Insight into the Role of Arbuscular Mycorrhizal Fungi in Sustainable Agriculture

P. Priyadharsini and T. Muthukumar

Abstract

Sustainable agriculture plays a vital role in agroecosystems and reduces adverse effects on the environment by utilizing the various natural processes. Optimum soil fertility is an essential goal to be achieved in sustainable agriculture system. The presence of beneficial microorganisms in the rhizospheric region and their activities are the main focal point which makes dynamic resources available to plants and conserve soil fertility. Majority of the agricultural and horticultural crops are associated with common soil fungi, the arbuscular mycorrhizal (AM) fungi. These fungi are crucial for plant health and fitness as they increase the efficiencies of the plant root systems. The hyphae of these fungi originating from roots grow into the soil and absorb nutrients especially phosphorus and deliver it to the roots. They also play a crucial role in imparting tolerance to plants against various stresses as well as modifying soil structure. Nevertheless, several agricultural practices involved in crop production can influence both AM formation and function. Consequently, AM fungal introductions or changes in crop management practices that enhance the proliferation, diversity and function of native AM fungi become essential. Optimization of agronomic practices that sustain maximum AM fungal presence and activity would enable to achieve increased plant production in sustainable agriculture.

Keywords

Sustainable agriculture • Arbuscular mycorrhizal fungi • Nutrients • Stress tolerance • Inoculum production

1 Introduction

In spite of the universal escalation of agriculture and tremendous growth in the major crop productivity over the last decades, the eradication of

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hunger facing mankind is far from being realized (FAO 2004). Factors that deter maximum crop productivity include several abiotic and biotic stresses like unfavourable climate, drought, diseases and pests. Recently, increased crop productivity has been achieved through crop breeding along with huge input of chemicals in the form of fertilizers and biocides. These chemicals not only disturb agricultural ecosystems but are also detrimental to the environment (Chapin et al. 2000; Barabasz et al. 2002; Parmesan and Yohe 2003; Zhong and Cai 2007). The tolerance of crops to various abiotic and biotic stresses can also be evolved through the exploitation of the worldwide abundant endophytic associations, where microorganisms live in reciprocally beneficial relationship with plants.

Sustainable agriculture, by definition, is ecologically sound, economically viable, and socially responsible (Siddiqui and Pichtel 2008). Agroecosystems are characterized by major dependence on human interference and therefore are influenced by factors that extend into the system such as energy, agrochemicals and their residues (Odum 1984). In contrast to natural ecosystems, agroecosystems are created and controlled by humans through the management of ecological processes for production and conservation. Soil is the prime area for manipulation in agroecosystems, because it is a biologically dynamic resource. Within this soil, the rhizosphere is the locus of greater role of energy flow and mineral cycling among the physical, chemical and biological components; it can therefore be considered as a subsystem (Wright and Miller 1994).

Arbuscular mycorrhizal (AM) fungi are one of the imperative soil microorganisms that participate mainly in the plant uptake of nutrients, especially phosphorus (P) in diverse agroecosystems (Atkinson et al. 2002; Gadd 2005; Jansa et al. 2008). In addition, AM fungi can easily take up and translocate other macronutrients and several micronutrients to plants (Ortas and Akpinar 2006; Abo-Rekab et al. 2010). Hence, AM fungi are recipients of worldwide attention as they play an important role in sustaining an active and diverse biological community essential for increasing the sustainability of agricultural systems (Gianinazzi and Schüepp 1994). Arbuscular mycorrhizal fungi constitute around 50 % of soil microbial biomass in agricultural soils due to their profuse growth and abundance (Olsson et al. 1999). Most of the major crops are capable of forming AM associations naturally and are the most common mycorrhizal type involved in agricultural systems (Barea et al. 1993). As AM fungal association can improve plant growth and health, there is an increasing interest in ascertaining their effectiveness in plant production systems and, consequently, in manipulating them when feasible, so that they could be successfully incorporated into plant production systems.

The aim of this review is to discuss the developments and to provide insights regarding the potentials of AM fungi in agricultural systems. Given the overview of beneficial effects of AM association on plant growth and health, it is expected that the development of appropriate management practices that enable the proliferation of AM fungi would reduce the chemical inputs (fertilizers and biocides) in the upcoming years, a key aspect of sustainable agriculture.

2 General Aspects

The obligate endosymbiont, ‘AM fungi’ associating with more than 90 % of terrestrial plants (Graham 2008), belongs to the phylum Glomeromycota and acts as a bridge between soil and plants. Arbuscular mycorrhizal fungal hyphae are coenocytic and aseptate and reproduce asexually by spores (Kuhn et al. 2001). Formerly called ‘vesicular–arbuscular mycorrhiza’ or ‘VAM’, the name implies to the production of special structures, i.e. arbuscules and vesicles (Fig. 1), within the host roots. However, the lack of the production of vesicles within the host roots by certain genera belonging to the order Gigasporales (*Gigaspora*, *Scutellospora*) resulted in the modification of term to ‘arbuscular mycorrhiza’ or ‘AM’. At present, there are around 249 species in 17 genera of fungi involved in AM association (Schüβler and Walker 2010).

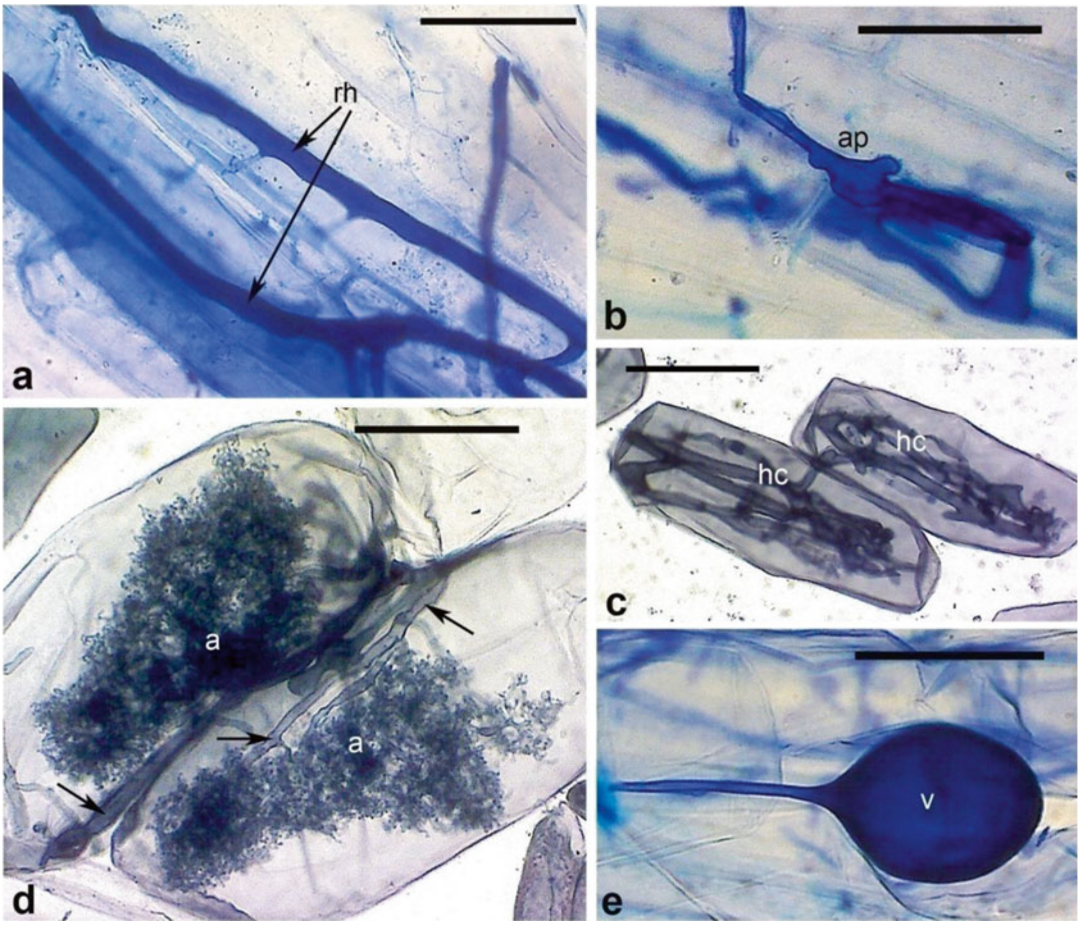

Fig. 1 (**a**–**e**) Arbuscular mycorrhizal colonization in crop plants. (**a**) Surface runner hyphae (rh) on root of *Allium cepa*. (**b**) Appressorium (ap) and hyphal entry in *Zea mays*. (**c**) Intracellular hyphal coils (hc) in *Capsicum annuum*. (**d**) Arbuscules (*a*) and arbuscular trunks (*black arrows*) in cortical cells of *A. cepa*. **e** Vesicle (*v*) in root of *Z. mays*. Scale bars = 50 µm

Like many host–microbe interactions, the colonization process begins with an exchange of signals between the two partners (host and the fungus), followed by the development of the symbiosis. The association is characterized by the adhesion and ingress of the fungus towards the host tissue. The host plant provides carbon source, the photosynthates to the fungus, whereas in turn, the extraradical hyphae of the fungus make available the soil nutrients that are not assessable to plant roots or to the host plant (Smith and Read 2008). The colonization of the root by an AM fungus begins with the fixation of the runner hyphae on the rhizoplane of a susceptible host through an appressorium (Fig. 1a, b). The AM fungal mycelium has dual phase: extraradical phase characterized by soil hyphae and intraradical phase characterized by exchange structures. The former is distinguished morphologically into two types: The first type is the runner hyphae (Fig. 1a) that actively transport nutrients and spread the hyphal network across the rhizospheric region extending the association to nearby plants (Smith and Read 2008; Neumann and George 2010). The second type is the finely branched fungal hyphae that play an important role in the uptake of nutrients from the soil. Intraradical phase consisting of intraradical hyphae, arbuscules and vesicles (Fig. 1c–e) plays an important role in nutrient exchange and uptake

