Chapter 25
Mycorrhizae: A Sustainable Industry for Plant and Soil Environment

Rouf Ahmad Bhat, Moonisa Aslam Dervash, Mohammad Aneesul Mehmood, Bhat Mohd Skinder, Asmat Rashid, Javeed Iqbal Ahmad Bhat, Dig Vijay Singh, and Rafiq Lone

Abstract The rhizosphere is an environment of plant roots in which most of the microbial activities of soil occur. The two vital components of soil rhizosphere are root exudates and soil microbes. Root exudates are the chemical compounds that are secreted by roots and act as a source of food for soil microbes especially for mycorrhizae. These chemical compounds plays significant role in soil microbe and plant interaction. The soil mycorrhizae are important for plant growth development and health. They are the main components that enrich the soil nutrients and maintain the soil health in sustainable manner. Furthermore, they enhance the plant growth regulators, provide defense mechanism to the plants, regulate enzymatic activities, increase rate of photosynthesis and supports in bioremediations, thus acting as eco-facilitator in sustainable agriculture both in terms of production and environmental protection.

25.1 Introduction

The rhizosphere is a soil environment that surrounds the plant roots and is crucial for plant life. This region around the plant root is highly active and is also described as a zone of maximum microbial activity. The microbial population present in this environment is relatively different from that of its surroundings due to the presence of root exudates that serve as a source of nutrition for microbial growth (Burdman et al. 2000). The microorganisms may be present in the rhizosphere, rhizoplane,

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R.A. Bhat • M.A. Dervash • M.A. Mehmood • A. Rashid • J.I.A. Bhat • D.V. Singh
Division of Environmental Sciences, Sher-e-Kashmir University of Agricultural Sciences and Technology, Shalimar, Kashmir 190025, India

B.M. Skinder
Department of Environmental Sciences, University of Kashmir, Hazratbal, Srinagar 190006, India

R. Lone (✉)
Department of Botany, SBBS University, Khiala, Jalandhar, Punjab 144030, India
e-mail: rafiqlone@gmail.com

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root tissue and/or in a specialized root structure called a nodule. Very important and significant interactions were reported among plant, soil, and microorganisms present in the soil environment (Antoun and Prevost 2005). These interactions may be beneficial, harmful and or neutral, and can significantly influence plant growth and development (Adesemoye and Kloepper 2009; Ahmad et al. 2011; Lau and Lennon 2011: Khanday et al. 2016). The microorganisms colonizing plant roots generally include bacteria, algae, fungi, protozoa and actinomycetes. Enhancement of plant growth and development by application of these microbial populations is well evident (Bhattacharyya and Jha 2012; Gray and Smith 2005; Hayat et al. 2010; Saharan and Nehra 2011). Fungi represent a significant portion of soil rhizosphere microflora and influence plant growth. The symbiotic association generated by fungi with plant roots (mycorrhizae) increases the root surface area, and therefore enables the plant to absorb water and nutrients more efficiently from large soil volume. The mycorrhizal association not only increases the nutrient and water availability, but also protects the plant from a variety of abiotic stresses (Evelin et al. 2009; Miransari 2010). Mycorrhizae play significant role in enhancing plant growth by way of different mechanisms. Exploring the mechanisms of growth promotion by mycorrhizae could be very useful for enhancing plant growth by using these microbial populations together, particularly under stressful environments. Although a number of studies have shown that combined application of mycorrhizae could be a meaningful approach for sustainable agriculture (Denton 2007; Najafi et al. 2012; Ordookhani et al. 2010), there are still certain aspects which need further investigations for obtaining maximum benefits in terms of improved plant growth from this naturally occurring population. The give and take, and vice-versa association between plant roots and fungi has great impact on crop quantity and quality. Ectomycorrhizae and arbuscular mycorrhizae are the two common kinds of fungi involved in such interactions and certainly the most plentiful fungi that are normally present in agricultural soils. They form symbiotic association with terrestrial as well as aquatic plants (Christie et al. 2004; Liu and Chen 2007; Willis et al. 2013). Almost 75–80% of all plants, including, terrestrial, aquatic mostly agricultural, horticultural, and hardwood crop species are able to establish this kind of symbiotic interaction that benefits both plant and fungi. These fungi enter into root cortical cells and form a particular haustoria-like structure called arbuscule that acts as a mediator for the exchange of metabolites between fungus and host cytoplasm (Oueslati 2003). The mycorrhiza hyphae also proliferate into the soil which helps plants to obtain mineral nutrients and water from the soil and also contribute to improving soil structure (Javaid 2009; Rillig and Mummey 2006). AM fungi play a very important role in ecosystems through nutrient cycling (Shokri and Maadi 2009; Wu et al. 2011a, b; Yaseen et al. 2012). Growth and productivity of several field crops have been observed by root colonization of mycorrhizal fungi (Cavagnaro et al. 2006; Nunes et al. 2010). Mycorrhizae increase the availability and supply of slowly diffusing ions, such as phosphate to the plant (Sharda and Koide 2010). In addition to their significant role in P acquisition, AM fungi can also provide other macro- and micro-nutrients such as N, K, Mg, Cu and

Zn, particularly in soils where they are present in less soluble forms (Meding and Zasoski 2008; Smith and Read 2008).

