Ecology of Arbuscular Mycorrhizae and Influence on Drought Tolerance in Crop Plants

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Kamlesh K. Meena, Praveen Kumar, Ajay M. Sorty, U. Bitla, and H. Pathak

Abstract

Drought stress critically affects plant growth and productivity. Alleviation of drought-induced detrimental effects in plants is urgently required to achieve sustainable crop production. Consequently, there is constant demand of controlling strategies that can sustainably promote growth, development, and productivity of plants under limited moisture conditions. Among the proposed strategies, use of arbuscular mycorrhizal fungi (AMF) has gained significant attention due to their multifaceted capabilities. AMF-induced tolerance in plants against abiotic stresses such as heat, salinity, drought, and extreme temperatures is well-known. AMF symbiosis significantly strengthens the host plant against multiple abiotic stresses including drought and improves productivity. This chapter will mainly explore the ecology of AMF, their interaction with host plant and soil microbial communities, and influence of AMF-plant-soil microbiome interactions on plant-drought tolerance.

Keywords

Arbuscular mycorrhizal fungi · Drought · AMF interactions · Soil microbiology · Triangular response

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K. K. Meena (✉) · P. Kumar
Division of Integrated Farming System, ICAR-Central Arid Zone Research Institute, Jodhpur, Rajasthan, India
e-mail: kk.meena@icar.gov.in

A. M. Sorty · U. Bitla · H. Pathak
Agricultural Microbiology Laboratory, School of Edaphic Stress Management, ICAR-National Institute of Abiotic Stress Management, Baramati, Maharashtra, India

N. K. Arora, B. Bouizgarne (eds.), *Microbial BioTechnology for Sustainable Agriculture Volume 1*, Microorganisms for Sustainability 33,
https://doi.org/10.1007/978-981-16-4843-4_8

8.1 Introduction

Drought is an increasingly detrimental abiotic stress that negatively affects the growth and development of plants. To restrict the ill effects of drought on crop productivity, availability of diverse adaptation and mitigation measures are needed (Nilsen and Orcutt 1996). Drought stress induces cellular damage through increased production of reactive oxygen species (ROS). These lethal molecules (ROS) can cause oxidative destruction of proteins, DNA, and lipids and critically affect vital cellular processes (Miller et al. 2010; Impa et al. 2012). To sustain crop yield under limited water supply, an effective rooting system is essential for plants to take up nutrients and water (Fohse et al. 1988). Arbuscular mycorrhizal fungi (AMF) are a unique class of beneficial soil microorganisms that can form a symbiotic association with plant roots forming arbuscular mycorrhizae (AMs), which play a vital role in regulating the plant growth even under variety of unfavorable abiotic circumstances including drought (Philippot et al. 2013). Most ancient, well-known mutualistic association is the endomycorrhizal symbiosis, in which specific soil fungi—arbuscular mycorrhizal (AM) fungi—actively colonize the roots of up to 74–90% of the land plants on earth (Bonfante and Genre 2010; van der Heijden et al. 2015). Generally, AMF exhibit a broad-spectrum symbiosis; Klironomos (2000) confirmed that AMF were not host specific but strong functional variants of fungal species. Owing to the multifaceted role of AMF, their symbiotic association with plant roots is a well-known approach to improve plant tolerance to environmental stress such as drought and phosphorus (P) limitation (Brachmann and Parniske 2006). AMF provide nutrients to their host plants by producing hyphae that grow out from plant roots, effectively increasing the soil volume from which immobile nutrients can be acquired. This fact is corroborated by the phenomenon that most agricultural crops perform better and are more productive when they are colonized by AMF compared with non-mycorrhizal plants. Apart from beneficial effects on plant biomass, AMF also frequently increase plant-nutrient concentrations by facilitating the nutrient uptake and improve the amounts of secondary metabolites in plants (Mohamed et al. 2014).

Microbial communities native to the soil also play key role in the germination and hyphal growth of AMF. Microbes promote the establishment of AMF and also participate in the process of plant growth promotion. More importantly AMF bring modification of the root architecture for improving access of water and nutrients (Hameed et al. 2014). AMF symbiosis-mediated growth elevation is not only due to enhanced uptake of water and mineral nutrients from the adjoining soil but also due to protection of the plants from fungal pathogens (Smith and Read 2008).

Despite having significant knowledge on influence of bacteria and AMF on plant growth and nutrition, there is a general lack of information on their performance under natural drought conditions. More studies elucidating the effect of these microorganisms are urgently needed to mitigate the influence of changing agro-climate conditions on crop productivity. Further, there is a dearth of knowledge on plant-AMF-soil microbe interactions under drought conditions. In this chapter we focus on importance of collective studies on plant-AMF-soil microbe interactions and their key role in alleviation of drought stress in plants.

8.2 Plant-AMF Interactions

Arbuscular mycorrhizal (AM) symbiosis is among the hoariest and most prevalent plant-fungal symbioses (Redecker et al. 2000; Smith and Read 2008). AMF can form symbiotic associations with plants and affect interspecific interactions by enlarging nutrient-absorbing part of plant root systems and further promote plant nutrient and water uptake and also induce tolerance to abiotic stress conditions (Smith and Read 2008). AMF are microscopic filamentous fungi that colonize the plant roots and rhizosphere and spread several centimeters in the form of ramified filaments (Bonfante and Genre 2010) that perform an array of biological interactions in the soil habitat.

