 family transporters such as the protein GintAMT1 characterised from *Glomus intraradices* (Lopez-Pedrosa et al. 2006). There is no evidence for fungal translocation of either ammonium or nitrate and it is thought that nitrogen transport occurs in the form of the amino acid arginine (Govindarajulu et al. 2005), and amino acids may be delivered directly to the interfacial apoplast for plant absorption. However, there is also evidence for an alternative route whereby arginine is broken down by ornithine aminotransferase and urease to release free ammonium. It has been proposed that ammonium is exported by protein-mediated mechanisms and a candidate fungal AMT transporter has been identified that is highly expressed in the internal hyphae (Govindarajulu et al. 2005). Gene expression analyses of medic and rice have identified

mycorrhiza-induced transcripts that putatively encode ammonium transporters that are candidates for this function. There is also the possibility for passive ammonia uptake across the periarbuscular membrane, perhaps facilitated by the presence of aquaporin proteins (Uehlein et al. 2007). The use of radiolabeled substrates has demonstrated that AM fungi take up plant carbohydrates in the form of hexose (Solaiman and Saito 1997). The route of this transport is specific to the arbuscule. There is little molecular evidence for the presence of hexose export proteins in the periarbuscular membrane; although a number of mycorrhiza-responsive sugar transporter genes have been identified in medic, they are thought to act as proton-sugar symporters in sugar import rather than export, possibly in support of high metabolic activity in arbuscules (Harrison 1996).

AM fungi deliver both P and N to the root through arbuscules. Previously MtPT4, a *Medicago truncatula* phosphate transporter located in the periarbuscular membrane that is essential for symbiotic P transport and for maintenance, was identified (Javot et al. 2011). In mtpt4 mutants arbuscule degeneration occurs prematurely and symbiosis fails (Javot et al. 2011). The MtPT4 arbuscule phenotype is strongly correlated with shoot N levels. On the other, the transport mechanism of sugars to the apoplast is passive movement. For example, when hexose reached in the apoplast is absorbed by the fungus via specific transport proteins. The characterisation of the GpMST1 hexose transporter from *Geosiphon pyriformis*, a Glomeromycotan fungus, provides a promising direction for further investigation (Schussler et al. 2006). In the intraradical hyphae, much of the C is changed to storage lipids, predominantly as triacylglycerides. Lipids not only act as storage C but also are the main form of C translocated from intra- to extraradical hyphae where they provide the major respiratory substrate.

AM fungi provide benefits to their plant hosts by enhancing mineral nutrition, increasing tolerance to water stress, inducing greater resistance to pathogens and reduce sensitivity to toxic substances present in the soil. However, the cost of colonisation can be ~20 % of the host's fixed C being consumed by the microbial symbiont. Nonetheless, under experimental conditions when nutrients are limiting, mycorrhizal crop plants typically exhibit a better performance over non-mycorrhizal plants in high-input agricultural systems, the relative advantages are reduced while the C costs remain same and the performance of colonised plants can fall below that of non-colonised plants (Janos 2007). Phillips et al. (2013) proposed a framework for considering how tree species and their mycorrhizal symbionts differentially couple C and nutrient cycles in temperate forests. Given that tree species predominantly colonise by a single type of AM fungi or ECM fungi and that the two types of fungi differ in their modes of nutrient acquisition, the abundance of AM and ECM trees in a paddock may provide an integrated index of biogeochemical transformations relevant to C cycling and nutrient retention.

AM fungi can obtain the photosynthates from host plants and can promote N uptake by host plants via the absorption of various N sources by mycorrhizal hyphae leading to improvement in nutrition and stress tolerance of host plants (Li et al. 2013). The symbiont absorbs and transfers N, but the mechanisms behind the N metabolism and translocation from AM fungi to host plants are still in debate.

The roles of AM fungi in N allocation in host plants and the ecological significance at community and ecosystem levels need to be studied in more detail because they vary widely (Hodge and Storer 2014).