25.2 Mycorrhizae to Improve Plant Growth Under Extreme Adverse Conditions

The growth support due to mycorrhizal relationship can be described by numerous ways of mechanisms performed by fungi under different conditions. These include release of metabolites viz., phytohormones, amino acids, vitamins, mineralization and solubilization processes. In addition to providing nutritional and structural benefits to plants, they also impart other benefits to them including production/accumulation of secondary metabolites, osmotic adjustment under osmotic stress, improved nitrogen fixation, enhanced photosynthesis rate, and increased resistance against biotic and abiotic stresses (Khaosaad et al. 2007; Ruiz-Lozano 2003; Schliemann et al. 2008; Selvakumar and Thamizhiniyan 2011; Sheng et al. 2009; Shinde et al. 2013; Takeda et al. 2007; Wu and Xia 2006). Many researchers have reported that mycorrhizae fungi can improve plant tolerance to heavy metals, drought, and salinity, and also protect plants from pathogens (Azcon-Aguilar et al. 2002; Gamalero et al. 2009a, b; Gosling et al. 2006; Marulanda et al. 2006, 2009; Vivas et al. 2003; Zhang et al. 2010). They can also improve crop growth and yield by alleviating the negative influence of allelochemicals (Bajwa et al. 2003; Khanday et al. 2016). These effects can be described by number of different ways of mechanisms that may differ depending on plant and mycorrhizae association as well as internal and external stress factors. For example, a number of studies have shown that improved P nutrition under salinity and water deficit environment is a primary mechanism for promoting stress tolerance in plants (Cantrell and Linderman 2001; Colla et al. 2008; Feng et al. 2002). There are many reports which show that mycorrhizae fungi can increase soil enzyme activities, such as phosphatase (Mar Vazquez et al. 2000). Some studies have also demonstrated that mycorrhizae association not only influences P nutrition but also affects the physiological processes of plants by increasing proline contents (Ruız-Lozano et al. 1995). Proline is known to act as an osmoregulator under stress conditions (Ashraf and Foolad 2007). The mechanisms used by mycorrhizae to alleviate effects induced adverse conditions of salinity on plant growth include: improvement of plant nutrition, variation in Na^+ and K^+ uptake, modification in physiological and enzymatic activities and alteration of the root architecture to facilitate water uptake (Evelin et al. 2009; Gamalero et al. 2010; Zhang et al. 2011; Zolfaghari et al. 2013). Physiological processes involved in osmoregulation like enhanced CO_2 rate, water use efficiency, and stomatal conductance are also influenced by the activities of mycorrhizae fungi (Birhane et al. 2012; Ruiz-Lozano and Aroca 2010). Mycorrhizae also increase the nitrogen availability of host plant under drought conditions (Subramanian and Charest 1999). It has been shown that mycorrhizal plants absorb water more efficiently under water deficit environment (Khalvati et al. 2005) that might be due to modification in root architecture which results in better root growth due to numerous branched roots (Berta et al. 2005). As abscisic acid regulates the stomatal conductance by closing stomata under water limited environment, the positive effect of mycorrhizae fungi on plant growth and development under drought stress might be due to its influence on abscisic acid concentration in plants (Jahromi et al. 2008). It has also been observed that mycorrhizae fungi increase salinity tolerance of host plants by improving water status of the inoculated plants by facilitating water transport in plants (Ouziad et al. 2006). Mycorrhizae also enhance soluble sugars and electrolyte concentrations in host plants. For example, improved osmoregulation capacity in mycorrhizae inoculated maize was related to higher soluble sugar and electrolyte concentrations (Feng et al. 2002). Porcel and Ruiz-Lozano (2004) and Al-Garni (2006) also reported increased sugar concentrations in mycorrhizal plants of soybean and *Phragmites australis*. It is also well documented that mycorrhizae fungi affect the expression of a number of antioxidant enzymes (Gamalero et al. 2009a, b), which protect the plants from reactive oxygen species produced under stress conditions. Similarly, improved nodulation due to increased activities of these enzymes under salinity stress has been observed along with other factors such as leghemoglobin content, nitrogenase activity and polyamine contents (Gamalero et al. 2009a, b; Garg and Manchanda 2008; Matamoros et al. 2010; Sannazzaro et al. 2007; Yaseen et al. 2012). Another mechanism used by mycorrhizae fungi to facilitate plant growth under salinity stress is the regulation of plant nutrition. High Na^+ concentration under salinity stress is detrimental for normal plant growth and low K^+/Na^+ ratio has been observed generally in salt sensitive plants (Ashraf et al. 2004). Therefore, improved K^+/Na^+ ratio is believed to be a potential indicator of salinity tolerance in most plants. The AM fungi also play an important role in maintaining a high K^+/Na^+ ratio in host plants exposed to saline conditions (Giri et al. 2007; Sannazzaro et al. 2006; Selvakumar and Thamizhiniyan 2011; Zhang et al. 2011). In general, mycorrhizae enhance plant growth under stressful environments by a number of mechanisms such as regulation of plant nutrition, production of hormones and antioxidant enzymes, and regulation of a multitude of physiological processes. However, it is also evident from the above discussion that the effectiveness of these mechanisms also depends on the extent of mycorrhizae and host plant association as well as a number of soil and plant factors.

25.3 Phytohormones

Plant growth regulators levels have been observed to change during mycorrhizae fungi development reported by many researchers and almost all hormones have been proposed as important regulators of the symbiosis (Hause et al. 2007; Ludwig-Muller 2010; Foo et al. 2013). Moreover, many of these hormones have been shown to be involved in root morphogenesis that enhances the development and improvement growth of plants especially crops (Rouached et al. 2010; Chiou and Lin 2011; Hammond and White 2011; Sato and Miura 2011; Niu et al. 2013).

25.3.1 Auxin

Auxin is an essential regulator of plant growth and developmental processes. In the roots, it positively regulates the size of the root apical meristem by promoting cell division antagonistically to cytokinin, and it is involved in the regulation of cell elongation with ethylene (Muday et al. 2012; Vanstraelen and Benková 2012). Moreover, it is the main regulator of each lateral root (LR) formation step (Fukaki and Tasaka 2009; De Smet 2011). Elevated levels of auxin, either due to exogenous application or to enhanced biosynthesis, are sufficient to increase lateral root formation, while mutations that reduce auxin signalling, such as solitary root of Arabidopsis, cause a strong reduction in lateral root formation (revised by Ivanchenko et al. 2008). Since mycorrhizae colonization increases root branching, the involvement of auxin in the root system architecture regulation of mycorrhizal plants has been suggested (Ludwig-Muller 2010; Hanlon and Coenen 2011; Sukumar et al. 2013). Auxin is involved in the mycorrhizae host–fungus interaction. The addition of auxin has been shown to increase spore germination and hyphal growth, and to influence the infection rate and percentage of colonization (Ludwig-Muller 2010). The auxin level in plant tissues increases in different plant–fungus associations (Ludwig-Muller 2010), probably independently of fungus production (Jentschel et al. 2007; Ludwig-Muller 2010).