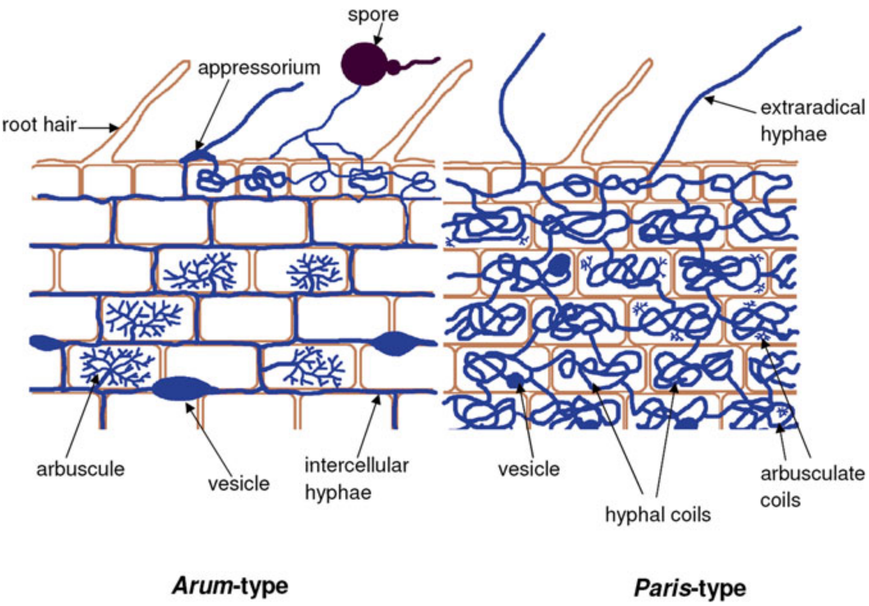

Fig. 2 Arbuscular mycorrhizal fungal structures showing *Arum*- and *Paris*-types

of carbon by the fungus. First, the AM hyphae receive suitable signals from host roots in the form of root exudates, and most specifically strigolactones (Akiyama et al. 2005; López-Ráez et al. 2008), which results in the branching of the hyphae. In response, the branched hyphae secrete a diffusible signal to the host roots, which initiates the expression of symbiotic-related genes (Kosuta et al. 2003). Based on the distribution of AM fungal structures within the roots, AM colonization patterns within host roots are divided into three types: *Arum*-, *Paris*- and intermediate-types (Dickson 2004).

In the *Arum*-type, the hyphae grow intercellularly in the root cortex and penetrate to form 'arbuscules' intracellularly, whereas in *Paris*-type association, intracellular hyphal coils frequently having intercalary arbuscules spread cell to cell in the cortex (Fig. 2). Intermediate-type AM exhibits characteristics of both *Arum*- and *Paris*-types. Most of the cultivated crops form *Arum* type, while *Paris*-type is common in plants of natural ecosystem (Ahulu et al. 2005).

Though most agricultural crops such as flax (*Linum usitatissimum*), corn (*Zea mays*), rice (*Oryza sativa*), sorghum (*Sorghum bicolor*), wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), potato (*Solanum tuberosum*), sugarcane (*Saccharum officinarum*), tomato (*Lycopersicon esculentum*) and sunflower (*Helianthus annuus*) can benefit from mycorrhizal association, certain crops belonging to Amaranthaceae, Brassicaceae and Chenopodiaceae do not form AM symbiosis (Brundrett 2009).

A wide range of AM fungi have been found to be associated with crop species (Fig. 3). In spite of the general assumption that the diversity of AM fungi is low in agricultural soils, several studies have reported high AM fungal diversity in agricultural soils (Jansa et al. 2002; Oehl et al. 2003, 2004; Ambili et al. 2012). Many studies on the diversity of AM fungi in agricultural soils have indicated the dominance of AM fungal communities by species belonging to the genus *Glomus* or the species that were once under *Glomus* (Jansa et al. 2002; Muthukumar and Udaiyan 2002; Sjoberg et al. 2004; Mathimaran et al. 2005). Nevertheless, spores of AM fungi belonging to *Acaulospora*, *Entrophospora*, *Gigaspora*, *Sclerocystis* and *Scutellospora* have also been reported along with *Glomus* in agricultural soils (Jansa et al. 2002; Muthukumar and Udaiyan 2002).

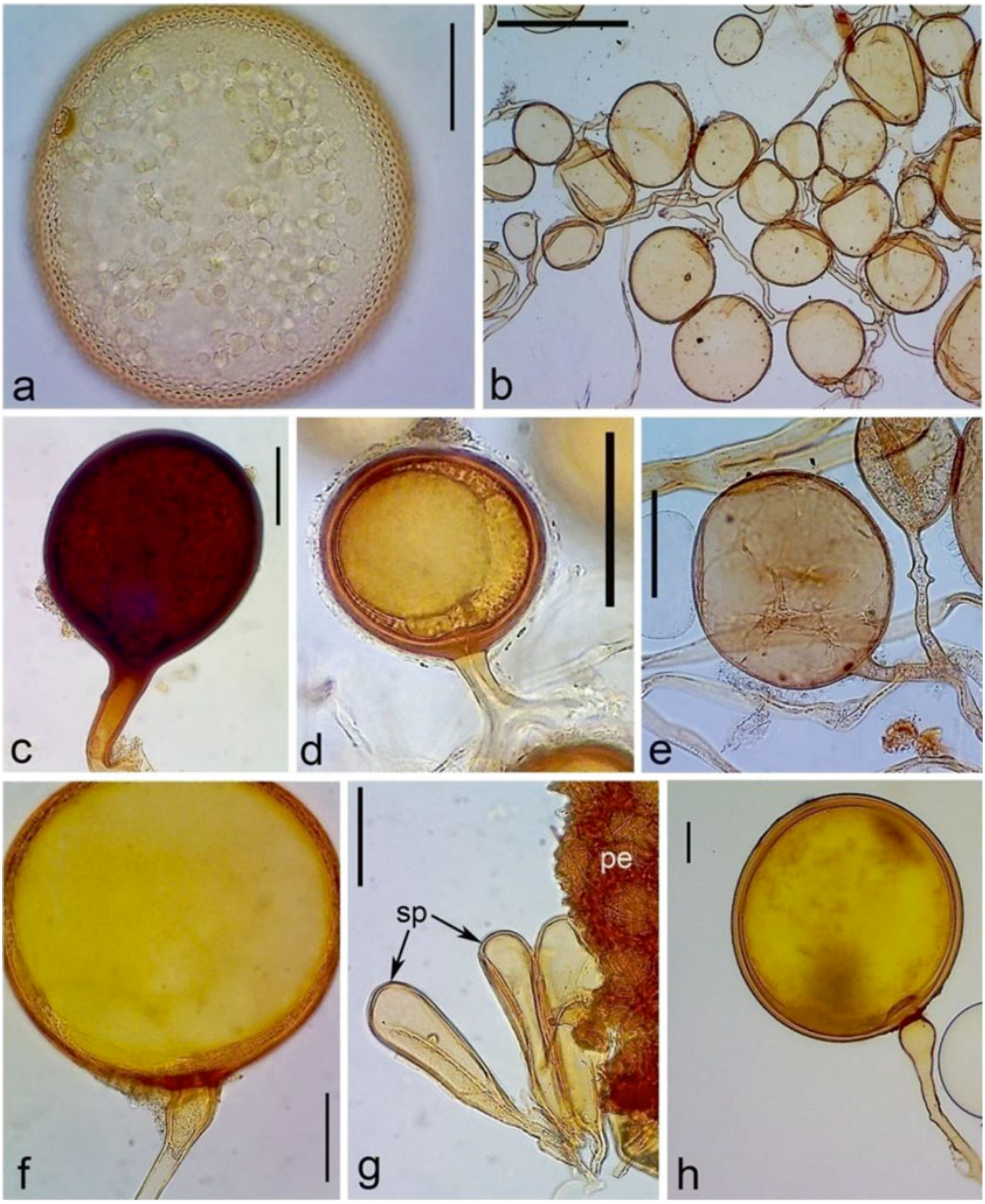

Fig. 3 (**a–h**) Spores of arbuscular mycorrhizal fungi associated with *Eleusine coracana*. (**a**) Spore of *Acaulospora scrobiculata*. (**b**) Loose cluster of *Glomus aggregatum*. (**c**) *Funneliformis geosporum*. (**d**) *Rhizophagus fasciculatus*. (**e**) *Rhizophagus intraradices*. (**f**) *Funneliformis mosseae*. (**g**) *Sclerocystis sinuosa* (*pe* peridium, *sp* spore). (**h**) *Scutellospora calospora*. Scale bars = 50 μm

3 Effects of AM Fungi

The major effects of AM association on host plants include enhanced uptake of low-mobile ions, nutrient cycling, rooting and plant establishment, plant tolerance to various biotic and abiotic stresses, improved soil quality and structure and enhanced plant community diversity. In agricultural ecosystems, AM fungi play a vital role in maintaining sustainability (Sanders 2004), by enhancing crop growth (Meir et al. 2010) and productivity (Lekberg and Koide 2005), soil constituents and fertility (Piotrowski et al. 2004; Li et al. 2007) and pathogen resistance (Sikes et al. 2009).

3.1 Improved Nutrient Uptake and Nutrient Cycling

Arbuscular mycorrhizal fungi improve plant uptake of nutrients by increasing the plant surface area of absorption. The narrow diameter of the absorbing hyphae allows more nutrients to be taken up from the soil solution. Generally, nutrient depletion zones develop around the root when the nutrients are removed from the soil solution by the plant roots (Fig. 4). For poorly mobile ions such as phosphate, a sharp and narrow depletion zone develops very close to the root. Hyphae of AM fungi can readily spread beyond this depletion zone and take up additional phosphate from the soil (Li et al. 1991) (Fig. 4). The uptake of other nutrients like N, K and micronutrients is also improved by AM fungi because many of these elements are also limited due to various reasons in the soil.

Two important factors that contribute to the effective uptake of nutrients by AM fungi from the soil are (i) the narrow diameter of the fungal hyphae and (ii) its longer lifespan relative to root and root hairs. As the diffusion gradient for a nutrient is inversely related to the radius of the absorbing unit, the soil solution should be less depleted at the surface of a narrow absorbing unit such as hyphae. Further, narrow hyphae can also grow into small soil pores that are not accessible to roots and root hairs (O'Keefe and Sylvia 1991). Therefore, crop species with well-developed root systems with fine roots or abundant root hairs like wheat, barley and oats (*Avena sativa*) remains little affected by AM colonization (Ryan and Graham 2002).