1.4 Role of AM Fungi in Sustainable Agriculture

Sustainable agricultural systems use natural processes to achieve satisfactory levels of productivity and food quality while decreasing fertiliser use, dropping input costs and preclude environmental pollution and its impacts (Siddiqui et al. 2008; Harrier and Watson 2004). It should also be ecologically feasible and socially responsible. Several soil factors contribute to sustainable agriculture through control of soil-borne diseases and increased soil microbial activity leading to increased antagonism and parasitism within the rhizosphere level (Jawson et al. 1993; Knudsen et al. 1995). Research approaches are presently focused on the search for suitable alternatives to the use of commercial artificial pesticides. However, progress has also been accomplished in exploring the use of microorganisms for improvement of soil fertility and ultimately increased crop productivity. Greater emphasis is being placed on enhancing exploitation of indigenous soil microbes which will contribute to soil fertility and increase plant growth as well as plant protection.

AM fungi have been difficult to study (Hamel and Strullu 2006), but they are now recognised as key components of soil ecosystems rather than only a plant root component. Recent advances in knowledge conveyed by new techniques for soil microbiology research open the way to AM fungi management in crop nutrition and production. AM fungi can influence crop growth, nutrition and production even in phosphorus-rich soils (Balzergue et al. 2013; Solaiman and Hirata 1997). However, growing crops in soil with lower levels of fertility could enhance the multiple beneficial effects of AM fungi in agroecosystem including decreased nutrient loss to the environment. Inclusion of mycorrhizal bioassays in soil testing protocol (Djuuna et al. 2009) for use in fertilisation recommendations and development of improved inoculants to manipulate AM fungi (Abbott et al. 1987) and screening of crop cultivars with improved symbiotic abilities (Smith et al. 1992) could contribute to agroecosystem stability and sustainability (Hamel and Strullu 2006).

In agriculture, several factors influence plant response and plant benefits from mycorrhizas such as host crop dependency on mycorrhizal colonisation, tillage, fertiliser application and the potential of mycorrhizal fungi inocula. Interest in AM fungal inoculation for sustainable agriculture is based on their roles in the improvement of plant growth through nutrient and water uptake (Augé 2004) and improvements in soil fertility as well as soil aggregate stability (Rillig et al. 2007; Rillig 2004).

1.5 Role of AM and ECM Fungi in Protection of Soil-Borne Diseases

Biological control of soil-borne diseases is currently accepted as a key practice in sustainable agriculture. AM fungi have shown potential in protecting host plants from soil-borne pathogens. While few AM isolates have been tested against these soil-borne pathogens, some appear to be more effective than others (Cameron et al. 2013; Azćon-Aguilar and Barea 1996). The degree of protection varies with the pathogen species involved and can be moderated by soil and other microclimatic conditions of the rhizosphere. Only weak responses to AM fungi colonisation have been found in some activities like lignification, production of phytoalexins and peroxidises and expression of genes encoding for PR proteins, indicating that AM fungi do not elicit typical defence responses (Azćon-Aguilar and Barea 1996). However, these compounds could make roots sensitive to the presence of pathogens and enhance defence mechanisms to subsequent pathogen infection (Benhamou et al. 1994). In this study, responses of AM and non-mycorrhizal transformed carrot roots to infection by *Fusarium oxysporum* f. sp. *Chrysanthemi* were investigated in mycorrhizal roots; the growth of the pathogen was usually restricted to the epidermis and cortical tissues, whereas in non-mycorrhizal roots the infection of pathogen reached at depth even up to the vascular stele. The *Fusarium* hyphae inside mycorrhizal roots exhibited a high level of structural disorganisation, probably induced by a strong reaction of the host cells characterised by the accumulation of phenolic-like compounds and the production of hydrolytic enzymes such as chitinases. This strong reaction was not induced by non-mycorrhizal roots, suggesting that the activation of plant defence responses by mycorrhiza formation provides a protection at a certain level against the pathogen. In contrast to the weak defence response towards AM fungi found in AM hosts, it is noteworthy that in myc$^-$ pea mutants, AM fungi trigger a strong resistance reaction. This suggests that the AM fungi are able to elicit a defence response but that symbiosis-specific genes have mechanism to control the expression of the genes related to plant defence during AM establishment (Gianinazzi-Pearson et al. 1996). The expression of several PRs in tobacco plants did not affect the level of colonisation by *Glomus mosseae* which was only reduced in plants constitutively expressing an acidic isoform of tobacco PR-2, a glucanase (Vierheilig et al. 1996).