25.3.2 Cytokinins

Cytokinins play a crucial role in regulating the proliferation and differentiation of plant cells, and also control many developmental processes. They are recognized as essential regulators of the plant root system, as they are involved, antagonistically to auxin, in the control of the size of the root apical meristem, and in the rate of root growth and lateral roots organogenesis (Sakakibara 2006; Werner et al. 2010; Marhavý et al. 2011). They can redirect assimilates and induce invertases, thus contributing directly to the plant carbon redistribution (Ludwig-Muller 2010). However, recent studies have suggested that cytokinins might not be involved to any great extent in the regulation of mycorrhizal development (Foo et al. 2013). A number of mycorrhizae plants accumulate more cytokinins than non mycorrhizal plants in both the shoots and the roots (Torelli et al. 2000; Shaul-Keinan et al. 2002). Since the main sites of cytokinin synthesis include the root tips (Aloni et al. 2006), the high cytokinin level found may be, in part, a consequence of increased root branching.

25.3.3 Ethylene

Ethylene plays an important role in coordinating internal and external signals, as well as in several stress responses and interaction of plants with other organisms (Lei et al. 2010; López-Ráez et al. 2010). In mycorrhizae symbiosis, ethylene and salicylic acid function as negative regulators of mycorrhizal intensity (Gamalero et al. 2008; Ludwig-Muller 2010). In fact, a strong ethylene inhibitory effect has been observed on early symbiotic gene expression, on fungus entry into roots (Mukherjee and Ané 2011) and on intra radical fungal spread (Martín-Rodríguez et al. 2011). The ethylene content is increased by a deficiency of ABA, which is in contrast necessary for arbuscule formation and is positively correlated to mycorrhizal establishment (Ludwig-Muller 2010; Martín-Rodríguez et al. 2011). Accordingly, most researchers indicate that ethylene production is diminished in mycorrhizae-infected plants (López-Ráez et al. 2010), although a few contradictory results have also been reported (Dugassa et al. 1996). Ethylene, like auxin and cytokinin, is an important regulator of root morphogenesis. It inhibits root elongation by reducing cell elongation synergistically with auxin (Muday et al. 2012). However, it also acts antagonistically to auxin by inhibiting LR formation in the earliest stages of LR initiation, as has been shown through treatments with ethylene.

25.4 Mycorrhizae Symbiosis a Sustainable Ecosystem Services

Plants in ecosystems perform a series of functions that are beneficial to the well-being of humans, providing multiple resources and processes (Daily 1997). Trade-offs and links between plants and soil microbial communities can act as drivers of a wide range of processes in ecosystems (Lavorel 2013; Grigulis et al. 2013). Given the beneficial functions of mycorrhizae fungi on plant fitness, resilience against environmental stresses, nutrient cycling, and soil quality, mycorrhizae symbiosis is now recognized to play a fundamental role as a provider of ecosystem services. Various ecosystem services delivered by mycorrhizae have been identified: biofertilization from the mycorrhizae promotion of plant growth, which in turn reduces fertilizer requirements, stabilization of soil structure, and bioregulation consequent to the plant metabolic modifications by mycorrhizae fungi (Gianinazzi et al. 2010). Linking functional traits of plants and soil microbes, such as mycorrhizae fungi, with their delivery of multiple ecosystem services is currently considered a rational mean for assessing the functioning of a given ecosystem (De-Bello et al. 2010). Less attention, however, has been given to beneficial soil organisms in general and mycorrhizae in particular and their influence on the processes of ecosystems that contribute to the ecosystem services in agroecology. The positive effect of mycorrhizae on the ability of plants to counteract the conditions of drought confers to mycorrhizae a pivotal role as a valuable technology not only for the sustainability of agricultural systems, but also for the restoration of degraded natural arid and semi-arid areas, where multiple environmental stresses, including drought, occur (Gianinazzi et al. 2010; Barea et al. 2011). In light of the assessment of the multiple ecosystem services provided by mycorrhizae, critical advances are required for elucidating the functional importance and value of plant and mycorrhizal diversity that are necessary for the functioning of ecosystems. These are also required for clarify the links among plant traits and their associated mycorrhizae fungal characteristics to quantify the contribution of plant–mycorrhizae fungi associations to ecosystem services under various environmental constraints (Barea et al. 2011; Grigulis et al. 2013; Lavorel 2013). The role of mycorrhizae symbiosis in the functional traits of both plants and microbes that could characterize above- and belowground ecosystem services has not yet been explored. The application of a trait-based approach to both plant and mycorrhizae fungal communities represents a promising opportunity to understand how functional mycorrhizae feedbacks between plant and mycorrhizae fungi translate into interactions between ecosystem services (Lavorel 2013).