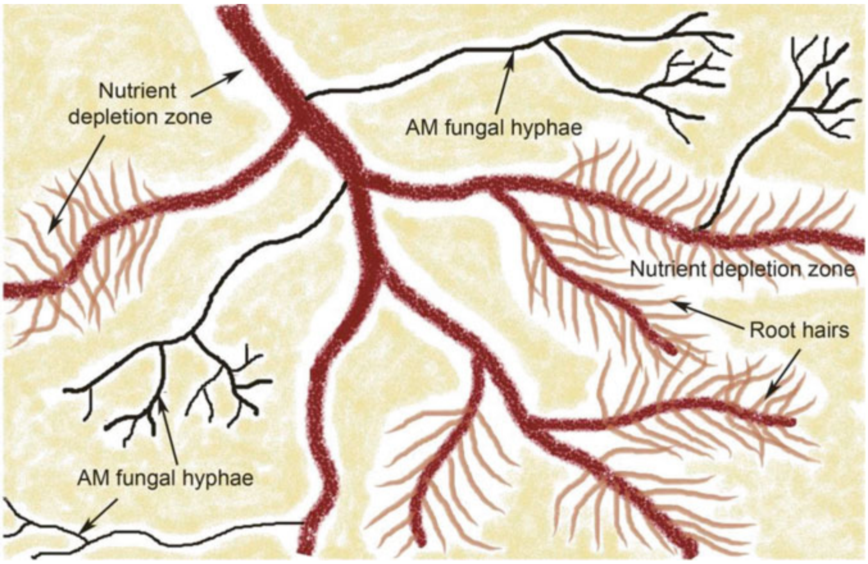

Fig. 4 Arbuscular mycorrhizal fungal hyphae and nutrient depletion zones around root

Arbuscular mycorrhizal fungi participate in N dynamics that relate in N cycling, plant growth and ecosystem functioning (Miransari 2011). The reduction of NO_3 is of environmentally significant concern. This has been accomplished with the presence of AM fungi (Hodge and Fitter 2010; Miransari and Mackenzie 2010), which absorb and transfer the N to the host under various conditions (Liu et al. 2007; Atul-Nayyar et al. 2009; Tian et al. 2010). Symbiotic N_2 fixation, the starting point in the N cycle, depends on an adequate and steady supply of P to the root and nodules (Barea et al. 1993). The AM fungi play an important role in enhancing growth, nodulation and N_2 fixation by legume crops symbiotic with nodulating bacteria. An increased N_2 fixation of mycorrhizal crop plants both under control (Kucey and Bonetti 1988; Barea et al. 1989a) and field conditions (Barea et al. 1989b; Shivaram et al. 1988) has been adequately demonstrated.

3.2 Plant Tolerance to Stresses

3.2.1 Abiotic Stresses

3.2.1.1 Water Relations

Water is an essential component for plant growth which is affected by global climatic change. Drought is one of the most important abiotic stresses that limit the crop growth and yield in agroecosystems in both arid and semiarid regions (Feng et al. 2002). The symbiotic association of plants with AM fungi has been shown to enhance plant tolerance to drought (Ruiz-Lozano et al. 2006; Boomsma and Vyn 2008). In arid regions, minimum moisture content in plants is balanced by an increased uptake of water by roots through AM fungal hyphae (Khan et al. 2003). Positive influence of AM fungi in improving plant water use efficiency and sustaining drought has been shown for wheat (Al-Karaki et al. 2004), oats (Khan et al. 2003), corn (Subramanian et al. 1997; Subramanian and Charest 1999), soybean (*Glycine max*) (Aliasgharzadeh et al. 2006), garden pea (*Pisum sativum*) (Quilambo et al. 2005), onion (*Allium cepa*) (Bolandnazar et al. 2007), tomato (Subramanian et al. 2006) and other crop species (see Augé 2001). It has been shown that an increased nutrient uptake mediated through AM fungi could impart more resistance to drought in mycorrhizal plants (Ruiz-Lozano et al. 1995). The increased uptake of P by AM plants under drought conditions results in higher yield than those without AM fungi (Smith and Read 2008). Therefore, improved P nutrition by AM fungi during the periods of water deficit has been postulated as a primary mechanism for enhancing host plant drought resistance under water stress conditions (Subramanian et al. 2006). In contrast, others consider that host plant drought tolerance is independent of P uptake stimulated by AM fungi (Davies et al. 1993; Augé et al. 1994). In addition to P, mycorrhizal plants can also absorb more N under drought conditions resulting in increased growth and yield (Tobar et al. 1994; Subramanian et al. 2006). One of the widely accepted mechanisms of AM symbiotic influence on plant water relation involves the AM fungal effect on plant size. The response of plants to mycorrhizal colonization is often related to the direct influence of AM fungus on plant size in conjunction with improved P nutrition (Ebel et al. 1994). However, mycorrhizal effect on metabolic changes (Subramanian and Charest 1995) and modified N assimilation pathways (Subramanian and Charest 1998) as shown earlier can also influence the size of host plants. The AM fungi could therefore to a certain extent replace genetic engineering and plant breeding techniques (Xu et al. 2008; Grover et al. 2011) by modifying the crop plant physiology as well as biochemical responses (Kohler et al. 2008; Grover et al. 2011) to stress tolerance. For example, AM fungal association has been shown to increase the stomatal conductance of mycorrhizal mutant bean (*Phaseolus vulgaris*) than non-mycorrhizal under water deficit condition (Augé 2004).

3.2.1.2 Salinity

Salinity is one of the cosmopolitan threats to crop production worldwide. Irrigation with groundwater and irrational use of easily soluble fertilizers are main causes for salinity in agroecosystems (Copeman et al. 1996; Al-Karaki 2000). It has been estimated that more than 250 million ha of groundwater irrigated lands is salinized, of which ten million ha is abandoned annually (Codevasf 2011). Salt deposition in the soil results in hyperionic and hyperosmotic stresses (Evelin et al. 2013). The presence of excess salts in the soil solution may limit the growth of an organism due to specific ion toxicity or osmotic stress. These factors tend to differ in relative importance depending on the species and concentration of ions involved, as well as the tolerance of the organism in question (Brownell and Schneider 1985). Salinity may affect certain stages of the life history of an organism more compared to other stages. Salt stress induced decline in crop productivity results from its negative impact on plant growth and development (Giri et al. 2003; Mathur et al. 2007). Arbuscular mycorrhizal fungi have been shown to increase crop yield under saline soils (Daei et al. 2009). Nevertheless, results on the influence of salinity on AM formation and function are often contradictory. Some studies have shown that soil salinity reduces root colonization by AM fungi and increases plant's mycorrhizal dependency (Tian et al. 2004; Sheng et al. 2008). In contrast, it has also been shown that AM colonization either remains unaffected (Yamato et al. 2008) or even increased under salt stress (Aliasgharzadeh et al. 2001). An increased soil salinity has also been shown to adversely affect the production of extraradical hyphae of AM fungal strains that are sensitive to salinity (Juniper and Abbott 2006; Evelin et al. 2009). The extent to which salinity reduces AM colonization depends on the stage of the association such that inhibition is more prominent during early stages of the symbiosis development than during the later stages (McMillen et al. 1998). For example, salinity inhibited early colonization of roots by *Gigaspora decipiens* more than by *Scutellospora calospora* (Juniper and Abbott 2006). It has been shown that AM fungi alleviate salt stress in some plants through modifications in physiological mechanisms (see Evelin et al. 2009; Porcel et al. 2012). However, the adjustment of osmotic potential by settling down of soluble sugars in mycorrhizal fungal parts has been suggested to protect the plant from salinity (Soliman et al. 2012). For instance, trehalose in spores and extraradical mycelium enables AM fungi to colonize host plants even under high salinity (Schubert et al. 1992). Several studies have reported that salt stress induces modifications in plants even at ultrastructure levels (Yamane et al. 2004; Miyake et al. 2006; Andrea and Tani 2009). Recently, Evelin et al. (2013) showed that the ultrastructural changes in AM-inoculated fenugreek (*Trigonella foenum-graecum*) plants exposed to four different levels of salt were less than non-mycorrhizal plants. Studies have also shown that some AM fungi are able to adapt to different environmental conditions better than others (Stahl and Christensen 1991). Thus, the varied observations reported by different workers may partly reflect the differences between the fungi used and their ability to adapt to various environments. Nevertheless, most of studies examining mycorrhiza and soil salinity to date have not considered these differences.

Arbuscular mycorrhizal fungal-mediated salt stress tolerance has been shown for crops like chilli (*Capsicum annuum*) (Çekiç et al. 2012), Chinese milk vetch (*Astragalus sinicus*) (Peng et al. 2011), pepper (*Piper nigrum*) (Turkmen et al. 2008; Kaya et al. 2009), fenugreek (Evelin et al. 2012), corn (Sheng et al. 2008, 2011), bajra (*Pennisetum glaucum*) (Borde et al. 2011), tomato (Hajiboland et al. 2010) and clover (*Trifolium alexandrinum*) (Gharineh et al. 2009). Like drought stress, an increased P uptake mediated by AM fungi has been suggested to alleviate saline stress (Tian et al. 2004). However, in certain cases, saline tolerance of mycorrhizal plants appears to be independent of P concentration (Feng et al. 2002). Both differences in the ability between AM fungi to obtain P from the soil and their ability to adapt to changing edaphic conditions (del Val et al. 1999) could reason for varied sensitivities of AM fungi to salinity. Therefore, it might be expected that an isolate originating from saline soil would have a higher adaptability and a greater capacity to promote plant growth under saline stress.