8.2.1 AMF, their Types, and Diversity

AMF are omnipresent root symbionts of above 90% of vascular plants and over 80% of the existing terrestrial plants (Wang and Qui 2006). Taxonomy of AMF is described in 214 known species in 4 orders, 13 families, and 19 genera, in the class *Glomeromycetes* of the phylum *Glomeromycota* (Muthukumar et al. 2009). According to the fossil archives and molecular data, AM symbiosis is evolutionarily primitive and could have had occurred with the first terrestrial plants (Lee et al. 2012). AMF or *Glomeromycota* are obligate symbiotic fungi that penetrate plant roots and form the arbuscules—a highly specialized hyphal structure that develops inside cortex cells and represents the main site of nutrient exchange between partners (Smith and Read 2008; Schußler and Walker 2010). AMF represent elements which are important to agricultural productivity and biogeochemical processes (van der Heijden et al. 2015). These fungi are known to play an important ecological role in management practices in low-input agricultural systems (Ma et al. 2005). There are two distinct kinds of AMF, categorized by intraradical hyphal adaptations which are also termed as the *Paris*-type where hyphal development is exclusively intracellular, forming the characteristic coil-like structures in host plants' cortical cells, while the other one is *Arum*-type, which is characterized by intraradical hyphal development that mostly remains intercellular and forms arbuscules in root cortical cells. AMF are mostly of asexual type in reproduction; however, exchange genetic material between genetically distinct strains takes place when their hyphae anastomose (Hijri and Sanders 2005).

8.2.2 Establishment of Symbiotic Association

The contribution of plant-derived and fungal signaling molecules that promote AM association encompasses a high degree of adaptation and genetic/metabolic coordination between mycorrhizal partners (Foo et al. 2013). Establishment of AM symbiosis is an intricate process involving a dedicated signaling pathway initiated by root-borne signal strigolactones, which are known to stimulate AM fungal activity (Van de Velde et al. 2017). AMF respond to the plant signals through consequent secretion of lipochito-oligosaccharide moieties, which induce a signal transduction pathway in plants upon perception. As this signal transduction pathway exhibits significant similarity with the one involved in root-nodule symbiosis, it is also known as the common symbiosis signaling pathway (CSSP), which has been elucidated in great detail in recent years (Gutjahr and Parniske 2013). Recent studies showed that formation of an infection structure called prepenetration apparatus (PPA) promotes cellular invasion (Genre et al. 2008) and development of the intracellular arbuscules that serve as nutritional edge between the associates (Gutjahr and Parniske 2013). Although the molecular mechanism involved in PPA formation is elusive, PPAs are thought to be a requirement for AMF contagion of host roots and to necessitate signaling through the CSSP (Genre et al. 2005). Establishment of AM is concomitant with an intricate process of reprogramming of the host cells including the stimulation of hundreds of genes (Calabrese et al. 2017) of which some are expressed absolutely in cells with arbuscules. Majority of these genes are thought to be indispensable for intracellular establishment, functioning of the fungus and for correlation of symbiotic activity.

8.3 Significance of AMF Symbiosis

AMF promote many aspects of plant life. In particular, AMF improve plant nutrition and enhance growth, stress tolerance, and disease resistance. In addition, the hyphal networks of AMF improve soil characters such as soil particle aggregation, thereby improving the resistance of soil towards erosion due to wind and water. Finally, AMF decrease nutrient leaching from the soil and contribute to retention of nutrients in the soil and also decrease the risks of groundwater contamination.

8.3.1 Nutritional Enhancement

Importance of AMF symbiosis in nutrient transport has been extensively studied. Capability of nutrient transport varies with AMF species and is highly dependent on their root colonization ability. For instance, members of *Gigasporaceae* are sluggish root colonizers; however, they are superior soil colonizers, where they form denser extraradical mycelium network than the members of the *Glomeraceae* (Hart and Reader 2002a). Therefore, it should be clearly noted that *Gigasporaceae* are more essential in soil structure establishment and maintenance than *Glomeraceae*.

Gigasporaceae seem to be less efficient in transferring P to the host plant when compared with *Glomeraceae* (Hart and Reader 2002b). AMF possess high-affinity inorganic phosphate (Pi) transporters; the expression of this Pi transporter was localized to the extraradical hyphae of *Glomus versiforme*, which is the main site of phosphate uptake from the soil. Accumulated as polyphosphate, Pi is then rapidly translocated along the aseptate mycelium to the host plant (Hijikata 2010). In mycorrhizal plants, nearly 70% of the whole phosphate uptake can be acquired via the AM pathway (Yang et al. 2012). Recent studies revealed nitrogen uptake in the AM symbiosis, with a significant role played equally for plant nutrition and for the regulation of the symbiosis functioning itself. In the soil, inorganic nitrogen is present as nitrate (NO_3) and ammonium ($NH4^+$), and AMF possess specific transporters for both the N forms. In *Rhizophagus irregularis*, three sequences refer to ammonium transporters, and one nitrate transporter has been identified (Tisserant et al. 2013). Role of sulfur (S) in AM symbiosis is poorly understood. However, some studies have reported AMF-mediated S transfer in plants. Allen and Shachar-Hill (2009) reported that AMF can take up both organic and inorganic S and transfer it to the host plant. *Lotus japonicas* and *Medicago truncatula* have sulfate transporters *LjSultr1;2* and *MtSultr1;2* that respond to mycorrhizal symbiosis (Guether et al. 2009). Macronutrient like potassium (K) is not well studied with respect to AMF-plant symbiosis. A few studies have been performed in this regard where a number of plant K transporters were identified like *Trk* (transporter of K), *HAK* (high-affinity towards K uptake), and *SKC* (Shaker-like channels), but their role in AMF symbiosis is still not demonstrated (Garcia and Zimmermann 2014).

