Chapter 5
Drought Stress and Mycorrhizal Plant

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Introduction

Interest in stressful conditions is rising with increasing the recognition that global changes can negatively affect ecosystems (Firbank et al. 2008; Scherr and McNeely 2008). The environment affects organisms in many ways named environmental factors, which can be biotic or abiotic. The effect of abiotic environmental factors (temperature, humidity, light, water supply, nutrients, and CO_2) (see Table 5.1) differs with their intensity as they regulate plant growth (Schulze et al. 2005).

Plant tolerance to abiotic stresses such as drought has been reported for different plant species. For example, Eucalypts species are known for their capacity to tolerate several stresses. Olive trees (Sofo et al. 2008), Agave, and native cactus from Mexico (Monroy-Ata and García-Sánchez 2009) as well as some native trees from semiarid of Brazil (Pagano et al. 2013) are able to survive under soil water conditions. It is worth noting, moreover, that these plant species require symbiotic fungal endophytes for growth under abiotic stress (see below).

Plants are sessile organisms exposed to natural climatic or edaphic stresses (drought, high irradiation, heat, frost, flooding, nutrient differences) and to environmental changes from human activities (air and soil pollution, soil degradation) (Schützendübel and Polle 2002). Nowadays, biotechnological techniques of stress tolerance in plants are increasingly pursued. For example, under stress, arbuscular mycorrhizal fungi (AMF) are able to modify plant physiology in a way so that the plant can subsist with those environmental factors (Miransari et al. 2008). Accordingly, the use of mycorrhizas as plant inoculants is being recommended to help plants to prosper in degraded arid/semiarid areas.

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Table 5.1 Abiotic plant stress factors. Adapted from Schulze et al. (2005)

Type			
Abiotic	Water	Drought	
		Flooding	
	Temperature	Heat	
		Cold	Chilling
			Frost
	Radiation	Light	
		UV	
		Ionizing radiation	
	Chemical stress	Mineral salts	Deficiency, over-supply
			pH, salinity
		Pollutants	Heavy metals
			Pesticides
		Gaseous toxins	
	Mechanical stress	Wind	
		Soil movement	
		Submergence	

Several reports have showed that mycorrhizal symbiosis improves plant health through increased protection against environmental stresses such as drought (Azcón and Barea 2010; Barea et al. 2005a, b). Additionally, recent investigations pointed to the increasing recognition of the occurrence of AMF in dry forests of Brazil (Pagano et al. 2010, 2012, 2013) and northern Ethiopia (Birhane et al. 2010, 2012). Moreover, some plant species need to cope the severe conditions caused by flooding and drought, as in the Netherlands, where riparian edge forests dominated by *Salix* (well adapted to anaerobic soil conditions) associate with only a limited number of mycorrhizal fungi (ectomycorrhizas) (Parádi and Baar 2006). Most of the research is based on limited experiments done in glasshouse or nursery. For example, in India, an important multipurpose fruit tree of arid and semiarid regions (*Ziziphus mauritiana*) showed great dependency on AMF under water stress conditions (Mathur and Vyas 2000).

To finish, there is an increased interest on biochar soil amendment not only to improve soil fertility and plant productivity, but also to alleviate drought stress (Elad et al. 2011). The mechanisms by which biochar increases water retention are scarcely understood; however, it promotes mycorrhizal fungi and modifies soil microbial populations and functions (Elad et al. 2011). The promotion of AMF by biochar is also poorly understood, further studies being needed (Warnock et al. 2007).

This chapter examines the current information on the AM symbioses with respect to the research results on plant growth as affected by drought. Additionally, soil amendments that may have a synergistic influence are discussed.

Plants and Drought Stress

Of severe significance are the effects of global change on soils: increased soil temperatures, increased nutrient availability, increased ground instability in mountainous regions, increased erosion from floods to name just a few (Simard and Austin 2010). It is known that abiotic stresses (Table 5.1), such as drought, adversely affect plant growth, productivity and generate morphological, physiological, biochemical, and molecular changes in plants. However, different plant species can vary in their sensitivity and response to water deficit (Schulze et al. 2005).