Ectomycorrhizas (ECM) have a positive effect on the performance of seedlings due to the beneficial relationship between plants and mycorrhizal fungi (Guerin-Laguette et al. 2004; Machón et al. 2006; Minchin et al. 2012). They are also effective against various plant root rot diseases (Duchesne 2000). Many studies have observed the protective role of ECM not only against fungal pathogens (Morin et al. 1999) but also against nematodes (Machón et al. 2006). Pine wilt disease is a globally severe forest disease and demonstrates the importance of ECM relationships (Akema and Futai 2005). In this study, the abundant ECM found in the upper slope enhanced water uptake by the pines, mitigated drought stress and thereby decreased the mortality of pine trees from pine wilt disease.

1.6 Role of AM and ECM Fungi in Restoration of Native Forest Ecosystems

Land clearing of terrestrial ecosystems claims several million hectares annually in Australia (Warren et al. 1996) which causes loss of essential physicochemical and biological soil properties (Skujins and Allen 1986). These properties largely determine soil quality and fertility that supports plant establishment and productivity. Soil degradation limits the potential for restoration of native plants (Agnew and Warren 1996), and erosion and desertification are accelerated. Desertification reduces the inoculum potential of mutualistic symbionts such as AM fungi that are key ecological factors in governing the cycles of major plant nutrients and hence in sustaining vegetative covers in natural habitats.

AM fungi improve the ability of plants to establish and cope in stressful conditions including nutrient deficiency, drought and soil disturbance (Schreiner et al. 1997). The fungal hyphae contribute to the formation of water-stable aggregates necessary for good soil tilth (Jeffries and Barea 2000). Loss of mycorrhizal propagules from degraded ecosystems can overcome either by natural or artificial revegetation where an increase of inoculum may be needed in these ecosystems (Requena et al. 1996). Inoculation of plants with mycorrhizal fungi in revegetation schemes should not only help plant establishment (Herrera et al. 1993) but also improve soil biological, chemical and physical properties thus contributing to soil quality (Carrillo-García et al. 1999). The introduction of a plant species along with a known AM fungus is a successful biotechnological tool to aid the recovery of desertified ecosystems (Azćon-Aguilar et al. 2003).

Many forest trees are dependent on a symbiotic association of their roots with ECM fungi and mobilise minerals from soil and transfer them to the plant. In exchange the trees deliver assimilated C to the fungi. The hyphae of ECM fungi are the source of C to soil microbes and depend on their tree hosts for their energy needs. In return, they take up P, N, S and Zn from soil and translocate them to their host and greatly extend the functional root system of the host plants (Allen 1991). An ECM fungus can connect roots of several trees by fungal hyphae network. Most ECM fungi are basidiomycetes such as *Amanita*, *Cortinarius*, *Lactarius*, *Russula* and *Suillus*, among the best-known ECM genera (Hacskaylo 1972). ECM are widespread particularly in temperate regions where many of the ecologically important tree species involve such as species of *Abies*, *Betula, Fagus, Picea*, *Pinus*, *Pseudotsuga*, *Quercus* and *Salix*.

Below-ground biodiversity is essential for the maintenance of forest growth and ecosystem functions as well as for reforestation of disturbed lands due to mining activities. ECM fungi are economically symbiotic soil fungi forming a sheath around the root tip and form a special structure called Hartig net (Smith and Read 2008). They gain C from the tree and in return support the tree in taking up nutrients, water and metabolites. The fungus also protects plants from parasites, nematodes and soil pathogens. The importance of ECM in forest plantations has received much attention when it was observed that trees often fail to establish at

new sites if the ECM symbiont was absent (Menkis et al. 2012). This effect has been found in exotic pine transplantation in different parts of the world. In Western Australia, *Pinus radiata* and *P. pinaster* failed to establish in nursery beds in the absence of ECM fungi (Lakhanpal 2000). Pine seedlings are known to be tolerant to environmental stresses such as acid mist when colonised with ECM fungi (Asai and Futai 2001). Tropical rainforests harbour the highest known tree diversity on the planet, and many ecological studies have attempted to explain the familiar symbiotic association of so many co-occurring species (Leigh et al. 2004; Valencia et al. 1994).