8.3.2 Abiotic Stress Tolerance

Importance of AMF-plant symbiosis in mitigation of abiotic stresses like drought, salinity, high temperature, and heavy metal in different agriculture crop is well-known (Moradtalab et al. 2019; El-Nashar 2017). AMF symbiosis protects plants against a variety of abiotic stresses through various processes such as improved photosynthetic rate, uptake and accumulation of mineral nutrients, cellular accumulation of osmoprotectants, upregulation of antioxidant enzyme activity, and change in the rhizosphere microecosystem (Table 8.1) (Bárzana et al. 2015; Calvo-Polanco et al. 2016; Yin et al. 2016). Exploiting AMF symbiosis may boost P and N uptake and improve plant growth and productivity. The mycorrhizosphere formed by roots and AMF mycelium in soil effectively enhances water and nutrient uptake because of its larger expanse (Smith and Smith 2012). AMF symbiosis decreases oxidative stress through declining membrane lipid peroxidation in plant under salinity stress (Abdel Latef and Chaoxing 2014). Further, it also improves integrity of the plasma membrane by lowering lipid peroxidation and alleviating electrolyte leakage due to membrane damage (Evelin et al. 2012). AMF defend plants against detrimental effects of ROS by increasing antioxidant enzymes like superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), and glutathione reductase (GR) (Table 8.1) (Evelin and Kapoor 2014). Improvement in cold

Table 8.1 Alleviation of abiotic stresses through AMF inoculation

Sr. no.	Types of AMF	Crop	Stress	Function	Reference
1	*Rhizophagus irregularis*, *Funneliformis mosseae*, *Funneliformis geosporum*, *Claroideoglomus claroideum*	*Triticum aestivum* L.	Heat	Increased grain quantity, nutrient distribution, and nutrient composition in root	Cabral et al. (2016)
2	*Glomus* sp.	Tomato	Salt stress	Amplified leaf area, and nutrient content, reflecting superior plant growth	Balliu et al. (2015)
3	*Glomus iranicum* var. *tenuihypharum* sp.	*Euonymus japonica*	Sewage water irrigation and salinity stress	Enhanced levels of P, Ca, and K	Gómez-Bellot et al. (2015)
4	*Glomus mosseae* and *Glomus intraradices*	*Pistachio* plants	Drought stress	Increased levels of P, K, Zn, and Mn	Bagheri et al. (2012)
5	*Funneliformis mosseae* and *Diversispora versiformis*	*Chrysanthemum morifolium (Hangbaiju)*	Salt stress	Increased root length, shoot and root dry weight, total dry weight, and root N concentration	Wang et al. (2018)
6	*Glomus intraradices*	*Medicago sativa* L.	Cd stress (heavy metal stress)	Plant growth enhancement, increased roots and shoot biomass	Wang et al. (2012)
7	*Rhizophagus intraradices*, *Funneliformis mosseae*, *Funneliformis geosporum*	*Zea mays*	High temperature	Increased leaf length, plant height, leaf number, chlorophyll a, photosynthetic rate, stomatal conductance, and transpiration rate	Mathur et al. (2018)
8	*Glomus monosporum*, *Glomus clarum*, *Gigaspora nigra*, and *Acaulospora laevis*	*Trigonella foenum-graecum* L.	Cadmium	Increased antioxidant enzymes activities and malondialdehyde content	Abdelhameed and Rabab (2019)
	Rhizophagus irregularis	*Solanum lycopersicum* L.	Salinity	Improved shoot FW, leaf area, leaf number, root FW, and levels of growth hormones	Khalloufi et al. (2017)

9	*Glomus intraradices*	*Solanum lycopersicum* L.	Salinity	Enhanced dry matter, ion uptake, growth parameters, and chlorophyll content	Hajiboland et al. (2010)
10	*Glomus mosseae*	*Leymus chinensis*	Salinity-alkali	Improved colonization level, seedling mass, water contents, and both P and N	Lin et al. (2017)

stress tolerance in plants due to inoculation of AMF was reported by Gamalero et al. (2009), where the authors linked AMF-induced mitigation through enhancement of photosynthesis. Cucumber root colonization by AMF might efficiently enhance the accumulation of phenolics, flavonoids, and lignin in the leaves and significantly reduce H_2O_2 accumulation under low-temperature conditions (Chen et al. 2013). Elevated temperature, however, negatively impacts the process of mycorrhizae development, which can also hamper AMF colonization, spore germination, and hyphal growth of the fungi (Jahromi et al. 2008). AMF-mediated improvements in photosynthetic rate, stomatal conductance, and transpiration rate indicate that AM symbiosis can deliver high gas exchange ability by reducing stomatal resistances and increasing CO_2 assimilation and transpiration fluxes (Zhu et al. 2012). These outcomes evidently demonstrate that AM symbiosis can efficiently protect the PSII reaction center and structural and functional disruption of photosynthetic apparatus from stress-induced damages. AMF symbiosis plays a key role and also improves the plant health in heavy metal-contaminated soils (Nadeem et al. 2014). AMF-induced enhanced plant tolerance towards heavy metals can be attributed to the mechanisms like restriction of heavy metals by AMF-secreted biomolecules, precipitation in polyphosphate granules in the soil, metal adsorption to chitin in the cell wall, chelation of metals inside the fungus, changes in rhizosphere pH, and regulation of variety of stress-responsive genes under stress conditions (Malekzadeh et al. 2011).