Plant reactions to water deficiency (including stress avoidance or tolerance) are complex. Stomata close in response to water deficit; however, it is more related to soil moisture than to leaf water status, involving chemical signals produced by roots (Chaves et al. 2002). Among abiotic stresses, drought and salinity stress are considered to be the most important factors limiting plant growth (Ruiz-Lozano 2003). The symptoms of drought are leaf wilting, reductions in the net photosynthesis rate, stomatal conductance, water use efficiency, relative water content, and gradually diminution in total chlorophyll content.

Plants can react to drought at morphological, physiological, and cellular levels with modifications that allow the plant to avoid the stress or to increase its tolerance (Ruiz-Lozano 2003). These morphological and physiological adaptations can be of vital importance for some plant species, but they are not a general response of all plant species. In contrast, the cellular responses to drought stress seem to be conserved in the plant kingdom. To date, reports including plant tolerance to drought (18,264 documents in SCOPUS from 1984 to June 2013) have increased in the last 10 years (69 % of which were published in the recent decade).

Mycorrhizal Fungi and Drought

It is known that drought can decrease plant growth and production. AMF can improve plant growth and production under different conditions, including various soil stresses (reviewed by Miransari 2010). This was explained in terms of plant allocation of more photosynthate to mycorrhizal hyphae to increase soil resource uptake as nutrient and water limitations increase and can be seen in high latitude and altitude ecosystems (see Simard and Austin 2010).

With regard to ectomycorrhizas, the complex transport of water from deep soil to the mycorrhizal sporocarps has served to understand the dynamic and important complex structural elements of the soil–fungal–plant interface (Allen 2007, 2009). Special attention on trees, e.g., in Europe, showed that oak species (*Quercus robur*, *Quercus petraea*, *Quercus pubescens*) inoculated with ectomycorrhiza (*Cenococcum geophilum*) tolerated strong drought. Moreover, the relative abundance of ectomycorrhizal species in the community will be manipulated by drought (Herzog et al. 2013).

With regard to AMF, they can promote plant growth increasing plant production under stress due to the establishment of extensive hyphal networks and secretion of glomalin, which enhance water and nutrient uptake meliorating soil structure (Miransari 2010).

Interestingly, biotechnology offers new strategies that can be used to develop transgenic crop plants with improved tolerance to stresses. Moreover, germplasm collected from high-altitude and low-temperature areas, cold-tolerant mutants, and wild species can be exploited for improved tolerant genotypes in other regions.

Earlier studies (Augé et al. 1987; Duan et al. 1996; Subramanian et al. 1995) showed a higher stomatal conductance, transpiration rate, and leaf water potential in mycorrhizal plants under drought. This was attributed to a higher water uptake, which allows plants to maintain higher rates of photosynthesis and higher water contents than non-mycorrhizal plants. The mechanism of modification of host-plant–water relations rests unknown.

However, different hypotheses have been tested with inconclusive results. Among those hypotheses, the following were proposed: (1) an indirect effect of improved *P* nutrition in mycorrhizal plants (Augé et al. 1986; Fitter 1988), (2) an improvement in water uptake in mycorrhizal roots by the extraradical hyphae (Ruiz-Lozano and Azcón 1995), by increasing effective root hydraulic conductivity or by modifying root architecture, (3) a biochemical modification of water regulation in the host plant through changes in hormonal signaling, (4) stimulation of osmoregulatory responses in mycorrhizal plants (Augé et al. 1986), and (5) changes in soil water retention properties (Morte et al. 2000).