25.5 Mycorrhizal Association Imparting Drought Tolerance in Crop Plants

Mycorrhizal association improving drought tolerance of agronomically important crop plants and has been reported by earlier workers in crops like wheat, soybean, onion, capsicum, maize, barley, cotton, etc. (Beltrano et al. 2013; Maya and Matsubara 2013). Improved growth and development of mycorrhizal plants especially in stressful environment is partly attributed to better water status of the leaf tissues (Colla et al. 2008), improved abilities to absorb nutrients from soil, higher root hydraulic conductivity and high photosynthetic rates of mycorrhizal plants (Yang et al. 2014). Therefore, it is evident that the mycorrhizal fungal association offers a number of benefits to the plants. Although the association is costly to the plant as it has to shell down some amount of carbon to the fungi, still the benefits derived in terms of protecting the plants under stress is much more than what the plant is losing. Under the conditions of water deficit, the external mycelium of *R. intraradices* may have a direct role in transport of considerable amount of nitrogen in the form of $NO^{-}{}_{3}$ as observed in maize plants where roots also had higher glutathione reductase activity and P status in host plants (Subramanian and Charest 1999). In general, drought affects the AMF colonization negatively (Ryan and Ash 1996), in wheat AMF has been shown to alleviate the drought stress and increase yield mainly through improved nutrient uptake (Al-Karaki et al. 2004). *Claroideoglomus claroideum* (*Glomus claroideum*) seems to play a key role in imparting drought tolerance in wheat by improved chlorophyll content and cell membrane permeability (Beltrano and Ronco 2008). Various horticultural crops have been shown to tolerate drought via AMF. For example, Wu et al. (2013) have reported that the AMF inoculated citrus exhibited higher drought tolerance than the non-AMF citrus. In lettuce, an important vegetable crop in Europe, the AMF association promoted secondary metabolite production thereby making the plants to withstand abiotic stress (Baslam and Goicoechea 2012). AMF has been shown to be associated with date palms indicating possible role of the AMF in withstanding droughts of deserts (Symanczik et al. 2014).

Inoculation of tomato plants with *R. intraradices* resulted in improved nutritional status, increased shoot dry matter, fruits and flowers with higher quantities of ascorbic acid and total soluble solids (Subramanian et al. 2006). Ballesteros-Almanza et al. (2010) observed that inoculation of common bean with AMF imparted drought tolerance by improving intraradical and extraradical hyphae, arbuscule development, and succinate dehydrogenase and alkaline phosphatase activity in root system. The list of AMF conferring drought tolerance on different crop species is given in Table 25.1.

25.6 Arbuscular Mycorrhizal Fungi as a Tool to Improve the Phytoremediation

Many large areas around the world are contaminated with heavy metals and organic compounds; most of these have not been remediated due to the high cost and technical drawbacks of currently available technologies. Heavy metals tend to accumulate in soils and aquatic sediments and can enter the food chain leading to the biomagnification phenomenon thereby representing a risk to the environment and to human health (Clijsters et al. 1999). Some essential elements, such as copper (Cu) and zinc (Zn), may be present in soils and waters at potentially toxic levels mainly as a result of agricultural and industrial practices (Ali et al. 2004). Alternative techniques for the clean-up of polluted soil and water, such as the cost-effective and less disruptive phytoremediation, have gained acceptance in recent years (Pilon-Smits 2005; Thewys et al. 2010). Trees have been suggested as suitable for phytoremediation due to their high biomass production (Dickinson and Pulford 2005) and because tree plantations can be multi-purpose (Tognetti et al. 2013). Poplar has many characteristics suitable for phytoremediation: a fast rate of growth, a deep and wide-spreading root system and a metal-resistance trait (Aronsson and Perttu 2001; Di Baccio et al. 2011; Sebastiani et al. 2004). Plant symbiotic fungi, such as mycorrhizae, and soil bacteria can confer increased tolerance to stress (Gamalero et al. 2009a, b). Arbuscular mycorrhizal fungi (AMF) form associations with the roots of the vast majority of land plants; the fungus colonizes the roots and forms arbuscules within root cortical cells thus improving plant nutrient uptake, especially phosphorus (Smith and Read 1997a, b; Khanday et al. 2016). Moreover, increasing evidence shows that symbiotic fungi contribute to plant adaptation to multiple biotic and abiotic stresses (Gohre and Paszkowski 2006; Lebeau et al. 2008, Lingua et al. 2002; Liu et al. 2007; Rodriguez and Redman 2008; Smith et al.

Table 25.1 Examples of AMF conferring drought tolerance in crop plants

Species	Crop	Stress	Mechanism	Reference
Claroideoglomus etunicatum	Maize	High temperature	Reduced membrane lipid peroxidation, membrane permeability and increased accumulation of osmotic adjustment compounds and antioxidant activity	Zhu et al. (2010)
Glomus versiforme	Citrus (*Citrus tangerine*)	Drought	Higher activities of catalase (CAT), ascorbate peroxidase (APX), superoxide dismutase (SOD)	Wu et al. (2006)
Funneliformis mosseae	Maize (*Zea mays*)	Drought	Accumulation of amino acids and imino acids, remarkable increase in trehalose content and higher trehalase activity	Schellenbaum (1998)
Funneliformis mosseae and *Claroideoglomus etunicatum*	Wheat (*Triticum asetivum*)	Drought	Higher biomass and higher grain yields, shoot P and Fe concentration in mycorrhizal plants	Al-karaki et al. (2004)
Glomus spp.	Wheat (*Triticum asetivum*)	Water stress	Mycorrhiza increased the content of free amino acids, proline, total soluble and crude protein, total carbohydrate, total soluble and insoluble sugars, and enhanced the activity of antioxidant enzymes like peroxidase (POX) and catalase (CAT)	Khalafallah and Abo-Ghalia (2008)
Rhizophagus intraradices	Sorghum (*Sorghum bicolor*)	Drought	Mycorrhiza minimized the adverse effect of drought and increased the grain yield by 17.8%	Alizadeh et al. (2011)
	Soybean (*Glycine max*)	Drought	Higher leaf water potential in mycorrhizal plants, and mycorrhiza protected the plants against oxidative stress	Porcel and Ruiz-Lozano (2004), Meddich et al. (2015)

(continued)

Table 25.1 (continued)