1.7 Conclusions

Mycorrhizal fungi are well known to have a wide range of benefits to their host plants. They can enhance nutrient uptake especially P, N and Zn. They can also suppress soil pathogens, enhance tolerance to drought stress and reduce sensitivity to toxic substances contaminated to the soil. The suitability of conditions needs to be managed for indigenous fungi to colonise hosts in their natural habitat or to minimise loss of these fungi with high-input farming/disturbance. Highly mycorrhizal host crop cultivars should be selected for use in crop rotations. Conventional plant breeding in soils with high nutrient contents may select against the most efficient fungal communities or even against the mycorrhizal association. Many efforts have been made in recent years to get benefits from mycorrhizas for agriculture, horticulture, forestry, land restoration and contaminated site remediation. The results have generally been consistently positive under controlled conditions, with some difficulties due to complications from diverse variables under field conditions. Mycorrhizal interactions between plants, fungi and the environment are complex and often indivisible. Mycorrhizas are an essential below-ground component in the establishment and sustainability of plant communities, but thorough knowledge is required to achieve maximum benefits from these microorganisms and their associations.

References

Abbott LK, Gazey C (1994) An ecological view of the formation of VA mycorrhizas. Plant Soil 159:69–78

Abbott LK, Robson AD, Gazey C (1987) Selection of inoculant VA mycorrhizal fungi. In: Sylvia DM, Hung LL, Graham JH (eds) Mycorrhizas in the next decade, practical applications and research priorities. Abstract. Proceedings of the 7th North American Conference on Mycorrhizas, pp 10–12. Institute of Food and Agricultural Sciences, University of Florida

Agnew C, Warren A (1996) A framework for tackling drought and land degradation. J Arid Environ 33:309–320

Akema T, Futai K (2005) Ectomycorrhizal development in a *Pinus thunbergii* stand in relation to location on a slope and effect on tree mortality from pine wilt disease. J For Res 10:93–99

Allen MF (1991) The ecology of mycorrhiza. Cambridge University Press, Cambridge, p 184. Chapman and Hall, New York, NY, p 534

Asai E, Futai K (2001) Retardation of pine wilt disease symptom development in Japanese black pine seedlings exposed to simulated acid rain and inoculated with *Bursaphelenchus xylophilus*. J For Res 6:297–302

Augé RM (2004) Arbuscular mycorrhizae and soil/plant water relations. Can J Soil Sci 84:373–381

Azćon-Aguilar C, Barea JM (1996) Arbuscular mycorrhizas and biological control of soil-borne plant pathogens – an overview of the mechanisms involved. Mycorrhiza 6:457–464

Azćon-Aguilar C, Palenzuela J, Roldan A, Bautista S, Vallejo R, Barea JM (2003) Analysis of the mycorrhizal potential in the rhizosphere of representative plant species from desertification-threatened Mediterranean shrublands. Appl Soil Ecol 22:29–37

Balestrini R, Bonfante P (2005) The interface compartment in arbuscular mycorrhizae: a special type of plant cell wall? Plant Biosyst 139:8–15

Balzergue C, Chabaud M, Barker DG, Becard G, Rochange SF (2013) High phosphate reduces host ability to develop arbuscular mycorrhizal symbiosis without affecting root calcium spiking responses to the fungus. Front Plant Sci 4, article no 426. doi: 10.3389/fpls.2013.00426

Bedini S, Avio L, Sbrana C, Turrini A, Migliorini P, Vazzana C, Giovannetti M (2013) Mycorrhizal activity and diversity in a long-term organic Mediterranean agroecosystem. Biol Fertil Soils 49:781–790

Benhamou N, Fortin JA, Hamel C, St-Arnaud M, Shatilla A (1994) Resistance responses of mycorrhizal Ri T-DNA-transformed carrot roots to infection by *Fusarium oxysporum* f. sp. *chrysanthemi*. Phytopathology 84:958–968

Brito I, Carvalho M, Goss MJ (2013) Soil and weed management for enhancing arbuscular mycorrhiza colonization of wheat. Soil Use Manage 29:540–546

Brundrett MC (2002) Coevolution of roots and mycorrhizas of land plants. New Phytol 154:275–304

Brundrett MC, Nanjappa A (2013) Glomeromycotan mycorrhizal fungi from tropical Australia III. Measuring diversity in natural and disturbed habitats. Plant Soil 370:419–433

Bucher M (2007) Functional biology of plant phosphate uptake at root and mycorrhiza interfaces. New Phytol 173:11–26

Cameron DD, Neal AL, van Wees SCM, Ton J (2013) Mycorrhiza-induced resistance: more than the sum of its parts? Trends Plant Sci 18:539–545