3.2.2 Biotic Stress

3.2.2.1 Protection Against Pests and Pathogens

In agriculture, pest and pathogen infestations severely damage the crops, resulting in a decline in crop yield. In spite of constant efforts to eradicate these pests and pathogens using chemical agents, little and temporary success has been achieved. Alternatively cost-effective biological methods involving microbes could be used to improve host plant resistance against pests and pathogens. There is a direct competition in host roots for nutrient uptake and proliferation between AM fungi and pathogens as they colonize the same niche. Some of the recent studies do provide evidence that AM fungi and their interaction with plants could substantially reduce the damage caused by soilborne pathogens (Whipps 2004; St-Arnaud and Vujanovic 2007; Smith and Read 2008). Further, the extent of protection imparted by AM fungi could vary with the pathogens and the host plant involved. Nevertheless, the degree of protection imparted by AM symbiosis against pests and pathogens could be modified by soil and other environmental conditions. Mechanisms by which AM fungi control root pathogens include (i) improved nutrient status of the host, (ii) damage compensation, (iii) competition for host photosynthates, (iv) competition for infection sites, (v) anatomical and morphological changes in the root system, (vi) microbial changes in the mycorrhizosphere and (vii) activation of plant defence mechanisms. In some cases, the direct biocontrol potential of AM has been demonstrated, especially for plant diseases involving pathogens like *Phytophthora*, *Rhizoctonia* and *Fusarium* (Abdel-Aziz et al. 1997; St-Arnaud et al. 1997; Vigo et al. 2000). A recent study by Singh et al. (2013) has clearly demonstrated the AM fungal ability to efficiently control *Fusarium* wilt disease under all conditions in three chickpea (*Cicer arietinum*) varieties tested. Further, several studies have also confirmed the existence of synergism between AM fungi and biocontrol agents such as *Burkholderia cepacia* (Ravnskov et al. 2002), *Pseudomonas fluorescens* (Edwards et al. 1998), *Trichoderma harzianum* (Datnoff et al. 1995) and *Verticillium chlamydosporium* (Rao et al. 1997). These interactions suggest that AM might affect plant and soil microbial activity by stimulating the production of root exudates, phytoalexins and phenolic compounds (Norman and Hooker 2000; Bais et al. 2005). A small increase in the activity of plant defence genes, especially those involved in the production of chitinases, glucanases, flavonoid biosynthesis and phytoalexins, has been observed during mycorrhizal growth; however, these mycorrhizal defence induction mechanisms remain transitory (Guillon et al. 2002; Harrier and Watson 2004). Further, AM-mediated resistance to biotic stress could vary with the mycobiont involved. For example, Ozgonen and Erkilic (2007) used three different species of Glomeraceae [*Funneliformis mosseae* (=*Glomus mosseae*), *Claroideoglomus etinicatum* (=*Glomus etunicatum*), *Rhizophagus fasciculatus* (=*Glomus fasciculatum*)] and a Gigasporaceae species (*Gigaspora margarita*) to control blight disease caused by *Phytophthora capsici* in pepper. The results of the study clearly showed a significantly higher plant growth and reduced disease severity in AM-inoculated plants. Of the different species of Glomeraceae screened, *F. mosseae* was found to be more efficient than others.

Many studies have also reported the suppressive effect of AM fungi on sedentary endoparasitic nematodes (Elsen et al. 2003; de la Peňa et al. 2006). In some crops, this effect is significant enough to the level, to consider AM fungi to be more or less an efficient means of biological control (Castillo et al. 2006). With migratory endoparasitic nematodes, studies have demonstrated a decrease in nematode population development like *Meloidogyne incognita* on cucumber (*Cucumis sativus*) (Zhang et al. 2008), *Radopholus similis* on banana (*Musa* spp.) (Elsen et al. 2004; Jefwa et al. 2010), *Pratylenchus* on dune grass (*Ammophila arenaria*) (de la Peña et al. 2006) and *Rhizoctonia solani* (Yao et al. 2002) on potato. Recently, Affokpon et al. (2011) evaluated native and commercial AM fungi for their efficacy to protect plants against root-knot nematode, *Meloidogyne* spp. The results of this study indicated that the

Table 1 Interaction of arbuscular mycorrhizal fungi with beneficial soil microorganisms

Group of microorganisms	Results
Symbiotic and asymbiotic N_2 fixers	N_2 fixation, N cycling, N transfer
Phosphate solubilizers	P cycling, use of sparingly soluble P source
Phytostimulators	Increased rooting and seedling establishment
Biocontrol agents	Increased resistance/tolerance to root disease
Other fungi and bacteria related to soil aggregation	Important to soil quality

Adapted from Azcón-Aguilar and Barea (1997) with permission

nematode attack could mask the magnitude of AM fungal benefits to the host plant, but AM fungal isolates could modify the severity of stress on plants to different levels (Veresoglou and Rillig 2012).

3.2.2.2 Interaction with Other Soil Organisms

Arbuscular mycorrhizal fungi interact with a diverse group of organisms in the rhizosphere. These interactions can range from positive to neutral and to negative on the AM association or a particular component of the rhizosphere (Azcón-Aguilar and Barea 1992; Rillig 2004). Different types of positive interactions between AM fungi and other soil microorganisms are presented in Table 1. The microflora in the rhizosphere of mycorrhizal roots most aptly termed as the 'mycorrhizosphere' quantitatively and qualitatively differs from the non-mycorrhizal roots (Bansal and Mukerji 1994). Mainly two groups of bacteria, namely, saprophytes and symbionts, interact with AM fungi that may be either detrimental, neutral or beneficial in their response (Johanson et al. 2004). 'Mycorrhiza helper bacteria' (MHB) found mostly in temperate and tropical ecosystems (Frey-Klett et al. 2007) initiate AM fungal root colonization, stimulate mycelia growth and also assist spore germination (Gryndler et al. 2000; Vivas et al. 2006). The interaction between AM fungi and nodulating nitrogen fixers has received considerable attention because of the high P demand involved in N_2 fixation (Barea and Azcón-Aguilar 1984; Veresoglou and Rillig 2012). The two symbionts act synergistically under low fertile conditions, resulting in greater N and P content in dually inoculated plants than when the organisms are inoculated separately. Even at low water potential, AM fungal inoculation improves nodulation and N_2 fixation by the bacterial symbiont (Goicoechea et al. 1998), thereby neutralizing the effects of salinity. An early association of the seedling with AM fungi can moderate the stressed condition of the host (Evelin et al. 2009). It has been noted that the premature nodule senescence in soybean under drought conditions could be ameliorated through AM fungal inoculation (Porcel et al. 2003).

Synergistic interactions have also been reported between AM fungi and plant growth-promoting rhizobacteria (PGPR) (Muthukumar et al. 2001; Muthukumar and Udaiyan 2006; Sala et al. 2007). However, the nature and the extent of benefit from interaction could vary. For instance, Chandanie et al. (2005, 2006) noted that co-inoculation of *Trichoderma* with an AM fungus (*F. mosseae*) positively stimulated plant growth. However, no such effect on plant growth was evident when *Penicillium* was co-inoculated with the same AM fungus.

3.2.2.3 Nutrient Transfer in Intercropping Systems

Intercropping is an ancient technique of growing more than one crop species simultaneously in the same field. It plays an important role in agriculture rendering advantages to both soil and plant. Intercropping improves soil texture and soil water availability and supplies various organic matters for most efficient proliferation of symbiotic and non-symbiotic microorganisms (Burner 2003; Muok et al. 2009). The wide and diverse plants in an intercropping favour an increased and viable population of AM fungi. However, the capability of legumes to form dual symbiotic association with both bacteria and AM fungi is important in intercropping systems from improving soil fertility point of view (Pagano et al. 2008; de Carvalho et al. 2010). As plants from different species could be linked by the common AM mycelia network, intercropping of legume crops can benefit nonleguminous crops through the transfer of N via common mycelia network (CMN) (Simard and Durall 2004). This CMN aids nutrient transfer between different host plants, thereby acting as an extension of the root systems, and also provides signalling molecules (Xiaolin and Shang 1997). For example, the cocultivation of citrus (*Citrus tangerine*) which is highly dependent on AM fungal association due to the poor root development (Wu and Xia 2006), along with a leguminous herb, *Stylosanthes gracilis*, consequently increased both soil quality and citrus yield in Southern China (Yao et al. 2008).

Other features of intercropping like the nutrient cycling and organic matter turnover can maximize the resource use by plants, thereby improving soil fertility. For example, Li et al. (2007) showed that the root exudates of faba bean containing organic acids and protons increased P content of maize plants in a maize–faba bean (*Vicia faba*) intercropping system. The CMN of AM fungi also enhances P balance as well as the N and P levels between plants (Giovannetti et al. 2004). Each AM fungal species tends to have different effects in relation to plant systems. For instance, AM fungal taxa that reduce plant growth in one plant species can enhance it in another (Klironomos 2003). Recently, Hu et al. (2013) examined the effect of intercropping *Sedum alfredii* with *Ipomoea aquatica* inoculated with two different AM fungal species ([Funneliformis caledonium (=*Glomus caledonium*) 90036, *Glomus versiforme* HUN02B)] in cadmium (Cd)-contaminated soil. The AM fungus *F. caledonium* 90036 increased P acquisition and plant biomass of *S. alfredii*, whereas *G. versiforme* HUN02B had the same effect on *I. aquatica*. Some of the studies also suggest that intercropping is beneficial and far better than monoculture system (Harinikumar et al. 1990; Ishii et al. 1996).

3.2.2.4 Rooting

Nutrient supply by the AM mycelium activity exerts a feedback regulation, especially in the aerial parts of the plant like photosynthesis and the translocation of the photosynthates. Generally, fewer photosynthetic products are allocated to the root due to an increased efficiency of the roots in response to AM symbiosis (Smith et al. 2003; Gamalero et al. 2004); the shoot/root ratios of AM plants are usually higher in AM plants than in their corresponding non-AM controls (Smith 1980). It has also been recently recognized that AM colonization could affect a wide range of morphological parameters in developing root systems including root branching (Atkinson et al. 1994; Berm et al. 1995). Enhanced root proliferation in response to AM fungal inoculation has been reported in black pepper (*Piper nigrum*) (Anandaraj and Sarma 1994; Thanuja et al. 2002) and cashew (*Anacardium occidentale*) (Krishna et al. 1983). Therefore, it has been speculated that changes in the plant hormonal balance and meristematic activity in response to AM association were responsible for the AM-induced effects on root development.

Changes in root morphology and P uptake alter the rhizosphere through predominantly affecting the microbial community (Linderman 1988). The variation in the root architecture of mycorrhizal plants from that of a non-mycorrhizal plant clearly indicates the involvement of some compounds from root system responsible for these traits. For example, Wu et al. (2010) showed that polyamines in addition to improving plant growth could also significantly alter the root system architecture in AM plants.

4 Management of AM Fungi

In agroecosystems, various management practices such as the degree and type of fertilization, plant protection, fallow period and soil tillage could influence AM association.