Species	Crop	Stress	Mechanism	Reference
Funneliformis mosseae *Rhizophagus diaphanum* *Glomus versiforme*	Trifoliate orange (*Poncirus trifoliata*)	Drought	Higher plant growth and biomass, acid and total phosphatase activity, leaf and root P contents in drought stressed mycorrhizal seedlings particularly in *F. mosseae*	Wu et al. (2011a, b)
Funneliformis mosseae	Sunflower	Drought	Inoculated plants produced more dry matter, heavier seeds and greater seed and oil yields with *F. mosseae*. Despite of reduction in N percentage due to drought, N percentage was higher in inoculated plants compared to control	Gholamhoseini et al. (2013)
Glomus spp.	*Boswellia papyrifera*	Pulsed water availability conditions	Higher level of AM colonization under irregular precipitation regime where mycorrhizal seedlings had higher biomass, increased transpiration, higher water	Birhane et al. (2012)
Funneliformis mosseae + *Rhizophagus intraradices*	Lettuce (*Lactuca sativa*.)	Water deficit	Under water deficit, the accumulation of potential antioxidants (mainly carotenoids, anthocyanins and to a lesser extent chlorophyll and phenolics) in the leaves of mycorrhizal lettuce plants were more. Shoot biomass in AM lettuce under moderate water deficit was equal to well watered AM plants. Improved lettuce quality and reduced irrigation without affecting lettuce production	Baslam and Goicoechea (2012)

2010). In the case of heavy metals, the beneficial effect varies according to plant and fungal species, metal and concentration (Bois et al. 2005; Lebeau et al. 2008; Takacs et al. 2005; Todeschini et al. 2007). The mechanisms by which AMF offer protection from stress has not been clarified, although decreased metal uptake has been reported in some cases (Christophersen et al. 2012; Mrnka et al. 2012). The potential of plant–microbe interactions in enhancing phytoremediation potential has been reviewed extensively elsewhere (Doty 2008; Lebeau et al. 2008; Rajkumar et al. 2012; Khanday et al. 2016). Also in poplar, the effects of bacterial endophytes (van der Lelie et al. 2009), and of endo- and ectomycorrhiza (Mrnka et al. 2012) on phytoremediation capacity have been described. Information regarding basic molecular processes underlying metal detoxification/tolerance is scarce especially in tree species. Metallothioneins are among the plant components that respond to metal stress. They are small proteins encoded by a multigene family whose members appear to be differentially regulated in relation to organ and developmental stage, and in response to a number of stimuli including heavy metals (Cobbett and Goldsbrough 2002). A role for metallothioneins in heavy metals detoxification and homeostasis has been proposed either because they bind to HMs or because they function as antioxidants (Akashi et al. 2004). The evidence is largely based on metallothioneins gene expression studies and yeast complementation experiments with plant metallothionein genes, and some of it comes from studies on poplar species or hybrids (Balestrazzi et al. 2009; Castiglione et al. 2007; Hassinen et al. 2009; Kohler et al. 2004).

25.7 Significance of Arbuscular Mycorrhizal Fungi (AMF) in Global Sustainable Development

25.7.1 Soil Fertility

Arbuscular mycorrhizal fungi can overcome nutrient limitation to plant growth by enhancing nutrient acquisition (Clark and Zeto 2000). Most studies have investigated P uptake but mycorrhizae have been implicated in the uptake of other essential nutrients also (Khanday et al. 2016). The increase in inorganic nutrient uptake in mycorrhizal plants is mainly because fungal hyphae provide the large surface area for nutrient acquisition to external root surface as compared to uninfected roots. As the fungal mycelium grows through soil, it scavenges for mineral nutrients and is able to make contact with uninfected roots, sometimes of different host species.

25.7.2 Phosphorus Uptake

Phosphorus is a major plant nutrient required in relatively large amounts and plays a vital role in all biological functions in energy transfer through the formation of energy-rich phosphate esters and is also an essential component of macromolecules such as nucleotiodes, phospholipids and sugar phosphates (Marschner 1995). The benefits of mycorrhizae are the increase in the phosphorus uptake by the plant. The general process of phosphorus uptake consists of three sub-processes; (i) absorption from soil by AMF hyphae, (ii) translocation along the hyphae from external to internal (root cortex) mycelia, (iii) the transfer of phosphate to cortical root cells (Barea 1991). The various mechanisms proposed to account for enhanced nutrient uptake include (i) increased exploration of soil; (ii) increased translocation of phosphorus into plants through arbuscules; (iii) modification of root environment; (iv) efficient utilization of P within plants; (v) efficient transfer of P to plant roots; and (vi) increased storage of absorbed P. Uptake of phosphate by roots is much faster than diffusion of ions to the absorption surfaces of the root (Bhat and Kaveriappa 2007). This causes phosphate depletion zone around the roots. The extensive extrametrical hyphae of AMF extend out into the soil for several centimeters so that it bridges the zone of nutrient depletion.

25.7.3 Nitrogen Uptake

Nitrogen (N) is essential for the formation of amino acids and is indirectly involved in protein and nucleic acid synthesis. AMF associated plants have increased N content in shoots. A number of mechanisms are suggested for this effects, namely (i) improvement of symbiotic nitrogen fixation; (ii) direct uptake of combined nitrogen by mycorrhizal fungi; (iii) facilitated nitrogen transfer, a process by which a part of nitrogen fixed by nodulated plants benefits the non-nodulated plants; (iv) increased enzymatic activities involved in nitrogen metabolism like pectinase, xyloglucanase and cellulose which are able to decompose soil organic matter (Barea 1991). The hyphae of AMF have the tendency to extract nitrogen and transport it from the soil to plants. They contain enzymes that breakdown organic nitrogen and contain nitrogen reductase which alters the forms of nitrogen in the soil. AM improves growth, nodulation and nitrogen fixation in legume-*Rhizobium* symbiosis. According to McFarland et al. (2010) more than 50% of plant N requirement is supplied by mycorrhizal association. Mycorrhizal inoculation enhanced activities of nitrate reductase, glutamine synthetase and glutamine synthase in the roots and shoots of mycorrhizal corn (*Zea mays* L.) as reported by Subramanian and Charest (1999). Recently, a plant ammonium transporter, which is activated in the presence of AMF has been identified and indicated that the way by which N is transferred in plant may be similar to P transfer (Guether et al. 2009).