Carrillo-García A, Leon de la Luz JL, Bashan Y, Bethlenfalvay GJ (1999) Nurse plants, mycorrhizae, and plant establishment in a disturbed area of the Sonoran Desert. Restor Ecol 7:321–335

Chalot M, Blaudez D, Brun A (2006) Ammonia: a candidate for nitrogen transfer at the mycorrhizal interface. Trend Plant Sci 11:263–266

Cooper KM, Tinker PB (1981) Translocation and transfer of nutrients in vesicular arbuscular mycorrhizas. IV. Effect of environmental variables on movement of phosphorus. New Phytol 88:327–339

Cox G, Sanders FE, Tinker PB, Wild JA (1975) Ultrastructure evidence relating to host/endophyte transfer in a vesicular–arbuscular mycorrhizae. In: Sanders FE, Mosse B, Tinker PB (eds) Endomycorrhizae. Academic Press, London, pp 297–312

Daniell TJ, Husband R, Fitter AH, Young JPW (2001) Molecular diversity of arbuscular mycorrhizal fungi colonising arable crops. FEMS Microbiol Ecol 36:203–209

Djuuna IAF, Abbott LK, Solaiman MZ (2009) Use of mycorrhiza bioassays in ecological studies. In: Varma A, Kharkwal AC (eds) Symbiotic fungi, vol 18, Soil Biology. Springer, Berlin

Duchesne LC (2000) Role of ectomycorrhizal fungi in biocontrol. In: Pfleger FL, Linderman RG (eds) Mycorrhiza and plant health. APS Press, St Paul, MN, pp 27–46

Ellerbeck M, Schüßler A, Brucker D, Dafinger C, Loos F, Brachmann A (2013) Characterization of three ammonium transporters of the Glomeromycotan fungus Geosiphon pyriformis. Eukaryot Cell 12:1554–1562

Gamper HA, Young JPW, Jones DL, Hodge A (2008) Real-time PCR and microscopy: are the two methods measuring the same unit of arbuscular mycorrhizal fungal abundance? Fungal Genet Biol 45:581–596

Gianinazzi-Pearson V, Dumas-Gaudot E, Gollotte A, Tahiri-Alaoui A, Gianinazzi S (1996) Cellular and molecular defence related root responses to invasion by arbuscular mycorrhizal fungi. New Phytol 133:45–57

Gollotte A, van Tuinen D, Atkinson D (2004) Diversity of arbuscular mycorrhizal fungi colonising roots of the grass species Agrostis capillaris and Lolium perenne in a field experiment. Mycorrhiza 14:111–117

Govindarajulu M, Pfeffer P, Jin H, Abubaker J, Douds DD, Allen JW, Bücking H, Lammers PJ, Shachar-Hill Y (2005) Nitrogen transfer in the arbuscular mycorrhizal symbiosis. Nature 435:819–823

Guerin-Laguette A, Shindo K, Matsushita N, Suzuki K, Lapeyrie F (2004) The mycorrhizal fungus Tricoloma matsutake stimulates *Pinus densiflora* seedling growth in vitro. Mycorrhiza 14:397–400

Hacskaylo E (1972) Mycorrhiza: the ultimate in reciprocal parasitism? BioSci 22:577–582

Hamel C, Strullu D-G (2006) Arbuscular mycorrhizal fungi in field crop production: potential and new direction. Can J Plant Sci 86:941–950

Harrier LA, Watson CA (2004) The potential role of arbuscular mycorrhizal (AM) fungi in the bioprotection of plants against soil-borne pathogens in organic and/or other sustainable farming systems. Pest Manag Sci 60:149–157

Harrison MJ (1996) A sugar transporter from Medicago truncatula: altered expression pattern in roots during vesicular-arbuscular (VA) mycorrhizal associations. Plant J 9:491–503

Harrison M (1999) Biotrophic interfaces and nutrient transport in plant/fungal interfaces. J Exp Bot 50:1013–1022

Harrison MJ, van Buuren ML (1995) A phosphate transporter from the mycorrhizal fungus *Glomus versiforme*. Nature 378:626–629

Harrison MJ, Dewbre GR, Liu J (2002) A phosphate transporter from *Medicago truncatula* involved in the acquisition of phosphate released by arbuscular mycorrhizal fungi. Plant Cell 14:2413–2429

Herrera MA, Salamanca CP, Barea JM (1993) Inoculation of woody legumes with selected arbuscular mycorrhizal fungi and rhizobia to recover desertified Mediterranean ecosystems. Appl Environ Microbiol 59:129–133