It has been shown that Arbuscular mycorrhizal (AM) symbiosis can modify water relations and drought responses of host plants (Augé 2001). Numerous reports have compared mycorrhizal plants with control plants; however, more suitable comparisons (with different fungal species) are nowadays required (Augé et al. 2003). Among the AM symbiotic characteristics associated with water relations, some authors focused on the extent of extraradical hyphal development in the soil. This was explained in terms of contribution to root water absorption (Ruiz-Lozano and Azcón 1995) or by moisture retention and modification of drainage properties (Augé et al. 2001; Bearden 2001).

Several authors suggested that extraradical hyphal development in mycorrhizal fungi was associated with greater drought resistance of plants growing in those soils or observed a significant occurrence of extraradical hyphae in semiarid ecosystems. To such aim, glasshouse experiments by Augé et al. (2003) showed that soil hyphal colonization (extraradical hyphae) had superior effects on both lethal leaf water potential and soil water potential than did root hyphal colonization, root density, soil aggregation, soil glomalin concentration, and other variables. Moreover, a semiarid mix of mycorrhizal fungi used as inocula was superior to the single inoculation of *Glomus intraradices*. They highlighted the importance of soil hyphae on the water relations of host plants. In semiarid plants of Mexico, Monroy-Ata and García-Sánchez (2009) also showed better water

Table 5.2 Some recent book and reviews* dealing with occurrence of AMF in drought-stressed conditions

Reports	References
Reports on plant–water relations, drought, and AM symbiosis	Augé (2001)*
Reports on molecular studies of Arbuscular mycorrhizal symbiosis and alleviation of osmotic stress	Ruiz-Lozano (2003)*
AMF and soil stresses	Miransari (2010)*
Drought tolerance and AMF in Grassland, Argentina	Busso and Bolletta (2010)
AMF and alleviation of soil stresses	Miransari et al. (2008)
AMF and alleviation of soil stresses	Siddiqui et al. (2008)
AMF and environmental stresses	Smith and Read (2008)

reviews

relations, plant growth, and survival in plants associated with AMF. They tested species of Fabaceae, Cactaceae, and Agavaceae mainly in greenhouse, showing the magnitude of AMF inoculation.

Since the publication of the seminal books of Sieverding (1991), Smith and Read (2008), van der Heijden and Sanders (2003) and Miransari et al. (2008, 2011) and several reports (see Table 5.2), the need for more information on how AMF influence plant drought stress in different plant and crop species was highlighted. However, to increase our ability to optimize AMF research, experiments under field situations are still urgently needed. Most recently, Gholamhoseini et al. (2013) showed that inoculation of AM such as *Glomus mosseae* can be more benefic under drought stress, e.g., for the cultivation of sunflowers under arid and semiarid ecosystems, where water is the most important factor in determining plant yield. Additionally, inoculation of *Glomus* spp. offered a better seedling resistance (improved plant growth and physiological performance) in *Sophora davidii*—spiny, multistemmed, deciduous shrub native to southwestern China, under water stress (Gong et al. 2013). The last plant species has important use for revegetation in the semiarid Loess Plateau and arid valley areas of China.

Mycorrhizal plants under drought conditions increase stomatal conductance, transpiration rate and leaf water potential due to a higher water uptake (Augé 2001) than non-mycorrhizal plants. The mechanism by which mycorrhizas modify host-plant–water relations remains unknown (different hypotheses have been tested with inconclusive results (Morte et al. 2000) and the contribution of AM symbiosis to plant drought tolerance is now seen as the product of accumulative effects (physical, nutritional, physiological, and cellular) (Ruiz-Lozano 2003).