25.7.4 Supply of Organic Mineral Nutrients

Although many mycorrhizal fungi can access inorganic forms of N and P, some litter-inhabiting mycorrhizal fungi produce proteases and distribute soluble amino compounds through hyphal networks into the root and *Glomus* has been shown to transport the amino acids glycine and glutamine into wheat (Hawkins et al. 2000).

25.7.5 Micronutrients

The extrametrical hyphae of AMF take up and transport potassium (K), calcium and sulphates and AM colonization affects the concentration and amounts of K in shoots. AM plants accumulate large quantities of some micronutrients (Zn, Cu, Co) under conditions of low soil nutrient availability (Feber et al. 1990). The absorption is attributed to the uptake and transport by external hyphae due to wider exploration of soil volume by extended extrametrical hyphae. Uptake and concentration of manganese (Mn) in plants may not be affected by AM and more often it may be lower in AM plants, thus contributing to higher Mn tolerance in plants. The enhanced iron (Fe) uptake may be due to specific Fe chelators.

25.7.6 Water Uptake in Mycorrhizal Association

AMF also play an important role in the water economy. The AMF association improves the hydraulic conductivity of the roots and improves water uptake by the plants or otherwise alters the plant physiology to reduce the stress response to soil drought (Safir and Nelson 1985). Mycorrhizal plants show better survival than non-mycorrhizal plants in extreme dry conditions. It reveals that mycelial network extends deeper and wider in the soil in search of water and nutrients. The permeability of cell membrane to water may also be altered by mycorrhizal colonization though the improved phosphorus nutrition and colonization by AMF can improve the drought resistance of plants (Sylvia and Williams 1992). Under conditions of drought stress, AMF exert their influence by increasing the transpiration rate and lowering stomatal resistance or by altering the balance of plant hormones (Huang et al. 1985). The change in leaf elasticity due to AMF inoculation improves water and turgor potential of leaf and also increase root length and depth (Kothari et al. 1990) and may also influence water relations and therefore, the drought resistance of the plants.

25.7.7 Soil Aggregation and Soil Stabilization

Disturbances in ecosystem affect the physical, chemical and biological processes in the soil. AMF help in the binding of soil particles and improve soil aggregation and soil conservation (Dodd 2000). Arbuscular mycorrhizal fungi are also known to enhance soil fertility, as they produce glomalin which upon accumulation in soil, along with the AMF hyphae forms micro aggregates and finally macro aggregates and, thus, acts as a backbone for soil aggregation and soil stabilization directly. It also releases exudates in the soil and thus promotes aggregate stability and also boost up other microorganism growth (Johnson et al. 2002; Khanday et al. 2016).

25.7.8 Role of AMF in Wasteland Reclamation

AMF have a great potential in the recovery of disturbed lands and these can be used in reclamation of wastelands. Inoculation with AM fungi can improve the growth and survival of desirable revegetation species. Colonization with AMF can cause a beneficial physiological effect on host plant in increasing uptake of soil phosphorus (Gerdemann 1975). Nicolson (1967) suggested that plant growth in wastelands could be effectively improved by incorporating AMF. It has been suggested that many plants may require mycorrhizal infection in order to survive on disturbed land. The absorptive surface area contributed by soil mycelium allows phosphorus uptake from a much greater volume. Host growth is also enhanced particularly in phosphorus-deficient soils (Mosse 1973). AM fungi have been conclusively shown to improve revegetation of coal spoils, strip mines, waste areas, road sites and other disturbed areas (Jha et al. 1994). Addition of AMF provides a nutritional advantage to associated plants in addition to providing possible resistance to low pH, heavy metal toxicants and high temperature. Presence and utilization of AMF has markedly increased the success of rehabilitation to these moisture deficient zones. Pre-inoculation of nursery seedlings with appropriate mycorrhizal fungi would benefit in revegetation of disturbed mined land. Rani et al. (2001) from our laboratory had worked on the effect of *Glomus mosseae, G. fasciculatum* along with *Rhizobium* and *Trichoderma* on better biomass yield of *Prosopis cineraria* and *Acacia nilotica* and reported further that co-inoculation with AM and *Rhizobium* resulted in maximum growth and best nodulation.

25.7.9 Role of AMF in Agriculture

The AMF symbiosis has also been shown to contribute substantially to soil conservation via its role in the formation of water-stable soil aggregates by the extrametrical hyphae. These aggregates are crucial for creating and maintaining a macroporous, water permeable soil structure, which is prerequisite for erosion resistance and also necessary for efficient nutrient cycling. The profuse use of phosphate fertilizers and chemicals causes pollution problems and health hazards. So the use of AMF is being encouraged in agriculture. The exploitation of mycorrhizal fungi is not easy because large scale production of AMF on field scale is not yet possible. But there is a possibility of mass production of AMF by means of appropriate crop and soil management practices. More farm management practices can influence the types of AMF found in agriculture soils. Apart from effects of fertilizer application on AMF, other practices like crop rotation, minimal cultivation, monoculture, tillage, organic amendments, and application of biocides affects the AMF (Kaur and Mukerji 1999) Mycorrhizal symbiosis plays an important role in the tropical agricultural crops because in tropical region, the soil is phosphorus deficient. Mosse (1973) reported that 75% of the phosphorus applied to the crops is not utilized by them but get converted to forms unavailable to plants.

25.7.10 Crop Dependency on Mycorrhizae

The relative dependency on AMF for nutrient uptake in crop plants depend on root factors such as surface area, root hair abundance and length, growth rate, response to soil conditions and exudations (Smith and Read 1997a, b). Crops such as corn (*Zea mays*) and flax (*Linum usitatissiumum*) are highly dependent on AMF to meet their early phosphorus requirements. Legumes, beans and potatoes also benefit significantly from mycorrhizae. Barley, wheat and oat benefit from mycorrhizal symbiosis.