4.1 Fertilizer

Crops require adequate nutrients especially P during early stages of growth for optimum crop production (Grant et al. 2001). Limited P supply frequently limits crop production and P fertilizer is commonly applied to ensure that sufficient P is available for optimal crop yield and maturity (Grant et al. 2005). The total soil P usually ranges from 100 to 2,000 mg P kg^{-1} soil representing approximately 350–7,000 kg P ha^{-1} in surface 25 cm of the soil, although only a small portion of this P is immediately available for crop uptake (Morel 2002). However, for AM fungi which are known for its P uptake (Hu et al. 2009), soil P is one of the major deterrent soil factors in agricultural systems that affects AM. It has been well proved that the AM fungal benefit tends to decline as the concentration of P in the plant increases (Valentine et al. 2001). Higher tissue P reduces the production of external hyphae (Bruce et al. 1994), hyphal branching (Nagahashi and Douds 2000) and sporulation (De Miranda and Harris 1994) of AM fungi. As available P in the soil increases, AM association may depress plant growth, as there is a carbon cost associated with supporting the association (Kahiluoto et al. 2000). For example, cucumber plants inoculated with AM fungi and raised on full-strength nutrient solution had 19 % lower biomass than uninoculated plants (Valentine et al. 2001). In contrast, mycorrhizal plants had 66 % higher biomass compared to non-mycorrhizal plants under reduced P concentration in the nutrient solutions. However, the effect of P fertilization on AM fungi may vary with P sources. While readily soluble or available, forms of P (inorganic) affect AM association to a greater extent than less soluble forms of P (e.g. rock phosphate) (Linderman and Davis 2004). Similar results have also been observed for N fertilization (Gryndler et al. 1990; Liu et al. 2000). The effect of P fertilization often changes with the response or balance of other nutrients present. The AM fungal benefit and mycorrhization tend to be highest when low P is combined with an ample supply of other nutrients (Grant et al. 2005). For instance, Guttay and Dandurand (1989) observed an increased mycorrhization in corn with N and K fertilization at low P levels but a decrease at high P levels. This clearly suggests the interactions among N, P and K fertilization in corn. The application of NPK fertilizer along with AM fungi has been shown to increase plant growth in potato (Eliopoulos et al. 2007), onion (Gergon et al. 2008) and cucumber (Ahmed et al. 2009). Using AM as a bioinoculant, instead of phosphate, was found to have a direct impact on sugarcane growth and yield (Surendran and Vani 2013). Like for AM colonization, some reliable evidence does indicate that the use of fertilizers can reduce AM fungal spore populations in the soil (Bhadalung et al. 2005; Emmanuel et al. 2010).

In organic farming, the use of synthetic fertilizers is avoided which enables the crops to depend on AM fungi for soil nutrients (Galvez et al. 2001). In addition, organic fertilization enhances AM fungal association and formation of AM fungal propagules in the soil (Gryndler et al. 2005; Gaur and Adholeya 2005), thereby improving soil quality. Though organic fertilizers generally have a positive effect on crops as evidenced by enhanced growth and accumulation of nutrients (Silva et al. 2007; Sharif et al. 2012), results of some studies are found to be opposite (Martin et al. 2002; Elorrieta et al. 2003). A consortium of seven AM fungi isolated from the soils of coffee (*Coffea arabica*) plantations with different fertilizer inputs (low, intermediate and high) was examined for their growth-promoting ability in coffee both under nursery and field conditions. The results of this study clearly showed that greater fertilizer inputs negatively influenced the spore abundance and plant growth, whereas intermediate input increased the AM fungal abundance (Trejo et al. 2011).

4.2 Tillage

Tillage is an integral part of modern agriculture that modifies the physical, chemical and biological properties of a soil. Consequently, tillage practices may also affect AM fungi (Gálvez et al. 2001; Kabir 2005; Neelam et al. 2010). The extent of extraradical AM fungal networks can be several metres per cubic centimetre of soil, providing the major nutrient–absorbing interface between plants and soil (Jakobsen et al. 1992). The persistence of AM fungi in ecosystems depends on the formation and survival of propagules (e.g. spore, hyphae and colonized roots). While spores are considered to be a resistant structure that may be viewed as long-term propagules in the absence of a viable host, hyphae are considered to be the main source of inocula for plants in undisturbed soils. The damage to these hyphal networks by tillage not only affects AM fungal growth but also reduces root colonization due to death or lowers infectivity of the hyphal fragments compared with intact hyphal networks (Johnson et al. 2001; Garcia et al. 2007).

Different AM fungi responded variedly to different tillage management practices (Gálvez et al. 2001; Kabir 2005; Borie et al. 2006). Tillage can reduce the root length colonized by AM fungi and subsequently AM-mediated P, Zn and Cu uptake by plants (Mozafar et al. 2000; Goss and de Varennes 2002). Certain AM fungal species may survive in tilled soils, while others may disappear. Because AM fungi are more abundant in the topsoil, deep ploughing may dilute their propagules in a greater volume of soil, thereby reducing their chance of association with a plant root. Soil aggregation is an important process that maintains soil porosity, hydraulic activity, organic matter and also soil erosion (Caesar-TonThat et al. 2011). But these processes are disturbed by long-term tillage systems, which subsequently not only affects the carbon stabilization and sequestration but also the microbial populations (Sainju et al. 2009). In undisturbed soil, roots follow preformed channels, making close contact with the AM-colonized root systems of the previous crop, resulting in enhanced mycorrhization of roots (Evans and Miller 1990). Furthermore, no-tillage favours the accumulation of organic matter, changes in soil structures and increased availability of C, N and water (Doran and Linn 1994; Shirani et al. 2002) in the surface horizons, thereby maximizing their benefits to crops (Kabir et al. 1999). Sheng et al. (2012) showed that long-term tillage and P fertilization invertedly affected the fine root development and AM fungal colonization in corn roots. In a recent study, Schalamuk et al. (2013) demonstrated that the effect of no-tillage or conventional tillage system on the abundance of AM fungal propagules in wheat crops depends more on the phenological stages of the crop.

4.3 Organic Manures

Organic manure consists of materials of biological origin which are used to restore the soil fertility and plant growth. According to Lee et al. (2008), general principles of organic farming include (1) exclusion of synthetic biocides; (2) addition of organic fertilizers to the soil, including farmyard manure, compost and crop residue and slow-release mineral fertilizers such as rock phosphate; and (3) use of crop rotation (IFOAM 1998). Manure application may increase or decrease root colonization by AM fungi. Tarkalson et al. (1998) found that manure application increased AM colonization, P and Zn uptake by plants and crop yield. Muthukumar and Udaiyan (2000) showed that manure applications could increase spore populations and root colonization by AM fungi. Gaur and Adholeya (2000) also found that organic amendments supported both high crop yield and AM fungal populations in onion, garlic (*Allium sativum*) and potato. The benefit of organic amendment on AM fungi has been attributed to changes in soil structure with manure amendments like increased porosity, enlarged mean weight diameter of aggregates, improved water retention capacity and greater activity of beneficial soil microbes in the soil profile (Celik et al. 2004; Pagliai et al. 2004). However, the effects of compost application on AM colonization appear to be inconsistent (Ellis et al. 1992; Allen et al. 2001). For example, the low levels of root colonization by AM fungi in soybean and sorghum in compost-amended soils were attributed to high soil P availability (Garcia et al. 2007). Muthukumar and Udaiyan (2002) showed that the growth and yield of the cowpea (*Vigna unguiculata*) varied in response with various organic amendments based on changes in indigenous AM fungal populations.

The response of plants to AM fungal inoculation in organic-amended soils has been shown to either increase (Rydlová and Vosátka 2000; Gryndler et al. 2002, 2006) or decrease (Ravnskov et al. 1999, 2006). Composted organic amendments in soil promote AM fungal hyphal growth and establishment (Douds et al. 2000), consequently aiding the transfer of mineral N (Hamel 2004) and amino acids (Govindarajulu et al. 2005) from the organic manures to the host plant. Minimal C:N ratio in the organic manures also has a positive influence on AM fungi (Groaker and Sreenivasa 1994). Likewise, the application of organic manures to soils with different nutrient levels affects the AM fungal colonization and abundance variedly. Both soil factors and N:P ratio of host roots can influence AM fungal colonization, but the mechanism remains unresolved (Liu et al. 2000; Johnson et al. 2003). Available phosphorus and mycorrhization in coconut (*Cocos nucifera*) were found to be higher in organic manure-amended soils than in inorganic fertilizer-applied soils, even though the later contain higher nutrient contents (Karunasinghe et al. 2009). The application of various combinations of organic manures (farmyard + poultry + humic acid) along with AM fungal inoculation showed enhanced plant growth and nutrient uptake and spore density in eroded soils (Sharif et al. 2012). This suggests AM fungal ability to reduce the effect of soil erosion and shield the soil fertility (Valarini et al. 2009). Numerous studies have also revealed the beneficial effects of organic manure application on AM fungi (e.g. Limonard and Ruissen 1989; Lee and Pankhurst 1992; Hole et al. 2005). Dai et al. (2011) conducted an experiment with various levels of organic amendments on chilli and showed an increased mycorrhizal colonization and a higher plant tissue nutrient in response to organic amendments.

The application of organic manures not only stimulates the AM fungal colonization of roots but also improves in spore populations in the soil. Organic manure amendment along with AM fungal inoculation has been shown to enhance plant growth and spore numbers of *C. etunicatum* and *F. mosseae* in soils than those fertilized with conventional fertilizers and inoculated with AM fungi (Douds et al. 2000). During early stages of plant growth, the spore numbers in organic manure-amended soil tend to decline and then increase subsequently due to alterations in nutrient content arising from decomposing manures (Harinikumar and Bagyaraj 1989; Muthukumar and Udaiyan 2002; Gryndler et al. 2009; Ijdo et al. 2010).

4.4 Biocides

Biocides, the chemical agents used to control pests and pathogens, are an inherent component of conventional agriculture. In plant production systems involving horticultural crops such as vegetables, most cultivators are unwilling to risk low production through reduced fertilizer or biocide inputs. Information on the effect of agricultural chemicals on AM fungi is largely empirical and poorly understood. Thus, biocide application may have inadvertent or unrecognized effects on AM fungi. Biocides used with the intention on promoting plant health may either impair or eliminate AM fungal activity causing damage to plant health. There are two beneficiary effects of biocides like fungicides on AM fungi: (a) modification of host plant physiology by enhancing root exudates that indirectly stimulate root colonization and (b) reduction of AM fungal antagonistic community (Tataranni et al. 2012). Most studies examining the effect of biocides on AM fungi are often conducted under greenhouses or in plant growth chambers, involving sterile media or media which have very little similarity to field conditions (Udaiyan et al. 1995). Soil fumigants used to reduce the abundance of pathogen cause stunting in a range of crops including onion, pepper (Hass et al. 1987), soybean (Ross and Harper 1970) and corn (Jawson et al. 1993). This reduction in plant productivity has often been attributed to decreased AM formation, which results in poor nutrient uptake. However, results of field studies do suggest that the elimination of co-occurring soil microorganisms might also substantially contribute to this effect (Hetrick et al. 1988).