Evidence from different continents indicates that most vegetation types subjected to drought stress present AMF. Monroy-Ata and García-Sánchez (2009) compiled the benefits of AMF in semiarid plants of Mexico. They showed more improved water relations and plant growth in such environments in comparison with uninoculated control plants. In southeastern Spain, Barea et al. (2011) compiled the diversity of mycorrhizas found in semiarid Mediterranean ecosystem. They showed the benefit of mycorrhizal fungi to help plants to establish and deal

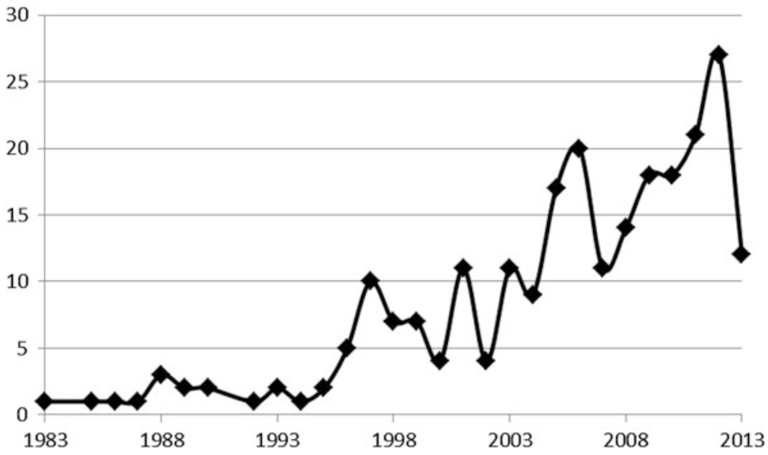

Fig. 5.1 Number of papers on AMF and drought published annually since 1983, included in the SCOPUS. Database survey conducted on June 2013

with nutrient deficiency, drought, soil disturbance, and other environmental stresses characteristically involved in soil degradation.

Modern research (Fig. 5.1) suggests a high diversity of AMF in natural ecosystems, since reports from highland fields as well from deciduous forest (see Pagano and Araújo 2011; Pagano 2012) pointed out a total of ~28 AM plant species and at least 36 AM species that occurs in those ecosystems (Pagano et al. 2013). Additionally, de Carvalho et al. (2012) reported 49 AMF species in highland fields from Brazil (23 AMF species are in common with the reports cited above). It is worth noting, moreover, that arid and semiarid regions of Argentina present in general xerophytic plants, forming dry forests, open scrublands, shrub steppe, etc. Different vegetal types such as Jarillal and Puna presented 225 AM plant species (Pagano et al. 2012), some of them also associated with dark septate endophytic fungi (DSE) (Lugo and Cabello 2002; Lugo et al. 2008). Moreover, in dry Puna ecosystem (2,000–4,400 m above the see level), ten AMF species were found, and *Glomus* was the predominant genus.

Reverse flows (hydraulic redistribution from plant to fungus) were recognized but we know little about this (they could play a critical role in supporting hyphae through drought). Moreover, the crucial importance of mycorrhizae in plant–water relations is influenced by the drying patterns, the soil pore structure, and the number of hyphal connections extending from the root into the soil (Allen 2007, 2009).

Recently, Li et al. (2013) revealed higher relative water content in colonized roots of maize by *G. intraradices*. The increased expression of two aquaporins genes in both root cortical cells containing arbuscules and extraradical mycelia under drought stress was reported. Moreover, the observed higher hyphal growth can be related to extension of the water absorption area.

Thus, new directions in microbial ecology must include the integration of microbial physiological ecology, population biology, and process ecology as microorganisms have a diversity of evolutionary adaptations and physiological mechanisms to cope with the environmental stress (Schimel et al. 2007).

Drought Stress and Agriculture

Maintenance of soil health has become a serious issue of agriculture, and the sustainable management of agricultural land has gained increasing relevance (Pagano et al. 2011). Moreover, the current intensive farming and agriculture are based on high-yielding cultivars which demand more nutrients, water, and chemicals (Tilman et al. 2002). Additionally, drought has proved to be a usual stress affecting agriculture and forestry, being able to change soil microbial abundances, including mycorrhizas composition. Few projects were based on field experiments (Pagano and Covacevich 2011; Schalamuk and Cabello 2010; Oehl et al. 2010) and showed that AMF occurs in high diversity in the fields (also in soil depth).