Hibbett DS, Gilbert LB, Donoghue MJ (2000) Evolutionary instability of ectomycorrhizal symbioses in basidiomycetes. Nature 407:506–508

Hodge A, Storer K (2014) Arbuscular mycorrhiza and nitrogen: implications for individual plants through to ecosystems. Plant Soil. doi:10.1007/s11104-014-2162-1

Hodge A, Campbell CD, Fitter AH (2001) An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. Nature 413:297–299

Janos DP (2007) Plant responsiveness to mycorrhizas differs from dependence upon mycorrhizas. Mycorrhiza 17:75–91

Jansa J, Mozafar A, Kuhn G, Anken T, Ruh R, Sanders IR, Frossard E (2003) Soil tillage affects the community structure of mycorrhizal fungi in maize roots. Ecol Appl 13:1164–1176

Javot H, Penmetsa RV, Terzaghi N, Cook DR, Harrison MJ (2007a) A *Medicago truncatula* phosphate transporter indispensable for the arbuscular mycorrhizal symbiosis. Proc Natl Acad Sci U S A 104:1720–1725

Javot H, Pumplin N, Harrison MJ (2007b) Phosphate in the arbuscular mycorrhizal symbiosis: transport properties and regulatory roles. Plant Cell Environ 30:310–322

Javot H, Penmetsa RV, Breuillin F, Bhattarai KK, Noar RD, Gomez SK, Zhang Q, Cook DR, Harrison MJ (2011) Medicago truncatula mtpt4 mutants reveal a role for nitrogen in the regulation of arbuscule degeneration in arbuscular mycorrhizal symbiosis. Plant J 68:954–965

Jawson MD, Franzlubbers AJ, Galusha DK, Aiken RM (1993) Soil fumigation within monoculture and rotations—response of corn and mycorrhizae. Agron J 85:1174–1180

Jeffries P, Barea JM (2000) Arbuscular mycorrhiza—a key component of sustainable plant-soil ecosystems. In: Hock B (ed) The mycota. IX. Fungal associations. Springer KG, Berlin, pp 95–113

Kjøller R, Rosendah S (2001) Molecular diversity of glomalean (arbuscular mycorrhizal) fungi determined as distinct *Glomus* specific DNA sequences from roots of field grown peas. Mycol Res 105:127–132

Knudsen IMB, Debosz K, Hockenhull J, Jensen DF, Elmholt S (1995) Suppressiveness of organically and conventionally managed soils towards brown foot rot of barley. Appl Soil Ecol 12:61–72

Kohout P, Sudová R, Janousková M, Ctvrtlíková M, Hejda M, Pánková H, Slavíková R, Stajerová K, Vosátka M, Sýkorová Z (2014) Comparison of commonly used primer sets for evaluating arbuscular mycorrhizal fungal communities: is there a universal solution? Soil Biol Biochem 68:482–493

Lakhanpal TN (2000) Ectomycorrhiza – an overview. In: Mukerji KG, Chamola BP, Singh J (eds) Mycorrhizal biology. Kluwer Academic/Plenum, New York, NY, pp 101–118

Leigh EG, Davidar P, Dick CW, Puyravaud J, Terborgh J, ter Steege H, Wright SJ (2004) Why do some tropical forests have so many species of trees? Biotropica 36:445–473

Li YJ, Liu ZL, He XY, Tian CJ (2013) Nitrogen metabolism and translocation in arbuscular mycorrhizal symbiote and its ecological implications. J Appl Ecol 24:861–868

Liu RJ, Jiao H, Li Y, Li M, Zhu X-C (2009) Research advances in species diversity of arbuscular mycorrhizal fungi. J Appl Ecol 20:2301–2307

Lopez-Pedrosa A, Gonzalez-Guerrero M, Valderas A, Azcon-Aguilar C, Ferrol N (2006) GintAMT1 encodes a functional high-affinity ammonium transporter that is expressed in the extraradical mycelium of *Glomus intraradices*. Fungal Genet Biol 43:102–110

Machón P, Santamaria O, Pajares JA, Alves-Santos FM, Diez JJ (2006) Influence of the mycorrhizal fungus *Laccaria laccaria* on pre-emergence, post-emergence and the late damping-off by *Fusarium moniliforme* and *F. oxysporum* on Scots pine seedlings. Symbiosis 42:153–160