8.3.2.1 Rhizosphere Microbiology and Biochemistry

AM colonization exerts significant influence on the species composition of the soil microbial community by aggregating some groups and declining the others (Krishnaraj and Sreenivasa 1992). Participation of AM symbiosis in numerous physiological and biochemical processes including direct uptake and transfer of water and nutrients by AMF improves osmotic regulation, enhanced gas exchange and water use efficiency, and superior protection against oxidative damage has also been reported (Rapparini and Penuelas 2014). Sustenance of AMF hyphae improves physical defense of SOM by stimulating soil aggregation, which is important for sandy soils and reclaimed mine soil where other binding agents are scarce (Birgitte and Leif 2000). AM symbiosis can enhance decomposition and increase N capture from organic material; mycorrhizal hyphae can also produce phosphatase to hydrolyze the organic P compounds (Hodge and Fitter 2010). Available nutrient content in the rhizosphere soil directly affects soil enzyme activity (He et al. 2010). Soil enzymes activity is related to the nutrients such as mineralization of N, P, and C and can be used as indicator to detect changes in the fertility and microbial functioning of soil. Saccharase enzyme imitates the law of accumulation and decomposition of soil organic carbon and indicates soil C cycling and important biochemical activities. The saccharase activity in the AMF-inoculated plants appeared significantly higher than that in the AMF-non-inoculated treatments; also enhanced activity of dehydrogenase, urease, and phosphatases in AMF-inoculated treatments remained higher than those in AMF-non-inoculated plants (Qian et al. 2012). Esterase, trehalase, phosphatase, and chitinase activities were higher in the rhizosphere of mycorrhiza-inoculated maize (Vázquez et al. 2000). Enhanced invertase, catalase, urease, and alkaline phosphatase activities were observed in rhizospheric soil of AMF-inoculated *Amorpha fruticosa* (Qin et al. 2018) and also showed higher root mycorrhizal colonization, glomalin-related soil protein concentrations, as well as an increase in soil organic carbon (SOC), total N, Olsen P, and available K.

8.4 AMF Interactions with Indigenous Soil Microbes

Rhizospheric microbial communities contribute a vital role in plant health and development. Bacteria appear to represent the third component of AM symbiosis because there exists an influence by bacteria associated with the mycorrhizosphere on establishment and function of AMF (Frey-Klett et al. 2007). Diverse types of bacterial communities thrive within the mycorrhizosphere, where they form association with mycorrhizal roots, spores, sporocarps, and extraradical hyphae (Rambelli 1973). From *Rhizoglomus irregulare* spores, as many as 374 bacterial strains were isolated (Battini et al. 2016).

In general, three ways of interaction of between AMF and other microbial communities could be possible—synergistic, antagonistic, and neutral. Literature is available to generate an overview of these interactions. Mycorrhizospheric microbiota performs characteristic functional activities such as contributing as mycorrhiza helpers, in addition to direct plant growth promotion. Mycorrhizae helper bacteria may accelerate the germination of spores and establishment of mycorrhizal symbiosis. As an example, *Streptomyces* spp., *Pseudomonas* sp., and *Corynebacterium* sp. improved the germination of *Funneliformis mosseae*, *G. versiforme*, and *Glomus margarita* spores (Frey-klett et al. 2007). The enhancement of spore germination was credited to *Actinobacteria*—a group of bacteria that regularly interact with AMF spores, able to hydrolyze chitin which is a key component of the spore walls (Agnolucci et al. 2015). *Klebsiella pneumoniae*, *Trichoderma* sp., and *Paenibacillus validus* increased germlings hyphal growth (Calvet et al. 1992; Hildebrandt et al. 2006), while a bacterial strain belonging to *Oxalobacteraceae* not only improved spore germination and germling growth but also enhanced root colonization to establish symbiosis (Pivato et al. 2009). In addition, the development of AMF extraradical mycelia may be promoted by strains of *Paenibacillus rhizosphaerae*, *Azospirillum* sp., *Rhizobium etli*, *Pseudomonas* spp., *Burkholderia cepacia*, and *Ensifer meliloti* (Bidondo et al. 2011; Ordoñez et al. 2016; Battini et al. 2017).