The use of different soil amendments in rotation to select AMF in order to benefit a particular crop as well as AMF inoculation is a topic that needs more detailed research and basic knowledge of AMF ecology (Jaison et al. 2011). Mycorrhizal plants can present higher water potential being capable to improve plant growth at a faster rate when irrigation is restored (van der Heijden and Sanders 2003; Miransari et al. 2011).

Little attention has been paid to the soil stresses and their effect on roots. Tillage promotes disruption of the AMF hyphal network and dilution of the propagule-rich topsoil (Schalamuk and Cabello 2010), which disturbs the soil physical and chemical properties, modifying the number, diversity, and activity of the soil microbiota, including both free and symbiotic fungal populations (Pagano 2011).

In this sense, anthropogenic alterations (perturbation stresses) to improve the productivity of crops (e.g., tillage, monoculture, crop rotation, irrigation, amendments and crop protection) result in disruption of the native soil microbial ecosystem. While moderate perturbation will be benefic in the short term, higher levels of stress may result in the degraded soils (Sturz and Christie 2003). The conventional tillage system, still commonly used in some countries, usually consists of moldboard plowing and additional secondary operations to prepare the seedbed. However, field traffic or intensive tillage result in excessive soil compaction and soil water loss. It is recognized that most plant species of agricultural interest associate with AMF (Miransari et al. 2011; Pagano and Covacevich 2011; Miranda 2008).

As tillage reduce AMF spore and hyphal length densities, AM fungi can be strongly decreased by conventional agricultural practices, possibly due to disturbance of AM fungal hyphal networks, changes in soil nutrient content, and altered microbial activity (Jansa et al. 2003, 2006), which can reduce glomalin content and thus the tolerance to drought.

In Argentina, earlier studies have found less management of AMF in order to increase plant productivity (Covacevich and Echeverría 2009). Soils of the Pampas region present high native AMF that colonize crop plants under different management systems (Covacevich et al. 2006, 2007; Schalamuk et al. 2006); however, they are not yet manipulated. More recently, Schalamuk and Cabello (2010) showed that different types of AM inocula from a field experiment with tilled and no-tilled wheat and from non-disturbed sites (spontaneous vegetation) presented different proportions of AM families, between field and trap cultures. Glomeraceae were higher in the trap cultures, which was attributed to the use of intra- and/or extraradical mycelium, showing advantages in the use of these propagules. Furthermore, those results suggested a huge importance of the selection of AMF species to be included under agricultural practices.

Biochar and Drought Stress

Biochar soil amendment can contribute to improved soil fertility and assumed the potential benefits to the agricultural productivity. However, the mechanisms by which it is effective in enhancing plant growth are scarcely understood, as well as the indirect effects (increased water and nutrient retention, improvements in soil pH, increased soil cation exchange capacity, effects on P and S transformations, neutralization of phytotoxic compounds, improved soil physical properties, and alteration of soil microbiota) (Elad et al. 2011).

In this regard, biochar promotes AMF, but few studies were performed in order to elucidate the "Biochar Effect" (Warnock et al. 2007), indicating the need to more future research to elucidate it (Elad et al. 2011). Recent studies, for example, showed that biochar addition improved AMF colonization of asparagus roots, contributing to the control of diseases (Elmer and Pignatello 2011; Elmer 2012). Nevertheless, the relevance of studies on biochar associated with AMF is still unknown since few studies have been published (13 documents in SCOPUS from 2007 to June 2013).

Reports including biochar and drought are lesser (only 10 documents in SCOPUS from 2009 to June 2013) and have increased in the last four years. Working with maize (*Zea mays* L.) under field conditions, Liu et al. (2012) demonstrated a synergistic positive effect of compost and biochar on soil fertility and water storage capacity. Working with wheat, Solaiman et al. (2010) suggest improved water supply to reduce drought stress with the addition of AMF. These fungi can prolong crop exploration of water from the wide inter-rows, improving grain yield and survival. Additionally, they tested the residual effect of biochar (after 2 years) and mineral fertilizers in a bioassay showing the improved conditions for root colonization after application of biochar.