Manoharachary C, Kunwar IK, Tilak KVBR, Adholeya A (2010) Arbuscular mycorrhizal fungi – taxonomy, diversity, conservation and multiplication. Proc Natl Acad Sci Ind Sect B Biol Sci 80:1–13

McNear DH Jr (2013) The rhizosphere – roots, soil and everything in between. Nat Educ Knowl 4 (3):1

Menkis A, Lygis V, Burokiene D, Vasaitis R (2012) Establishment of ecto-mycorrhiza inoculated Pinus sylvestris seedlings on coastal dunes following a forest fire. Baltic Forestry 18:33–40

Minchin RF, Ridgway HJ, Condron L, Jones EE (2012) Influence of inoculation with a Trichoderma bio-inoculant on ectomycorrhizal colonisation of *Pinus radiata* seedlings. Ann Appl Biol 161:57–67

Morin C, Samson J, Dessureault M (1999) Protection of black spruce seedlings against Cylindrocladium root rot with ectomycorrhizal fungi. Can J Bot 77:169–174

Morton JB, Redecker D (2001) Two new families of Glomales, Archaeosporaceae and Paraglomaceae, with two new genera Archaeospora and Paraglomus, based on concordant molecular and morphological characters. Mycologia 93:181–195

Oehl F, Sieverding E, Javier P, Kurt I, da Silva GA (2011) Advances in *Glomeromycota* taxonomy and classification. IMA Fungus 2:191–199

Olsson PA, Rahm J, Aliasgharzad N (2010) Carbon dynamics in mycorrhizal symbioses is linked to carbon costs and phosphorus benefits. FEMS Microbiol Ecol 72:125–131

Opik M, Vanatoa A, Vanatoa E, Moora M, Davison J, Kalwij JM, Reier U, Zobel M (2010) The online database MaarjAM reveals global and ecosystemic distribution patterns in arbuscular mycorrhizal fungi (Glomeromycota). New Phytol 188:223–241

Pellegrino E, Bedini S (2014) Enhancing ecosystem services in sustainable agriculture: biofertilization and biofortification of chickpea (*Cicer arietinum* L.) by arbuscular mycorrhizal fungi. Soil Biol Biochem 68:429–439

Phillips RP, Brzostek E, Midgley M (2013) The mycorrhizal-associated nutrient economy: a new framework for predicting carbon-nutrient couplings in temperate forests. New Phytol 199:41–51

Redecker D (2002) Molecular identification and phylogeny of arbuscular mycorrhizal fungi. Plant Soil 244:67–73

Redecker D, Morton JB, Bruns TD (2000) Ancestral lineages of arbuscular mycorrhizal fungi (*Glomales*). Mol Phylogen Evol 14:276–284

Renker C, Heinrichs J, Kaldorf M, Buscot F (2003) Combining nested PCR and restriction digest of the internal transcribed spacer region to characterize arbuscular mycorrhizal fungi on roots from the field. Mycorrhiza 13:191–198

Requena N, Jeffries P, Barea JM (1996) Assessment of natural mycorrhizal potential in a desertified semiarid ecosystem. Appl Environ Microbiol 62:842–847

Rillig MC (2004) Arbuscular mycorrhizae, glomalin, and soil aggregation. Can J Soil Sci 84:355–363

Rillig MC, Caldwell BA, Wosten HAB, Sollins P (2007) Role of protein in soil carbon and nitrogen storage: controls on persistence. Biogeochemistry 85:25–44

Rosendahl S (2008) Communities, populations and individuals of arbuscular mycorrhizal fungi. New Phytol 178:253–266

Saito M (2000) Symbiotic exchange of nutrients in arbuscular mycorrhizas: transport and transfer of phosphorus. In: Douds DD, Kapunik Y (eds) Arbuscular mycorrhizas: physiology and function. Kluwer, Dordrecht, The Netherlands, pp 85–106

Saks Ü, Davison J, Öpik M, Vasar M, Moora M, Zobel M (2013) Root-colonizing and soil-borne communities of arbuscular mycorrhizal fungi in a temperate forest understorey. Botany 92:277–285

Sanders IR, Alt M, Groppe K, Boller T, Wiemken A (1995) Identification of ribosomal DNA polymorphisms among and within spores of the Glomales – application to studies on the genetic diversity of arbuscular mycorrhizal fungal communities. New Phytol 130:419–427