Microbial biocontrol agents are capable to produce antibiotic effect, while some antifungal components originating from non-AMF microbes can affect the process of spore production and mycelial growth of AMF (Bitla et al. 2017). Germination rate of *G. mosseae* was accelerated, and expansions of mycelia from germinated spores were improved due to the presence of *Trichoderma* spp.; however, the presence of *Penicillium decumbens* and *Aspergillus fumigatus* inhibited spore germination of *G. mosseae* (Calvet et al. 1992). Some of the plant growth-promoting microbial agents could produce volatile, hormones and other secondary metabolites (Sorty et al. 2016; Meena et al. 2019) that can be detrimental to growth of AMF hypha and spores; *Bacillus subtilis* produces some unknown volatiles that inhibit the spore germination and hyphal growth of *Glomus etunicatum* (Xiao et al. 2008). Filion et al. (1999) observed that conidial germination of *Trichoderma harzianum* was enhanced by the fungal extract secreted by AMF while the *Fusarium oxysporum* f. sp. *chrysanthemi* were decreased; these effects were directly correlated with extract concentration. AMF- and phosphate-solubilizing bacteria (PSB) could interact synergistically because PSB solubilize thriftily accessible phosphorous compounds into orthophosphate that AMF can absorb and transport to the host plant (Nacoon et al. 2020).

8.4.1 Influence on Soil Microbial Community

The colonization of plants by AMF affects the quality and the quantity of the host plant root exudates and hence the structure of microbial communities in the rhizosphere and chemotactic responses of specific bacteria (Tahat and Sijam 2012). Presence of AMF also exerts an influence on soil microorganisms concomitant with their extraradical mycelium, principal to the formation of a specific zone of soil which is generally called the mycorrhizosphere (Artursson et al. 2006). Denaturing gradient gel electrophoresis (DGGE) profiles of 16S rRNA amplicons from total DNA extracts of pea rhizosphere appeared relatively similar between AMF-inoculated and AMF-non-inoculated rhizosphere. However, AMF (*Glomus intraradices*)-inoculated plants showed suppression of four to five specific bright bands (Wamberg et al. 2003). Direct root colonization with either *G. mosseae* or *G. intraradices* significantly modified the DGGE profiles of bacterial community from tomato rhizosphere. Both the AMF species had similar bacterial communities after 4 weeks. The bacterial taxa associated with the rhizosphere of tomato plants inoculated with *G. mosseae* were identified as *Pseudomonas*, *Herbaspirillum*, and *Acidobacterium*, while *Bacillus simplex* (clone TR03) was found to be affiliated only with *G. intraradices* (Lioussanne et al. 2010).

8.4.2 Long-Term Impact on Soil Microbiology

An AMF-rhizosphere microbial interaction significantly influences the soil microbiology and also affects the soil physiological and chemical characteristics. AMF influence the soil structure by binding and enmeshing soil particles into macroaggregates and by producing glomalin (Rillig and Mummey 2006; Treseder and Turner 2007). Carbon (C) fraction of glomalin can range from 9 to 22%, habitation time in soil from 6 to 42 years and may represent >5% of total soil C (Rillig et al. 2001). Soil aggregates are important for storage of C and nutrients. Soil aggregates are important for flourishing microbial communities, where they provide shelter in the form of micropores. Stable soil aggregates are long-lasting source of C because

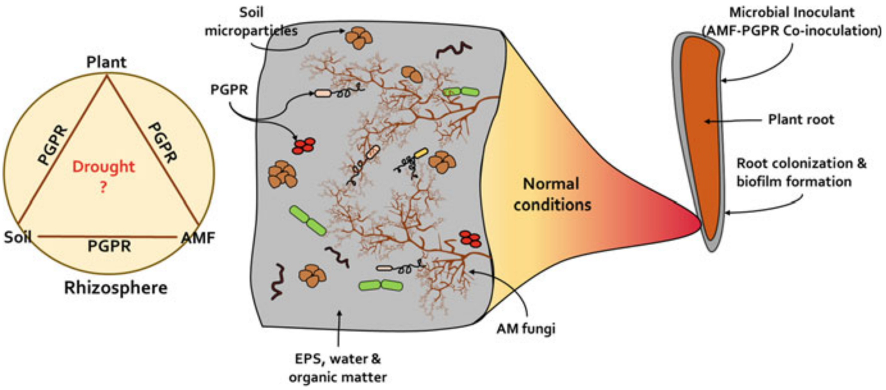

Fig. 8.1 An overview of AMF associations within the plant rhizosphere under normal conditions

they significantly enhance the microbial activity and the process of C sequestration in soil (Fig. 8.1). Soil C is important for all microbial activities that are connected to the phenomenon of microbial plant growth promotion. AMF-rhizosphere microbial interaction maintains the C:N ratio through symbiotic exchange of nutrients and C. Long-term mesocosm exploration with single AMF strain showed that there is significant influence on the diversity of associative microbial communities and on alterations in aggregate formation. In a diverse AM community, this may specify a highly composite biotic heterogeneity in mycorrhizosphere soils (Rillig et al. 2005). Fascinatingly, investigators constantly demonstrate enhanced concentration of available P in the smallest aggregates, in ultisols (Thao et al. 2008). AMF symbiosis affects the diversity of the microbial community as well as their function within the rhizospheric soil (Schreiner et al. 1997; Olsson et al. 1997). AMF can improve the quantity and movement of beneficial soil microorganisms including nitrogen fixers and phosphate solubilizers, which are important for growth, development, and productivity of plants (Linderman 1992).