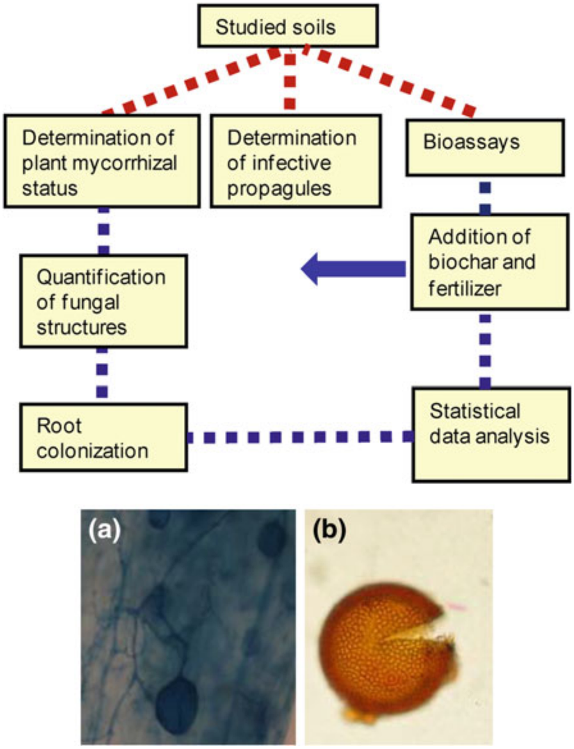

Fig. 5.2 Protocol for studying the effect of drought stress and biochar effect on AM plants. Roots of plants are stained for AM colonization (**a**). Determination of infective propagules including spores (**b**) and bioassays against soil samples are required (photos by M. Pagano)

Later, LeCroy et al. (2013) examined the interaction between biochar, AMF (*G. intraradices*), and nitrogen on sorghum seedling growth in greenhouse. They showed that addition of mycorrhizae and low nitrogen caused more oxidation (biotic oxidation) of the biochar surface than the other tested combinations and found a greater fraction of carbon present as carbonyl groups. Moreover, they suggested that the greater oxidation can be related to the AMF behavior with a more activity in their search for nutrients in a nitrogen-limited situation. A protocol for studying the effect of drought stress and biochar effect on AM plants is presented in Fig. 5.2.

It is also known that biochar may help to remove allelopathic effects via adsorption and detoxification (Wardle et al. 1998). However, further studies assessing the types of biochar (depending on original feedstock and pyrolysis conditions) (Downie et al. 2009; Krull et al. 2009) that induce resistance responses in plants against pathogens and parasites including fungi, bacteria, viruses, and nematodes are urgently needed.

Conclusion

In the introduction to this chapter, I briefly described plant stress factors and the benefits that mycorrhizal fungi provide to their plant hosts. Throughout the chapter, I have showed that stress affects soil physical and chemical properties, influencing the population, diversity, and activities of soil microbes, including symbiotic fungal populations. To identify mycorrhizal fungal species, which may contribute to plant growth under stress, the mycotrophic status of plant species is crucial, especially with regard to drought stress, as the fungi mediate the link of the plant to the soil. Additionally, anthropogenic alterations (tillage) were discussed with regard to drought although more detailed studies are lacking. The alleviation of drought stress would have great implication in the manipulation of AMF species able to colonize plants in arid and semiarid soils approving the potential of AMF to be inoculated. This chapter argues that AMF alleviate drought stress, which has great effect on plant growth; however, development of technologies and protocols to cope with drought are crucial. Lastly, the potential benefits to the agricultural productivity of biochar soil amendment and their interactions with mycorrhizal plants under drought were also pointed.

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