25.7.11 Crop Rotation

It has been well established that the AMF activity is decreased by non mycorrhizal fungi host plants and highly mycorrhizal host crop increase AMF inoculum potential of the soil and colonization of the subsequent crops (Karasawa et al. 2002). An increase in AMF colonization and growth in maize occurred following sunflower (*Helianthus annuus,* mycorrhizal) when compared to corn following mustard (non-mycorrhizal). Here non mycorrhizal plants in the rotation reduce the rate of AMF colonization in following crops. Gavito and Miller (1998) also observed delayed AMF colonization of corn (*Zea mays*) following canola (*Brassica napus*); a non-mycorrhizal host species, when compared to the colonization of corn following the AMF host species bromegrass (*Bromus* spp.) and alfalfa (*Medicago sativa*).

25.7.12 Phosphorus Fertility

The benefits of AMF are greatest in systems where P in the soil is low. As the level of P available to plants increases, the plant tissue phosphorus also increases and the plant carbon investment in mycorrhizae is not economically beneficial to the plant (Grant et al. 2001). Encouragement of mycorrhizal symbiosis may increase early uptake of phosphorus, improving crop yield potential without starter P fertilizer application (Grant et al. 2005).

25.7.13 Seedling Establishment

AMF also play an important role in successful reforestation and there are several reports of increased establishment of many of forest seedlings in the field, like *Quercus rubra* (Dickie et al. 2001). In a study conducted by Ramos-Zapata et al. (2006) on establishment of *Desmoncus orthacanthos* along with inoculation of AM fungi resulted in a threefold increase in survival of seedlings in the field.

25.7.14 Alleviation of Environmental Stress

AMF are able to alter plant physiological and morphological properties in a way by which plant can handle the stress (Miransari et al. 2008). AM fungi facilitate better survival of plants under stress conditions through a boost up in uptake of nutrients particularly P, Zn, Cu and water. They make the host resilient to adverse conditions created by unfavourable factors related to soil or climate. The role played by these fungi in alleviating the stress on the plant due to drought, metal pollution, salinity and grazing is briefly described.

25.7.15 Water Stress

Water stress is a major agricultural constraint in the semi-arid tropics. It is well known to have a considerable negative impact on nodule function. It inhibits photosynthesis and disturbs the delicate mechanism of oxygen control in nodules. The latter is essential for active nitrogen fixation. AMF symbiosis can protect host plants against detrimental effects caused by water stress. Quilambo (2000) reported that inoculation with indigenous inoculants resulted in increased leaf and root growth and prevented the expected increase in root to shoot ratio and root–weight ratio that is normally observed under phosphorus deficient and water stress conditions in peanut. AMF improve the uptake of nutrients like N and P in water stressed conditions (Tobar et al. 1994). Water scarcity in soil is conveyed to the shoots by means of non-hydraulic chemical signal that is relayed from the dehydrating roots to the aerial shoots by the transpiration system. The response is expressed by the leaves in terms of stunted growth and decreased stomatal conductance. AMF alters this non-hydraulic root–to–shoot signaling of soil drying by eliminating the leaf response (Auge et al. 1986). The extraradical AMF hyphae increase the absorptive surface area of the roots (Hampp et al. 2000) which in turns reduces the resistance to water uptake. Hence, the role played by AMF in alleviating water stress of plants has been investigated and it appears that drought resistance is enhanced. An increase reliance on AMF for nutrient uptake can frequently be detected. Hence, AMF help to alleviate the water stress conditions.

25.7.16 Increased Resistance Against Root Pathogens

AM are intimately associated with their host plants, particularly the roots. Therefore, an interaction between the symbionts and plant pathogens is bound to occur. By creating new environments in their zone of influence, AMF contribute to the proliferation of specific microorganisms, a few of them interact with pathogens by antibiosis, competition and parasitism (Filion et al. 1999). Plants are subject to attack by various organisms ranging from fungi, bacteria, viruses and nematodes. Mycorrhizal plants usually suffer less damage from infection than non-mycorrhizal plants (Dehne 1982; Filion et al. 1999). Soybean colonized with *Glomus mosseae* grown in soils infested with pathogenic *Macrophomina phaseolina, Fusarium solani* and *Rhizoctonia solani* had growth greater or comparable to plants grown in without AMF inoculated soils. Mycorrhizal tobacco and alfalfa are reported to be resistant to a plethora of fungal pathogens like *Phytophthora megasperma, Pyrenocheata terrestris*, *Fusarium oxysporum, Pythium ultimum* etc. (Kaye et al. 1984; Schenk 1981). Several mechanisms have been proposed to explain the protection extended by AMF to host plants against attack by pathogens. Mycorrhizal root tissues are more lignified than non-mycorrhizal ones, particularly in the vascular region. This restricts the endophyte to the cortex. The same mechanism may hold back the invading organism too (Dehne 1982) increasing root thickenings, and causing chemical differences. Amino acid content, particularly arginine has been found to be high in AM plants. AMF altered physiology of roots may prevent penetration and retard the development of nematodes (Schenk 1981). Some authors have suggested that improved nutrition may protect the plant against pathogens. Mycorrhizal fungi are believed to induce high activation of antimicrobial phenyl propanoid metabolism in roots. It has been reported that induced resistance of AMF sweet orange to *Phytophthora* root–rot disease does not appear to operate unless a P nutritional advantage is conferred on the AMF plant (Graham and Egel 1988).

25.7.17 Carbon Cycling

Significant amount of carbon flows through mycorrhizal mycelia to different components of soils. Production of glycoproteins such as glomalin that are involved in the formation and stability of soil aggregates may have also an important influence on other microorganisms associated with the AMF mycelium (Johansson et al. 2004).

