Chapter 6
The Role of Arbuscualr Mycorrhizae in Inducing Resistance to Drought and Salinity Stress in Crops

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Abstract Arbuscular mycorrhizal (AM) fungi are commonly occurring soil microbes whose association with roots can have wide ranging effects on growth of the host plants. These fungi are frequent root colonizers of trees, shrubs, terrestrial orchids and a broad range of plants in temperate and tropical habitats. During the establishment of AM symbiosis, a range of chemical and biological parameters are affected in plants. These fungi are considered instrumental in promoting plant establishment and growth in these environments by enhancing plant nutrient and water uptake, protecting plants from root herbivores and pathogens and improving soil structure. This symbiosis is alleged to improve plant resistance to drought and nutrient stress. There are several reports which show that AM induce physiological drought tolerance, involving both increased dehydration avoidance and dehydration tolerance. Majority of the experiments have shown that when the symbiosis improves host drought resistance it does so by aiding drought avoidance.

AM symbiosis has frequently increased resilience of host plants to salinity stress. The AM plants in the saline soils had increased phosphate and decreased Na concentrations in shoots compared to non-AM ones. Salt resistance has been shown to improve by AM colonization in a number of crops like maize, mungbean, clover, cucumber, lettuce, tomato, and many more. A correlation has been established between AM colonization and improved osmoregulation or proline accumulation. AM colonization has also been documented to improve NaCl resistance in tomato, with the extent of improvement related to salt sensitivity of a cultivar. AM improvement of salt resistance has usually been associated with AM-induced increases in P acquisition and plant growth. However, there are scanty reports of AM induced effects on host plants being more pronounced when plants were exposed to osmotic stress in salinized soils.

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1 Introduction

Only in the last few decades, botanists and mycologists have realized that most terrestrial plants live in symbiosis with soil fungi (Krishna 2005). The term mycorrhiza, coined to reflect this reality, comes to us, moreover, from the combination of two words, one Greek "mikes" (fungus) and the other Latin "rhiza" (roots). It therefore basically designates the symbiotic association between fungi and plant roots. Among the types of mycorrhizae observed in nature, one is found on the vast majority of cultivated plants. It is the arbuscular mycorrhiza, which lives in association with approximately 85% of herbaceous plants. This means therefore that in the plant world, mycorrhizal symbiosis is the rule rather than the exception.

Arbuscular mycorrhizal fungi (AMF), which are microscopic soil fungi, colonize the roots and their rhizosphere simultaneously and spread out over several centimeters in the form of ramified filaments. This filamentous network dispersed inside as well as outside the roots allows the plant to have access to a greater quantity of water and soil minerals required for its nutrition. In return, the plant provides the fungus with sugars, amino acids and vitamins essential to its growth (Harley and Smith 1983).

The colonized plant is better nourished and better adapted to its environment. It obtains increased protection against environmental stresses (Sylvia and Williams 1992), including drought (Augé et al. 2007, 2008), cold (Charest et al. 1993), salinity, and pollution (Leyval et al. 1997). In addition, symbiosis tends to reduce the incidence of root diseases and minimizes the harmful effects of certain pathogenic agents (Dehne 1982; St-Arnaud et al. 1995). By and large, the growth and health of colonized plants is improved. At the same time, they obtain increased protection against environmental conditions detrimental to their survival.

Given that the majority of cultivated plants used for human and animal food purposes are colonized by mycorrhizae, we can consider utilizing this symbiosis for the benefit of agriculture, by selecting the best plant-fungus combinations (Abbott and Robson 1991). It is then possible to promote healthier cropping systems and to reduce the use of chemical inputs (pesticides, fertilizers), while ensuring crop profitability and environmental quality.

2 Arbuscular Mycorrhiza and Environmental Stresses

Recent evidence suggests that colonization of root systems by VA mycorrhizal fungi affords host plants greater resistance to environmental stresses like drought stress (Sanchez-Diaz and Honorubia 1994; Allen and Bosalis 1983; Nelson and Safir 1982; Augé 2000, 2001). Mycorrhizal plants may avoid drought to some extent through enhanced water uptake at low soil moisture levels. In onion, the effects appear to be conferred through improved phosphorus nutrition (Nelson and Safir 1982). While in Bromus and rose, some other mechanism prevails (Bildusan et al. 1986). An influence on host osmotic potential has been observed in wheat (Allen and Bosalis 1983).