8.5 Impact of Drought Stress on Plant-AMF-Rhizosphere Microbial Interactions

8.5.1 Recognition of Drought Conditions and Consequences

Plant-microbe interactions at biochemical, physiological, and molecular levels established that microbial associations largely direct plant responses towards environmental stress(es) (Meena et al. 2017, 2020). Extended moisture stress decreases leaf water potential and stomatal opening; reduces leaf size; suppresses root growth; decreases seed number, size, and sustainability; delays flowering and fruiting; and restricts plant growth and productivity (Osakabe et al. 2014). Drought condition also affects the plant root exudation (Sorty et al. 2018; Bitla et al. 2017). Root exudates act as direct communication pathway between plant and rhizosphere microbial communities; deviation in the composition of root exudates governs the diversity and function of the colonizing microbial communities (Sasse et al. 2018). Drought-induced changes in amount or composition of root exudates may be a situation- or species-dependent phenomenon (Gargallo-Garriga et al. 2018). Drought-induced changes in root exudate profiles can alter the composition and movement of the surrounding soil microbiome, endorsing additional alterations to soil geochemistry that in turn alter enormousness and direction of soil community changes. Dynamics and structure of rhizosphere microbial communities depend on the type and quality of the decaying root materials and the composition of root exudates, ranging from simple sugars to complex aromatic compounds (Kos et al. 2015). Drought condition has a substantial influence on the biomass and structure of soil microbial communities and their involvement in nutrient cycling (Schimel 2018). Water stress not only directly affects microbial community but also modifies the relative significance of the impact on plant AMF interaction (Monokrousos et al. 2020). Although the available literature signifies beneficial interaction of AMF under drought conditions, the knowledge relating to the underlying mechanisms of AMF-mediated plant growth enhancement under drought conditions and the potential beneficial effects on soil structure and indigenous microbial community is very limited. Thus, rigorous initiatives are critically needed to address the major knowledge gaps in the area of AMF-plant-microbe interactions (Fig. 8.1).

8.5.2 Counter Responses of AMF to Drought Conditions

AMF symbiosis might play a significant role in alleviating the impact of drought on crop yield. AMF symbiosis could considerably enhance plant resistance to drought via increased dehydration avoidance and increased tolerance (Ruiz-Lozano and Azcon 2000). The root colonization by the AMF is represented by active absorptive surface zone and enhanced water and nutrient uptake even under limited moisture conditions. AMF symbiosis could increase drought tolerance via the increased soil water drive to the plant roots (Ruiz-Lozano et al. 2016). Impact of AMF on drought-plant relation also extends to the soil environment in terms of higher rate of soil aggregate formation and improved soil water conditions to the rhizosphere (Rillig et al. 2002). AMF also regulate plant physiological performance to alleviate drought stresses by the upregulation of antioxidant enzyme activity and jasmonate synthesis to reduce peroxidative damage and also improve stomatal conductance (Pedranzani et al. 2016). AMF-mediated enhancement of drought tolerance in C3 (*Leymus chinensis*) and C4 (*Hemarthria altissima*) plant species through upregulation of antioxidant system has been reported (Li et al. 2019). Colonization of AMF can modulate morphological adaptation to improve drought tolerance of the host plant (Table 8.2). Previous studies showed that less epicuticular wax and lower cuticle weight were observed in leaves of AMF-inoculated rose plants than non-AMF-inoculated plants during drought acclimation (Henderson and Davies 1990). Fluctuations are observed in root structure of trifoliate orange inoculated with or without *F. mosseae*. Considerably enhanced root total length, projected area, surface

Table 8.2 Alleviation of drought stress through AMF inoculation

Sr. no.	AMF strain	Host plant	Abiotic stress	Influence on host	Reference
1	*Funneliformis mosseae*	Rose geranium	Water stress	Increased the concentrations of N, P, and Fe	Amiri et al. (2017)
2	*Glomus mosseae* and *Glomus intraradices*	*Pistachio* plants	Drought stress	Nutrient content is improved	Bagheri et al. (2012)
3	*Glomus deserticola*	*Antirrhinum majus* cv. *Butterfly*	Water stress	Increase the shoot and root dry mass, rise the water use efficiency, flower yield, nutrient and chlorophyll content	Asrar et al. (2012)
4	*Septoglomus constrictum*	*Tomato*	Drought and heat stress	Enhanced stomatal conductance, leaf water potential, and relative water content	Duc et al. (2018)
5	*Rhizophagus irregularis*	Tomato and lettuce	Drought stress	Improved growth rate and efficiency of photosystem II, increase strigolactone production	Ruiz-Lozano et al. (2016)
6	*Glomus mosseae*	Sunflower	Drought	Increase dry matter, heavier seeds and greater seed and oil yield, increase the N percentage in leaves and seeds	Gholamhoseini et al. (2013)
7	*Rhizophagus irregularis*	Hybrid poplar	Drought	A higher net photosynthetic rate and Chl fluorescence, better water use efficiency and water uptake, enhanced growth, and reduced loss of biomass	Liu et al. (2015)
8	*Glomus intraradices*	Rice	Drought	Enhanced the photosynthetic efficiency and the antioxidative enzyme activity	Ruiz-Sánchez et al. (2010)
9	*Glomus versiforme*	Citrus	Drought	Improving reactive oxygen metabolism	Wu and Zou (2009)
10	*Funneliformis mosseae* and *Paraglomus occultum*	Trifoliate orange	Drought	Escalated the leaf sucrose and fructose concentration, significantly increase the leaf sucrose	Wu et al. (2017)