Arbuscular mycorrhizal fungal responses to biocides are varied and may be influenced by the host plant, specific chemical compounds, method of application, mode of action, growth stage of AM fungi and biotic and abiotic factors (Giovannetti et al. 2006). Fungicides applied as soil drenches generally have a detrimental effect on AM fungi (Udaiyan et al. 1999). In a recent study, Rotor and Delima (2010) assessed the influence of AM fungi with the addition of N fertilizer and biocides on corn growth and productivity. The results of this study clearly suggested that microbial inoculants could act as a substitute for biocide application. But the effect of fungicides on AM association can vary with host–fungal combinations. For example, the dicarboximide fungicide captan is known to stimulate mycorrhization of beans by *Glomus* spp. (De Bertoldi et al. 1977), had no effect on undetermined species colonizing onion (El-Giahami et al. 1976) and reduced colonization by *F. mosseae* in corn (Sutton and Sheppard 1976). Fungicides can also adversely affect different stages of AM fungal development and function (Trappe et al. 1984). The influence of three commonly used fungicides, i.e. benomyl, pentachloronitrobenzene, and captan, tested on mixed culture of AM fungi indicated that these fungicides could alter the species composition of AM fungal community (Schreiner and Bethlenfalvay 1996). Nevertheless, the biological response of AM to these fungicides depends not only on the fungus–fungicide relationship but also on the prevailing environmental conditions (Schreiner and Bethlenfalvay 1997). Systemic fungicides like carbendazim can completely inhibit P uptake by AM fungal hyphae even when applied at recommended field rates (Kling and Jakobsen 1997). In addition, carbendazim could disrupt hyphal P uptake at concentrations as low as 10 % of the recommended field dosage (Schweiger and Jakobsen 1998). However, under field conditions, carbendazim or a mixture of propiconazole and fenpropimorph applied at recommended rate did not affect AM colonization (Schweiger et al. 2001). In contrast to carbendazim, the benzimidazole fungicide benomyl has to be applied at a much higher rate than recommended levels to affect AM fungal colonization of roots (Gange et al. 1993).

Like certain fungicides, higher dosage of pesticides like malathion and mancozeb reduces plant growth parameters and also affects the extent of mycorrhizal colonization (Saleh Al-Garni 2006). Unlike other pesticides, the herbicide atrazine at lower concentration decreases mycorrhizal colonization, whereas at higher concentration, it stimulates colonization (Huang et al. 2006, 2007). However, it has been speculated that the application of higher concentrations of atrazine tends to induce tolerance in AM fungi, although the real mechanism behind the varied effect is yet to be elucidated (Huang et al. 2007).

4.5 Crop Rotation

In general, microbes in the soil affect the succeeding crop. From the biological view point, crop rotation is essential for proliferation of AM fungi (Douds et al. 2005). The AM fungi which proliferate with a host plant are not necessarily those best at promoting the growth of other crops in the rotation (Feldmann et al. 1999). The proliferation of such AM fungi has been attributed as a cause to yield decline in continuous monoculture (Schenck et al. 1989). This had been noted in soybean and sorghum grown as continuous cropping and also by crop rotation, which reflected less mycorrhizal colonization in the former method than the later (Ellis et al. 1992). In addition, the diversity of the AM fungal community is linked to the diversity and productivity of the plant community (van der Heijden et al. 1998; Bever et al. 2001). A more relaxed altitude towards weed management may increase both the diversity and effectiveness of the AM fungal community when the crops are non-mycorrhizal (Miller and Jackson 1998; Feldmann and Boyle 1999; Jordan et al. 2000). This is important under circumstances where the cultivation of non-host crop such as *Brassica* spp. is known to reduce AM fungal inoculum in the soil (Blaszkowski 1995).

Pre-cropping enhances mycorrhizal inoculum potential (Dodd et al. 1990a, b; Karasawa et al. 2001, 2002). The enhancement of mycorrhiza inoculum potential by a given pre-crop may improve the mycorrhizal activity of a subsequent crop in the rotation (Barea et al. 1993). This is because the fungi develop and sporulate mostly in the roots of those plant species, which are most susceptible to mycorrhizal colonization. Susceptible crops, which in the rotation follow non-host plants (or plants, which develop little mycorrhizal colonization), may carry less colonization than they would follow a strongly mycorrhizal crop (Ocampo and Hayman 1981). The composition of AM fungal spore communities tends to change significantly if crop rotation was practiced along with P fertilization (Mathimaran et al. 2007). According to Vestberg et al. (2005), improved P nutrition of rice grown under acidic and phosphorus deficiency conditions without using P fertilizer could be achieved by crop rotation (maize and horse gram) along with AM fungal inoculation.

4.6 Fallow Period

Fallow, the reinstatement period to trim down the weed growth, may negatively influence AM fungi. Crops including corn, sorghum, sunflower, chickpea and linseed, when grown in southern Queensland, Australia, after long periods of bare fallow, exhibited poor growth with P and Zn deficiency. This syndrome, termed long-fallow disorder, was associated with low AM colonization, failure of AM fungal mycelia networks in soil to take up sufficient nutrients and reduced AM fungal spore density and diversity (Kabir and Koide 2000; Karasawa et al. 2002). The application of P and Zn fertilizers to soils following long fallow not only alleviated the negative effects of low AM colonization and fertility, but crops responded better than in soils with higher AM fungal inoculum levels (Thingstrup et al. 1998). Poor growth of linseed after prolonged fallowing in a semiarid cropping system was improved by inoculation with AM fungal propagules obtained from sorghum-cropped field soil (Thompson 1994). A 1-year fallow in an oxisol reduced the number of AM fungal propagules by 40 % and the growing of non-mycorrhizal crops like mustard (*Brassica juncea*) reduced them by 13 % (Harinikumar and Bagyaraj 1988). Wagner et al. (2001) observed an exponential decline in spore counts of *Claroideoglomus claroideum* (=*Glomus claroideum*) with time during soil storage. with time during soil storage. Ellis (1998) also showed that the absence of host roots could drastically reduce AM fungal populations in the soil. The findings of Troeh and Loynachan (2003) suggest that continuous cropping of maize and soybean increases AM fungal spore numbers, whereas spore numbers tend to decrease under fallow. Recently, Karasawa and Takebe (2012) reported that fallow condition could reduce the abundance of AM fungal propagules (spores and mycelium), due to the disruption of AM fungal mycelial network and alteration of available nutrients and microbial activities in soil (Jansa et al. 2003). To overcome the defects, the maintenance of high AM fungal abundance in cropping systems could ensure tolerance to prolonged fallow periods and their activity (Hijri et al. 2006).

4.7 Management Considerations

Reports of improved plant growth responses in response to AM inoculation under controlled conditions in low fertile soils led to a flurry of activities during 1980s, aimed at utilizing AM fungi as bioinoculants. However, the magnitude of responses was different under field conditions, especially under conventional high-input agricultural systems. Further studies, however, have shown that most crop species are mycorrhizal and AM fungi can have a substantial positive or negative impact on crop productivity (Johnson et al. 1997). Therefore, there is a need to elucidate the role of AM fungi in agroecosytems and to understand the impact of management practices on the symbiosis. The introduction of appropriate fungi to the plant production systems may be appropriate under conditions where the native AM fungal inoculum potential is low or inefficient. The initial step in any inoculation programme is to identify and isolate organisms that are both infective (able to associate) and effective (able to impart desired effects) under a given set of conditions. Isolates of AM fungi may vary widely in these properties. So, screening trials are needed to select isolates that will perform efficiently and successfully. Screening under actual field conditions is preferred than under controlled conditions, because the influence of indigenous AM fungi, soil organisms and cultural practices on the introduced fungi could be more clearly understood. Factors that should be considered when assessing the potential role and introduction of AM fungi in agroecosystems include:

4.7.1 Mycorrhizal Growth Response (MGR) and Mycorrhizal Dependency (MD) of the Host Crop

Mycorrhizal growth response (MGR) is the responsiveness of change in the total biomass of mycorrhizal (M) versus non-mycorrhizal (NM) crop plants from the symbiosis (Hetrick et al. 1992):

$$\mathrm{MGR} = \left[(\mathrm{M} - \mathrm{NM}) / \mathrm{NM}\right] \times 100$$

Mycorrhizal dependency (MD) is defined as the growth response of the total dry matter in mycorrhizal (M) versus non-mycorrhizal (NM) plants at a given phosphorus level (Plenchette et al. 1983):

$$\mathrm{MD} = \left[(\mathrm{M} - \mathrm{NM}) / \mathrm{M}\right] \times 100$$

All mycorrhizal agricultural crops are not equally benefitted from the association. Generally, coarse-rooted plants like legumes benefit more from AM symbiosis than fine-rooted cereals (Jeffries and Dodd 1991). Mycorrhizal dependency of a crop species may differ with the cultivars as well as with the AM fungal species involved (Table 2; Figs. 5 and 6).