25.7.18 Biohardening Tool

The technique of using AM fungi in micropropagation has been applied recently for clonal selection in woody plants (Salamanca et al. 1992). The inoculation of AMF to nursery plants has been proved both necessary and feasible and it has been extended to micropropagated plants (Adholeya et al. 2005). Salamanca et al. (1992) studied mycorrhizal inoculation of micropropagated woody legumes used in revegetation programmes for desertified Mediterranean ecosystem. Inoculation of micropropagated plantlets with active culture of AMF appeared to be critical for their survival and growth (Yadav et al. 2011). This avoids ‘transient transplant shock’ and stunted growth on transfer in the field. Endomycorrhization can modify root architecture to give a root system which is better adapted for uptake of mineral nutrients and water as well as increasing hormone production and resistance to pesticides and root pathogens. Micropropagated plantlets inoculated with AM spores increases the survival rate and growth in potted conditions.

25.7.19 Ornamental Flowering Plants

Vase life is an important consideration of choosing flowers. The longevity or potential of vase life of flower is determined by environmental conditions under which the flowers are produced and post harvest factors such as increase in the activity of peroxidase enzyme, increase in level of ethylene and due to tissue deterioration caused by microbes in the vase solution. Colonization by mycorrhizal fungi has been shown to increase the vase life of cut flowers (Wen and Chang 1995) but the mechanism involved is still unknown. Some of the reasons of having better and prolonged vase-life of cut flowers in mycorrhizal inoculated plants can be because of better vascular development by mycorrhizal fungi (Chang 1994) or due to decreased ethylene production. Besmer and Koide (1999) also attributed the increased vase-life of cut flowers of *Antirrhium majus* to the reduction of ethylene production in mycorrhizal plants. Parish (1968) suggested that increase in peroxidase activity is one of the most reliable indicators of maturity. Enhanced peroxidase activity was associated with an increase in the level of peroxides and free radicals, which reacted with cellular constituent (Fridovich 1975). AMF inoculated plants show less increase in peroxidase activity because AMF increase the activity of antioxidative enzymes such as superoxide dismutase (SOD) and catalase (CAT) (Blilov et al. 2000). Also, these anti-oxidative enzymes constitute an important primary defense mechanism of cells against superoxide free radicals generated under stress condition (Bowler et al. 1992).

25.7.20 Physiological and Biochemical Parameters

25.7.20.1 Photosynthesis

AM fungi may function as a metabolic sink causing basipetal mobilization of photosynthates to roots thus providing a stimulus for greater photosynthetic activity (Bevege et al. 1975). Increase in activity of hormones like cytokinin and gibberellin could elevate photosynthetic rates by stomatal opening influencing ion transport and regulating chlorophyll levels (Allen et al. 1982). AMF symbiosis need carbon source from symbiotic partner synthesized by the process of photosynthesis and upto 20% of the total photoassimilates substances can be transferred to the fungal partner (Graham 2000). AMF are known to enhance the uptake of phosphorus (P) from the soil which, in turn, has an important role as energy carrier during photosynthesis.

25.7.20.2 Production of Growth Hormones

Plants with mycorrhiza exhibit higher content of growth regulators like cytokinins and auxins as compared to non mycorrhizal ones. AMF colonized roots show changes in root morphology by getting much thicker and carry fewer root hairs. Hormone accumulation in the host tissue is affected by mycorrhizal colonization with changes in the levels of cytokinins, abscissic acid, gibberellins like substances. The effect of AMF on photosynthesis and host morphology could also be hormonal. *Glomus mosseae* has been shown to synthesize phytohormones.

25.7.20.3 Alters Soil Enzyme Activity

Enzyme activity is often used as an index of total microbial activity in the soil as well as its fertility (Dhruva-Kumar et al. 1992) and is also useful in the study of changes caused in soil due to land degradation. Xyloglucanases, a hydrolytic enzyme is involved in the penetration and development of AM fungi in plant roots (Garcia-Garrido et al. 2002); esterase indicates catabolic activity in the soil, directly correlated with microbial activity of soil; phosphatases include acid as well as alkaline phosphatase that helps in release of inorganic phosphorus from organically bound phosphorus returned to soil (Kumar et al. 1992); chitinases are known to catalyses degradation of chitin, a major component of most fungal cell wall and are also known to enhance defense mechanism, thus helps in providing protection against diseases; trehalose catalyses the hydrolysis of trehalose which is known to be a very common signal in plant symbiosis (Mellor 1992). Peroxidase enzyme activity increases in diseases and injured plant tissue but AM symbiosis is known to retard this enzyme activity by enhancing root penetration and colonization. Inoculation with AMF *G. vessiforme* enhanced soil proteinase, polyphenoloxidase, urease and saccharase activities compares with control in watermelon (Zhao et al. 2010). AM fungi are known to alter the soil enzymes activity and, thus, increase plant establishment and transport problems.

25.7.20.4 AMF in Weed Control

Sustainable system targeting *Striga* management can be achieved by the AM fungi inoculation technique. Several reports have suggested that AM fungi can change the nature/composition of weed communities in mixed culture system in a variety of ways, including changing the relative abundance of mycotrophic weeds species (colonized by AMF) and non-mycorrhizal species (noncolonized). For example, witch-weed (*Striga hermonthica*) has been found to seriously affect cereal production in many tropical countries. Infection of *Striga* resulted in a significant reduction in cereal grain yield between 20 and 100%. AMF could provide a new means of ecologically based weed management by affecting the fruiting of weed communities. According to Lendzemo (2004), *Striga* performance in the presence of AMF was negatively impacted with reduced and/or delayed germination, attachment and emergence.

25.8 Conclusion

The soil mycorrhizae are important for plant growth development and health. The use of mycorrhizae has great potential to protect plants from diseases through their biocontrol mechanism. This offers an alternative environment-friendly strategy by reducing the use of chemicals. They are the main components that enrich the soil nutrients and maintain the soil health in sustainable manner. Furthermore, they enhance the plant growth regulators, provide defense mechanism to the plants, regulate enzymatic activities, increase rate of photosynthesis and supports in bioremediations, thus acting as eco-facilitator in sustainable agriculture both in terms of production and environmental protection. Such microbial populations need systematic strategy so that their potential can be utilized in an effective way in future prospects.

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