Schreiner RP, Milhara KL, McDaniel H, Bethlenfalvay GJ (1997) Mycorrhizal fungi influence plant and soil functions and interactions. Plant Soil 188:199–209

Schüßler A, Schwarzott D, Walker C (2001) A new fungal phylum, the Glomeromycota: phylogeny and evolution. Mycol Res 105:1413–1421

Schussler A, Martin H, Cohen D, Fitz M, Wipf D (2006) Characterization of a carbohydrate transporter from symbiotic glomeromycotan fungi. Nature 444:933–936

Schwarzott D, Walker C, Schussler A (2001) Glomus, the largest genus of the arbuscular mycorrhizal fungi (Glomales), is nonmonophyletic. Mol Phylogenet Evol 21:190–197

Siddiqui ZA, Akhter MS, Futai K (eds) (2008) Mycorrhizae: sustainable agriculture and forestry. Springer Science + Business Media B.V., 365 pp

Skujins J, Allen MF (1986) Use of mycorrhizae for land rehabilitation. MIRCEN J 2:161–176

Smith SE, Read DJ (2008) Mycorrhizal symbiosis. Academic Press, London, 800 pp

Smith SE, Smith FA (2012) Fresh perspectives on the roles of arbuscular mycorrhizal fungi in plant nutrition and growth. Mycologia 104:1–13

Smith SE, Robson AD, Abbott LK (1992) The involvement of mycorrhizas of genetically-dependent efficiency of nutrient uptake and use. Plant Soil 146:169–179

Solaiman ZM, Abbott LK (2003) Phosphorus uptake by a community of arbuscular mycorrhizal fungi in jarrah forest. Plant Soil 248:313–320

Solaiman ZM, Abbott LK (2008) Influence of arbuscular mycorrhizal fungi, inoculum level and phosphorus placement on growth and phosphorus uptake of *Phyllanthus calycinus* in jarrah forest soil. Biol Fertil Soils 44:815–821
Solaiman ZM, Hirata H (1997) Effect of arbuscular mycorrhizal fungi inoculation of rice seedlings at the nursery stage upon performance in the paddy field and greenhouse. Plant Soil 191:1–12
Solaiman ZM, Saito M (2001) Phosphate efflux from intraradical hyphae of Gigaspora margarita in vitro and its implication for phosphorus. New Phytol 151:525–533
Solaiman ZM, Saito M (1997) Use of sugars by intraradical hyphae of arbuscular mycorrhizal fungi revealed by radiorespirometry. New Phytol 136:533–538
Solaiman ZM, Ezawa T, Kojima T, Saito M (1999) Polyphosphates in intraradical and extraradical hyphae of arbuscular mycorrhizal fungi. Appl Environ Microbiol 65:5604–5606
Stürmer SL (2012) A history of the taxonomy and systematics of arbuscular mycorrhizal fungi belonging to the phylum Glomeromycota. Mycorrhiza 22:247–258
Tinker PB (1975) Effects of vesicular–arbuscular mycorrhizas on higher plants. Symp Soc Exp Biol 29:325–350
Uehlein N, Fileschi K, Eckert M, Bienert GP, Bertl A, Kaldenhoff R (2007) Arbuscular mycorrhizal symbiosis and plant aquaporin expression. Phytochemistry 68:122–129
Valencia RH, Balslev H, Paz H, Mino CG (1994) High tree alpha-diversity in Amazonian Ecuador. Biodiv Conserv 3:21–28
Vandenkoornhuyse P, Ridgway KP, Watson IJ, Fitter AH, Young JPW (2003) Co-existing grass species have distinctive arbuscular mycorrhizal communities. Mol Ecol 12:3085–3095
Vierheilig H, Alt M, Gut-Rella M, Lange J, Boller T, Wiemken A (1996) Colonization of tobacco constitutively expressing pathogenesis-related proteins by arbuscular mycorrhizal fungi. In: Azcón-Aguilar C, Barea JM (eds) Mycorrhizas in integrated systems: from genes to plant development. European Commission, EUR 16728, Luxembourg, pp 270–273
Warren A, Sud YC, Rozanov B (1996) The future of deserts. J Arid Environ 32:75–89
Willis A, Rodrigues BF, Harris PJC (2013) The ecology of arbuscular mycorrhizal fungi. Crit Rev Plant Sci 32:1–20