4.7.2 Inoculum Density, Rate and Extent of AM Colonization

Rapid and extensive spread of AM fungal colonization is a crucial factor for effectively enhancing plant growth and ably competing with indigenous AM fungi. Therefore, the formation of entry points is important, and their number is controlled by inoculum level, more specifically by inoculum density, that is, the number of propagules per given unit of soil. Experiments are preformed either with unknown quantities of AM fungal inoculum or state only the spore numbers. However, the spore numbers alone do not constitute total propagules, as dried root bits, sporocarps, soil hyphae and mycorrhizal roots can also act as propagules. Therefore, currently, the total

Table 2 Mycorrhizal dependency of agricultural crops under low soil P

Mycorrhizal dependency	Agricultural crops
Strong	Cassava, onion, legumes, peppers
Medium	Soya, wheat, barley, cowpea, grain legumes, tomatoes
Weak	Potato, rice, melon, sunflower, beans, maize, sorghum

After Jeffries and Dodd (1991) with permission

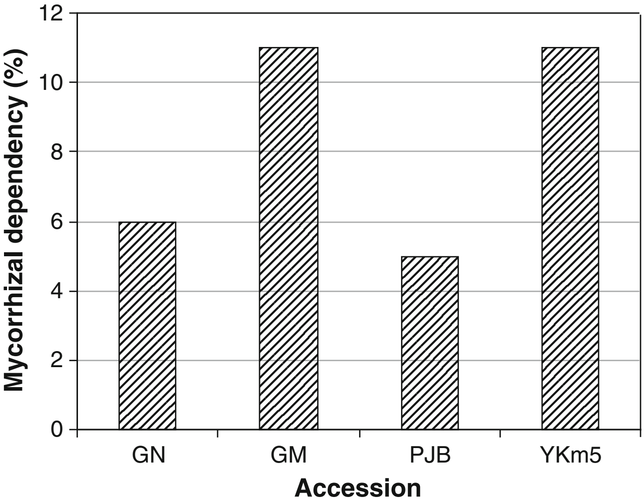

Fig. 5 Relative mycorrhizal dependency of four *Musa* cultivars (*GN* Grande Naine, *GM* Gros Michel, *PJB*, Pisang Jari Buaya, *YKm5*, Yangambi Km5) inoculated with *Funneliformis mosseae* (Data from Elsen et al. 2003, with permission)

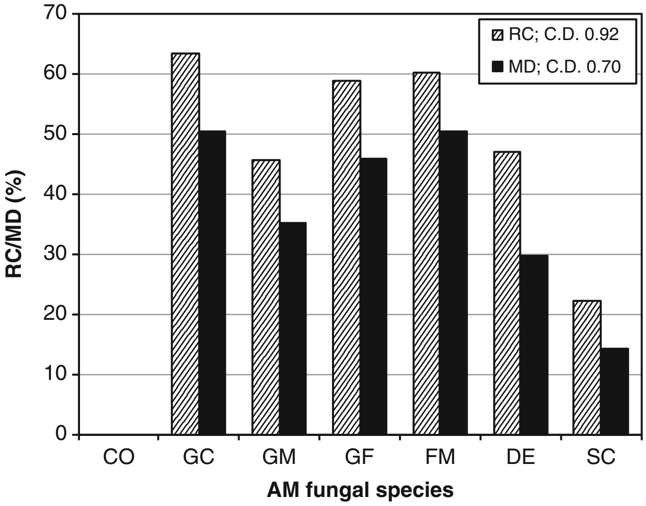

Fig. 6 Effect of different arbuscular mycorrhizal fungi on root colonization (RC) and mycorrhizal dependency (MD) of *Eleusine coracana* var. HR-374. *CO* Control, *GC Glomus caledonium*, *GM Gigaspora margarita*, *GF Glomus fasciculatum*, *FM Funneliformis mosseae, DE Diversispora epigaea* (=*Glomus epigaeum*), *SC Scutellospora calospora*, *C.D* critical difference ($P < 0.05$) (Data from Tewari et al. 1993, with permission)

number of propagules available for colonization is used to measure the AM fungal propagule density in field soil or inoculum (Muthukumar and Udaiyan 2003). For example, the reduction in plant growth had been shown under field conditions under reduced spore density and root colonization (Zangaro et al. 2008, 2012). Similarly, comparisons between different AM fungi should be made at similar inoculum densities. A study by Rajan et al. (2000) showed that the infectivity and rate of colonization development of *Gigaspora margarita* were greater than those of *Rhizophagus intraradices* (=*Glomus intraradices*). Likewise, propagules of *F. mosseae* were found to be most effective compared to those of *R. intraradices* (Rajan et al. 2000). Studies have also shown that inoculum consortia of AM fungi perform better than inoculum containing single taxa (Khade and Rodriguez 2009). In a recent study, Jin et al. (2013) using plant growth parameters and molecular techniques to detect the presence of AM fungi within plant roots showed that a mixed culture [*Rhizophagus irregularis* (=*Glomus irregulare*), *F. mosseae* and *Rhizophagus clarus* (=*Glomus clarum*)] functioned better than a single species (*R. irregularis*) inoculation in field-grown pea plant.

4.7.3 Efficiency of Inocula

For field applications, it is always essential to confirm that the inoculated microorganisms possess all the qualitative characteristics of an inoculum. The efficiency of the inoculum primarily depends on the performance of the AM fungal strain adapted to the host plants for their establishment. However, this tends to vary with the fungus and the host plants. To characterize the efficiency of inoculum, various approaches including the identification of the spore, estimation of root fungal colonization (Dalpé 1993) and an assessment on spore germination rate are often used. Further, molecular techniques are also handy for the detection of the introduced AM fungal strain among the indigenous AM fungal strains naturally occurring in the soil. These techniques are not consistent with morphological identification, due to the large genetic variability in AM fungi, and these techniques are rarely used. Consequently, internal transcribed spacer (ITS) sequences of ribosomal DNA genes (rDNA) were also used in some discrimination. Current researches focus on the development of consistent molecular techniques to trace the inoculated strains using PCR and species-specific primers (Séguin et al. 2003) and also for the entrapment of AM fungal propagules in natural polysaccharide gels (Vassilev et al. 2005; Siddiqui and Kataoka 2011) are under study. Such technological breakthroughs would greatly facilitate both fundamental and applied researches on mycorrhizae as well as improve quality control of commercial inocula.

5 Methods of Inoculum Production

The production of inoculum is more essential for AM fungi due to its obligate symbiotic nature. Traditionally, AM fungi are propagated through open pot cultures. Starter cultures are usually initiated from spores or colonized root fragments, which are later incorporated into the growing medium for seedling production (Brundrett et al. 1996). The fungi spread in the substrate and colonize the roots of the seedlings. Both colonized substrates and roots can then serve as mycorrhizal inoculum. Soilless culture systems such as aeroponic cultures enable the production of cleaner spores and facilitate uniform nutrition of colonized plants (Singh et al. 2012). The successful propagation of some AM fungal strains on root-organ cultures has facilitated the development of monoxenic strains that can be used directly as inoculum for in vitro plant production systems or for large-scale inoculum production (Fortin et al. 2002).

5.1 Off-Farm Methods

The various advantages and disadvantages of different off-farm inoculum production methods are shown in Table 3. Highly infective soil-based inocula are quite easy to produce and handle. However, the time span required to produce appreciable quantities of soil-based inocula can range between 6 and 12 months. An inoculum form produced using light expanded clay aggregates as substrate is of interest (Dehne and Backhaus 1986), as the porous material containing infective mycelium and spores can be easily separated from the plant roots (Feldmann and Idczak 1992). The aggregates can later be surface sterilized and applied to field-grown crops in small quantities (Baltruschat 1987). Vermiculite is an inorganic carrier for AM inoculum production, as it is an ideal substrate for AM fungal sporulation (Barea et al. 1993). Sheared-root inocula (Sylvia and Jarstfer 1992), prepared from aeroponic cultures (Hung and Sylvia 1988; Jarstfer and Sylvia 1999), are also routinely used in inoculation programmes. Surface-disinfected AM fungal propagules can also be used especially under in vitro conditions. Two methods of off-farm inoculum production (open pot culture and root-organ culture) are detailed below.

Table 3 Arbuscular mycorrhizal fungal inoculum types with their advantages and disadvantages

Inoculum type	Advantages	Disadvantages
Soil based	Long shelf life	Bulk and heavy
	Useful at transplanting	Needs soil sterilization
Soilless substrate	Weightless than soil	Needs careful control of watering and fertilizer application
	Uniform composition	
	Can be dried and stored	
Surface-sterilized AM propagules	Aeroponically developed colonized roots can be sheared	Needs highly skilled technique
Entrapment in polymer gel, alginate, hydrogel, hydroponic, aeroponic and root-organ culture	Can be kept free of extraneous organisms	Relatively expensive
	Can be dried and stored	

Modified from Azcon-Aguilar and Barea (1997) with permission

5.1.1 Open Pot-Culture Production

Arbuscular mycorrhizal fungi are obligate symbionts, which require a suitable host plant for its establishment and proliferation. Conditions for large-scale inoculum production need to be optimized. Care should be taken to identify and avoid contamination from undesired species during monoculture. The process to attain huge amount of targeted inoculum is rather lengthy. The inoculum production through open pot cultures involves the following steps.

5.1.1.1 Isolation of AM Fungal Strain

Spores of desired AM fungal strain are collected from the plant's rhizosphere by wet-sieving and decanting technique (Gerdemann and Nicolson 1963). However, for raising monoculture, AM fungal propagules can be acquired from trap cultures. The trap culture constitutes the host plant rhizospheric soil diluted equally with sterilized sand (Menge 1984). The resulting AM fungal spore densities are higher compared to the initial rhizosphere soil. In fact, undetected spores in the initial extraction of field soil could be detected in trap culture (Mortan et al. 1995). Liu and Wang (2003) evaluated the presence of AM fungal spores by using different trap plants. The results of this study suggested that the numbers of AM fungal spores and species were higher in trap cultures and clover (*Trifolium repens*) was found to be a suitable host for identifying the AM fungal diversity. Using spores for initiating cultures certainly has some benefits like easy detection of undesired fungal spores, quick enumeration and evaluation of spore viability and germination and a reduction of pathogen inclusion (Dodd and Thomson 1994). On the other side, AM fungal spores sometimes exhibit dormancy, which reduces the potential of the inoculum (Gemma and Koske 1988).

5.1.1.2 Choice of a Host Plant

The selection of a suitable host plant should be based on high mycorrhizal dependency, adaptability to in vitro or greenhouse conditions and in having an extensive root system. The host plants commonly used for raising pot cultures are corn, onion, leek (*Allium porrum*), *Sorghum halepense*, Bahia grass (*Paspalum notatum*), Guinea grass (*Panicum maximum*), buffell grass (*Cenchrus ciliaris*) and subterranean clover (*Trifolium subterraneum*) (Chellappan et al. 2001). Generally, monocots are preferred as hosts, because the fibrous root system enables uniform spreading of the roots in a given volume of soil than plants with tap roots. Further, the fibrous root system renders monocots less dependent on mycorrhizal fungi than dicots.