(continued)

Table 8.2 (continued)

Sr. no.	AMF strain	Host plant	Abiotic stress	Influence on host	Reference
				phosphate synthase and neutral invertase, regulating the sucrose- and proline-metabolized enzyme activities	
11	*Glomus mosseae* or *Glomus etunicatum*	Wheat	Drought	Improved growth, yield, and nutrient uptake	Al-Karaki et al. (2004)
12	*G. mosseae*	*Wheat*	Drought	Enhancement of P, Zn, Cu, Mn, and Fe uptake	Al-Karaki and Al-Raddad (1997)
13	*G. mosseae*	(*Zea mays* L.)	Drought	Increased P uptake	Abdelmoneim et al. (2014)
14	*Glomus* spp.	*Ipomoea batatas*	Drought	Proline and soluble sugars adjust osmotic potential	Yooyongwech et al. (2016)

area, average diameter, volume, and number of first-, second-, and third-order lateral roots are observed in AMF trifoliate orange seedlings under well-watered and drought situations compared with non-AMF seedlings (Liu et al. 2015, 2016). Comas et al. (2013) observed that alteration in root structure caused by AMF can deliver more exploration of soil volume to absorb water and nutrients from the soil, therefore potentially enhancing drought tolerance of the host plant.

8.5.3 Integrated Response Triangle of Plant-AMF-Rhizosphere Microbes

Under drought condition, root colonization by AMF generally decreases (Augé 2001). Still AMF inoculation in crop is one of the best biological methods to alleviate drought stress. AMF can promote plant drought fitness either via enhanced nutrition or more direct effects on stomatal conductance and enhanced water use efficiency (Augé 2001). Mycorrhizal helper bacteria play a vital role in establishment of AMF symbiosis under drought stress. The symbiotic relationship between legumes and nitrogen-fixing rhizobia is susceptible to drought which induces failure of the infection and nodulation developments (Bouhmouch et al. 2005); however, presence of AMF improves the performance of legume-rhizobial symbiosis under drought. Bacterial strains isolated from AMF spores also exhibit the ability of plant growth promotion; 17 actinobacterial strains were able to produce siderophores and IAA, mineralize phytate and solubilize inorganic phosphate and 10 putative N fixers to produce siderophore and solubilize P (Battini et al. 2016). Nitrogen and P are transported towards the host through AMF extraradical hypha. Inoculation of drought-adapted AMF and *Bacillus thuringiensis* consortium increased growth a of maize under drought stress; it was observed that the co-inoculation increased plant nutrition and plant drought tolerance including regulation of plant aquaporins with several putative physiological functions (Armada et al. 2015).

8.5.4 Influence of the Triangular Response on Plant Performance under Drought Conditions

Under drought conditions, plants undergo variety of morphological and metabolic changes that affect root exudations and soil microbial communities. Plant also alters the root-shoot ratio and stimulates root growth to gain access areas to the moisture from additional part of the adjacent soil. Drought-induced changes in root metabolites may also explain observed changes in root-associated microbiome (Xu et al. 2018). Most microbes are susceptible to limited C. A significant amount of C is provided through root exudates which are thus important governing factors of microbial processes and shaping root-associated microbial communities (Peterson 2003). AMF-induced improved soil aggregation and SOC are known to increase the abundance of plant growth promoting (PGP) bacteria that accelerate the processes like nitrogen fixation, phosphate solubilization, hormone production, and nutrient mobilization. Involvement of phytohormones such as strigolactones, gibberellins, auxin, abscisic acid, ethylene, jasmonic acid, salicylic acid, cytokinins, and brassinosteroids in AMF symbiosis and plant growth is extensively reviewed by Liao et al. (2018). These hormones improve extraradical hyphal growth of AMF (Bidondo et al. 2011) and also improve plant performance under varying abiotic conditions (Meena et al. 2011, 2017; Sorty et al. 2016, 2018). The hyphal growth regulates transport of nutrient and water to host plant under drought conditions. Thus the plant-AMF-soil microbe triangular interactions improve drought tolerance in plants and promote growth, development, and productivity.

Additional to nutrients mobilization, and phytohormones production, PGP microbes are involved in different activities of plant growth promotion through the production of wide types of metabolites and volatile compounds that directly or indirectly enhance plant growth and sustenance (Barea et al. 2002; Rouphael et al. 2015; Sorty et al. 2016, 2018; Meena et al. 2017). These activities also influence AMF-plant symbiosis, thus making it important to consider the activities performed by associative microbiota before selecting the AMF and bacterial combination for co-inoculation. P is quickly immobilized in the soil, forming insoluble compounds with aluminum/iron and with calcium in acid and alkaline soil, therefore becoming inaccessible to plants; P-solubilizing bacteria could work in interaction with AMF to enhance P availability and subsequent uptake by the plant. P-mobilizing bacteria, such as *Streptomyces* spp., *Leifsonia* sp., *Bacillus pumilus*, *Lysinibacillus fusiformis*, and *E. meliloti*, isolated from AMF spores of *Rhizoglomus irregulare*, showed synergistic action with AMF, promoting mineralization of soil phytate and facilitating P uptake by mycorrhizal plants (Battini et al. 2017).