5.1.1.3 Optimizing Growing Conditions

Properly sterilized substrate is essential not only to maintain the purity of a culture but also for avoidance of diseases. Usually, equal proportions of sterilized sand soil mixture are used for raising inoculum (1:1; sand/soil). A coarse-textured sandy soil (Gaur and Adholeya 2000) mixed with vermiculite or perlite or turface (Dehne and Backhaus 1986) can also be used. Inadequate mineral nutrient in the substrate may affect plant and in turn the fungal development. However, the excess of available P can inhibit AM fungal propagation. As N, K, Mg and microelement ratios may affect AM inoculum development, plant fertilization needs to be performed artificially especially when inert substrates are used for inoculum production (Dixon et al. 1999). In addition, other edaphic and climatic factors such as pH, soil temperature and aeration, light intensity and relative humidity need to be controlled for optimal AM fungal propagation (Rao and Tarafdar 1999). Some disadvantages of open pot-culture production include bulkiness, transportation problems, cross-contamination and lack of genetic stability (Abdul-Khaliq et al. 2001).

5.1.2 In Vitro Propagation on Root-Organ Culture

The root-organ culture involves the proliferation of excised roots under axenic conditions on an artificial nutrient media supplemented with vitamins, minerals and carbohydrates. This method was first used for in vitro AM fungal propagation by Mosse and Hepper (1975). Root-organ cultures with vigorous root formation and uniform growth under poor nutrient conditions (alteration in hormones) have been obtained through the transformation of roots by the soil bacterium *Agrobacterium rhizogenes* (Abdul-Khaliq et al. 2001). Nevertheless, when hairy root technique started to emerge, AM fungal propagules like spores or sporocarps, mycorrhizal root bits and even isolated vesicles were used in hairy root cultures to initiate in vitro AM fungal inoculum

(Kapoor et al. 2008). Surface sterilization of AM fungal spores is done using various sterilizing agents like chloramine-T or Tween 20 (Fortin et al. 2002) followed by antibiotic solution wash to remove contaminants from spore surfaces. All the above said processes need to be carried at reduced temperatures. The selection of culture medium is of prime importance, because both roots and AM fungal propagules require different media compositions for their growth. The negative geotropic nature of transformed roots facilitates its contact with the AM fungal hyphae, thereby initiating colonization. Recently, Abd-Ellatif et al. (2012) demonstrated the successful establishment of AM fungal association in root-organ culture using tomato hairy roots.

5.2 On-Farm Methods

On-farm production of AM fungal inoculum entails increasing the propagules of desired isolates and indigenous AM fungi in fumigated and unfumigated field soils, respectively, or transplanting pre-colonized host plants into compost-based substrate (Douds et al. 2005). This type of AM fungal inoculum production would enable farmers to obtain inoculum at a cheaper cost and make their transportation easy. Furthermore, farmers could easily produce locally adopted isolates and generate a taxonomically diverse inoculum in large quantities.

5.2.1 Method 1

The earliest method of inoculum production for an effective strain of the AM fungus *Rhizophagus manihotis* (= *Glomus manihotis*) was developed by Sieverding (1987, 1991) in Columbia. In this method, first, a 25 m^2 field plot was tilled and fumigated to eliminate the indigenous AM flora. After the fumigant has dissipated, the inoculum of the specific AM fungal strain (*R. manihotis*) was inoculated into holes drilled in the soil and then seeded with a grass host, *Brachiaria decumbens*. Simultaneously, pre-colonized *B. decumbens* plants were also transplanted to the inoculum preparation plots, thereby minimizing the amount of starter inoculum needed. After 4 months of growth, the soil and roots were harvested to a depth of 20 cm and used as inoculum.

5.2.1.1 Advantage

A postharvest analysis of the inoculum showed that fumigation of the soil was essential to increase the AM fungus spore production per given quantity of the soil. Further, fumigation also increased the relative proportion of spores of the desired AM fungal isolate relative to indigenous AM fungi compared to unfumigated and inoculated plots.

5.2.2 Method 2

The second method of on-farm AM fungal inoculum production involves preparing raised soil beds (60 × 60 × 16 cm) (Gaur 1997; Douds et al. 2000). After fumigation of the beds, the AM fungi from a starter inoculum were inoculated into furrows in the raised beds. A succession of hosts [(e.g. *Sorghum sudanese*, corn and carrot (*Daucus carota*)] were grown for 1 year of 4 months each. The growth cycle was carried over a course of 3 years. After the third cycle started to progress, the soil in raised beds was found to be ready to be used as inoculum.

5.2.2.1 Advantage

An approximately tenfold increase in AM fungal inocula was evident from year 1 to year 3, yielding around 2.5×10^6 propagules per bed.

5.2.3 Method 3

Gaur et al. (2000) and Gaur and Adholeya (2002) later modified the above method to yield a shorter inoculum production cycle without the use of fumigants. Raised beds were prepared as stated above (method 2) by using 2:1 (v/v) mixture of soil to leaf compost. The beds were either inoculated or left uninoculated to enhance the proliferation of indigenous AM fungi. In this method, only one plant growth cycle was used involving forage crops or vegetables as host plants.

5.2.3.1 Advantage

In this method, inoculum production was 15- to 20-fold greater than the starter inoculum used. This method produced only 55–69,000 propagules per bed, 40-fold lower than the 3-year method (method 2).

5.2.4 Method 4

In 2005, Douds et al. developed another method for on-farm production of AM fungal inoculum for temperate regions. Raised bed enclosures (0.75 × 3.25 × 0.3 m) were constructed with silt fence walls, weed barrier cloth floors and plastic sheeting dividing walls dividing the enclosure into 0.75 m square sections. The enclosures were filled to a depth of 20 cm with a 1:4 (v/v) mixture of compost and vermiculite. Pre-colonized ten Bahia grass plants were transplanted into the enclosures. One AM fungal isolate was used per enclosure section. The enclosures were tended for one growing season and watered as needed (Douds et al. 2005).

5.2.4.1 Advantage

The advantage of this method includes the production of significant quantities of the desired AM fungi. An average of 95×10^6 propagules could be produced per 0.75 × 0.75 m enclosure section.

5.2.5 Method 5

In 2006, Douds et al. suggested another method for on-farm production of AM fungus inoculum. Bahia grass seedlings colonized by AM fungi were transplanted into raised bed enclosures consisting of vermiculite mixed with either field soil or yard clipping compost or vermiculite mixed with yard clipping compost or dairy manure/leaf compost. The propagule yield was higher in compost and vermiculite mixture compared to soil-based mixture. Inoculum production in a 1:4 (v/v) mixture of yard clipping compost and vermiculite media was more (503 propagules cm^{-3}) than those with 1:9 and 1:99 (v/v) mixtures (240 and 42 propagules cm^{-3}), respectively (Douds et al. 2006).

5.2.5.1 Advantage

This method enables the production of concentrated AM fungal inoculum that can be readily used in horticultural potting media for vegetable seedling production. Supplemental nutrient additions are unnecessary during inoculum production.

5.2.6 Method 6

In 2010, Douds et al. modified the existing method for the production of AM fungal inoculum in temperate climates. Black plastic bags filled with approximately 20 L of a 1:4 (v/v) mixture of pasteurized compost and vermiculite served as the growing medium. To this growing medium, field soil (containing 12 propagules cm^{-3}) collected from the top 10 cm from a field was mixed at the rate of 100, 200 or 400 cm^3. Three-month-old non-mycorrhizal or mycorrhizal Bahia grass seedlings were planted in the bags at a rate of five plants per bag and grown for 3 months. Adding 100 cm^3 of field soil to the growing medium and planting with non-mycorrhizal seedlings produced 465 propagules cm^{-3} compared to 137 propagules cm^{-3} for planting with the pre-colonized seedlings (Douds et al. 2010).

5.2.6.1 Advantage

This modification to the existing method allows greater flexibility and makes it easier for the production of the AM fungal inoculum directly on the farm. This method could be readily adopted by farmers.

6 Determination of Infective Propagule Abundance

The most suitable and convenient method to determine the number of infective propagules of AM fungi in a crude inoculum, soil or mycorrhizal root bits is termed as the most probable number (MPN) technique (Alexander 1982). It has been assessed by using a statistical estimation of microbial population density (Cochran 1950).

6.1 Inoculum Management

Inoculum formulation procedure consists of placing fungal propagules (root fragments, mycelium and spores) in a carrier (perlite, peat, inorganic clay, zeolite, vermiculite, sand, etc.) for a given application (Gianinazzi and Vosátka 2004). The critical factor that determines the inoculum efficiency is the dosage and the time of inoculation. Although, theoretically, a single propagule of AM fungi is sufficient to initiate mycorrhization, the colonization process in such cases is very slow to be of agronomic interest. About 1–2 kg of soil inoculum (with 5,000–10,000 propagules) per m^2 of seedbed could be an appropriate application rate. However, the application rate for each crop species has to be standardized for a given set of environmental conditions (Muthukumar and Udaiyan 2003). The time of inoculation is also important, and in general, the earlier the inoculation, the greater the benefit to the plant (Barea et al. 1993).

6.2 Inoculation Methods

The aim of inoculation is to introduce desired AM fungal propagules into the rhizosphere of the target plant (Jarstfer and Sylvia 1992). Various methods of AM fungal inoculation for transplanted and field-sown crops have been detailed by Bagyaraj (1992). The most common method is to place the inoculum below the seed or seedling, prior to seeding or planting. Seedlings raised in sterilized or unsterilized nursery beds or containers containing selected AM fungi can be transplanted after mycorrhizal association is well established. This method has been successfully used for agronomic crops like chilli, finger millet, tomato and tobacco (*Nicotina tabacum*) (Govinda Rao et al. 1983; Sreeramulu and Bagyaraj 1986). For field-sown crops, AM fungi can be applied as seed coating (Hattings and Gerdemann 1975), mycorrhizal pellets (Hayman et al. 1981; Hall and Kelson 1981), fluid drilling (Hayman et al. 1981) and inoculation in furrows (Hayman et al. 1981; Powell and Bagyaraj 1982).

7 Conclusion

The role of AM fungi in enhancing plant growth is proved beyond doubt both under on-field and off-field conditions. Responses to AM fungal association are most widely to occur when mycorrhizal-dependent crop species are raised on substrates with low P levels. Therefore, it is important to determine the mycorrhizal dependency of the crops grown in a region and to select those which could respond to AM inoculation. Screening for selection of an efficient crop–AM fungal combination should be undertaken. Research should be intensified in the direction of manipulating AM fungi in the indigenous AM fungal community to achieve maximum crop productivity. The optimization of agronomic practices, reducing fertilizer input and use of cheap source of fertilizer (rock phosphate, organic manures) should be investigated. Top priority should be given to the development of new technologies for rapid and large-scale quality inoculum production. Further, one of the main tasks in AM research is to raise awareness in the growers' mind about the potentials of AM technology in sustainable crop production and soil conservation.

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