Co-inoculation of PGP bacteria and AMF is known to significantly enhance plant growth than inoculation with the PGP bacteria or AMF alone. Co-inoculation also improves crop yield and shows improvement in uptake of N and P than single inoculated crop (Kim et al. 1998; Singh and Kapoor 1998). Most of the researchers have already shown the importance of microbial co-inoculation in the mitigation of drought stress in crops under in vitro and field conditions (Meena et al. 2010). Drought-resistant *B. thuringiensis* inoculated with indigenous AMF isolate could decrease water requirement by 42% in *Retama sphaerocarpa*, a positive AMF-plant growth promoting rhizobacteria (PGPR) consequence on plants grown under drought stress (Marulanda et al. 2006).

8.6 Recent Trends and Advancements on AMF Inoculants in Modern Agriculture

A variety of strategies for application of AMF have been developed during the last few decades. The prominent ones include combination of different AMF sp., AMF-PGPR co-inoculation, AMF inoculation with organic compost, and liquid inoculum. Marketable inocula are prepared with *R. irregulare* (syn. *Rhizophagus irregularis*, formerly *G. intraradices*) and *F. mosseae* (formerly *G. mosseae*) that are generalist symbionts and are common all over the world in nearly all soils and climatic zones (Smith and Read 2008). However, recently a very common practice of using AMF with other commercial biofertilizers of PGP microbes has gained significant popularity. It is a proven fact that co-inoculation of AMF and PGPR under drought stress can induce several beneficial changes in plants. Some studies have reported that co-inoculation of more than one AMF species with bacterial inoculants can significantly promote plant growth in addition to alleviating the drought stress. For instance, co-inoculation of *G. mosseae* and *G. intraradices* along with *Bacillus* sp. alleviates drought responses in *Lactuca sativa* (Vivas et al. 2003). Consortium of *Claroideoglomus etunicatum*, *R. intraradices*, and *F. mosseae* inoculated with *B. subtilis* alleviates salt stress impact on *Acacia gerrardii* (Hashem et al. 2016), while a consortium of *B. thuringiensis*, *Bacillus megaterium*, and *Pseudomonas putida* inoculated with single *R. intraradices* sp. also enhances plant growth under drought stress (Ortiz et al. 2015). Compost-amended substrate inoculated with AMF *Glomus iranicum* in micropropagated date palm plantlets (cv. *Feggous*) revealed increased biomass, chlorophyll, and mineral nutrient contents than plantlets transplanted into compost-amended substrate or without compost amendment (El Kinany et al. 2019). Combination of biochar and AMF *C. etunicatum* (syn. *G. etunicatum*), *Rhizophagus irregularis* (syn. *G. intraradices*), and *F. mosseae* (syn. *G. mosseae*) enhanced the growth of chickpea by improving synthesis of chlorophylls, rate of photosynthesis, membrane stability index (MSI), and relative water content (RWC); it also enhanced the nitrogen fixation ability of *Cicer arietinum*. Plants may have considerably contributed to growth promotion and the superior drought tolerance by retaining the optimal concentration of amino acids and other stress-responsive metabolites (Hashem et al. 2019). Organic compost applied in combination with the inoculation of a native AMF synergistically promoted the growth of *Anthyllis cytisoides* in a neutral mine tailing under field conditions (Kohler et al. 2015). Organic compost amendment enhances soil nutrient status, stimulates mycorrhiza formation, enhances soil microbial function and soil enzyme activity, thereby inducing the nutrient turnover and plant performance. *Glomus hoi* applied as liquid inoculum form in *Oryza sativa* L promoted growth and development and improved the production of rice plants under saline conditions. Liquid inoculum also reduced the detrimental effect of salinity on AMF-like mycorrhizal colonization, and decreased the ectophyte growth in soil (Fernández et al. 2011). Liquid inoculum of AMF also increased the size and number of fruits, especially under deficit irrigation or low nitrogen input condition (Robinson Boyer et al. 2016).

8.7 Future Perspectives on AMF-Based Strategies for Agricultural Sustainability

Owing to their multifaceted function in agricultural systems, AMF are gaining significant popularity at grassroots level. Consequently, there is constantly increasing demand for AMF-based formulations. However, there is still a dearth of knowledge particularly with respect to the appropriate dosage, propagule density, optimization-related issues for varying agro-climatic conditions, post-inoculation survival, establishment and function of AMF under different biogeochemical and environmental regimes, etc. Further, a regulatory framework to determine quality standards of AMF-based products is yet to be formulated. Finally, there remains a huge scope for exploitation of new AMF strains from diverse natural habitats for promoting plant performances. Chronically stressed habitats can serve as excellent resources of resilient AMF diversity. Extensive use of mycorrhizal inocula in agriculture remains challenging due to their cost, variability in terms of quality, responses on plants, and incompatibility with high available P levels in soils under certain circumstances. Further, there is a need to develop the AMF products that are compatible with rhizospheric microbial communities and are tolerant to biotic and abiotic stresses. Although different types of combinations and amendments are already studied, there is a huge scope for optimization of AMF, crop, associated soil microbial communities, and soil physicochemical properties. Thus, there is a critical need to evaluate the AMF-plant-soil microbial response triangle and its importance in alleviation of abiotic and biotic stresses.

Acknowledgments Authors are grateful to the Indian Council of Agricultural Research (ICAR) for their financial support through the network program—Application of Microorganisms in Agriculture and Allied Sectors (AMAAS).

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