These fungi also play a vital role in alleviating the effects of salinity (Al-Karaki et al. 2001). By improved nutrient acquisition, AM fungi compensate for the nutritional imbalances imposed by salinization, (Sylvia and Williams 1992). Some other environmental stresses such as micronutrient imbalances, industrial effluents (Oliveira et al. 2001), heavy metal toxicity (Chaudhry et al. 1999; Leyval et al. 1997), biocide treatment, (Heggo et al. 1990), slurry application (Chistie and Kilpatrich 1992), sulfur dioxide fumigation (Clappert et al. 1990) and wild fire recovery (Puppi and Tartnlini 1991), involves the use of AM fungi, (Barea et al. 1993). Some AM fungi are adapted to adverse conditions so they can benefit plants under a variety of environmental stresses, (Mosse et al. 1981). AM can also reduce the toxicity of certain metals for plants, while at non-toxic or such optimal level, their acquisition is enhanced by symbioses, (Bethlenfalvay 1992; Sylvia and Williams 1992; Barea et al. 1993; Khan et al. 2000). AM also plays positive role in protecting plants from pH extremes, (Sylvia and Williams 1992).

Mycorrhizal fungi interact with a wide assortment of organisms in the rhizosphere. The results can either be positive, neutral, or negative on the mycorrhizal association or a particular component of the rhizosphere. For example, specific bacteria stimulate EM formation in conifer nurseries and are called mycorrhization helper bacteria. In certain cases, these bacteria eliminate the need for soil fumigation (Azcón-Aguilar and Barea 1992; Garbaye 1994; Gryndler 2000).

The interaction between *Rhizobia* and AM fungi has received considerable attention because of the relatively high phosphorus demand of N_2 fixation. The two symbioses typically act synergistically, resulting in greater nitrogen and phosphorus content in combination than when each is inoculated onto the legume alone.

Legumes are typically coarse-rooted and therefore inefficient in extracting phosphorus from the soil. The AM fungi associated with legumes are an essential link for adequate phosphorus nutrition, leading to enhanced nitrogenase activity that in turn promotes root and mycorrhizal growth.

Mycorrhizal fungi colonize feeder roots and thereby interact with root pathogens that parasitize the same tissue. In a natural ecosystem where the uptake of phosphorus is low, a major role of mycorrhizal fungi may be protection of the root system from endemic pathogens such as *Fusarium* spp. Mycorrhizae may stimulate root colonization by selected biocontrol agents, but our understanding of these interactions is meager. Much more research has been conducted on the potential effects of mycorrhizal colonization on root pathogens. Mycorrhizal fungi may reduce the incidence and severity of root diseases (Linderman 2000, 1994; Hooker et al. 1994). The mechanisms proposed to explain this protective effect include: (i) development of a mechanical barrier-especially the mantle of the EM to infection by pathogens, (ii) production of antibiotic compounds that suppress the pathogen, (iii) competition for nutrients with the pathogen, including production of siderophores, and (iv) induction of generalized host defense mechanisms (Duchesne 1994). Role of arbuscular mycorrhizae as biological control agents soil-born plant pathogens have been elucidated by Azcón-Aguilar and Barea, (1996) and Singh and Singh (1996).

3 Arbuscular Mycorrhiza and Abiotic Stresses

The concept of an arbuscular mycorrhiza (AM) has been intensively advocated as a temporally and spatially complex symbiosis representing a suite of hosts and fungi, as against the more traditional "dual organism" view. These associations are important on natural and managed ecosystems due to their nutritional and non-nutritional benefits to their symbiotic partners. They can alter plant productivity, because AMF can act as biofertilizers, bioprotectants, or biodegraders (Xavier and Boyetchko 2002). AMF are known to improve plant growth and health by improving mineral nutrition or increasing resistance to tolerance to biotic and abiotic stresses (Clark and Zeto 2000; Turnau and Haselwandter 2002; Takeda et al. 2007).

Reports are mounting concerning the role of AM in responses to elevated atmospheric CO_2. Measurements of the contributions of AM fungi at various levels require the use of different response variables. For example, hyphal nutrient translocation rates or percent AM root infection may be important measures at the individual plant level, but hyphal biomass or glomalin production and turnover are more relevant at the ecosystem level. There is a discrepancy between our knowledge of the multifaceted role of AM fungi in plant and ecosystem ecology and most of the current research is aimed at elucidating the importance of this symbiosis in global-change scenarios. A framework for more integrated and multifactorial research on mycorrhizal involvement in regulating CO_2 responses may also serve to enhance communication between researchers working at different scales on large global-change ecosystem projects. A series of investigations have summarized the role of

anthropogenic pollution in general and CO_2, SO_2, O_3 pollution in particular, affecting mycorrhizal fungal communities (Cairney and Meharg 1999; Rillig and Allen 1999; Staddon and Fitter 1998).

One major line of work entailed studying the responses of the mycorrhizal communities to pollution stress, since under field conditions these fungi are crucial for the transfer of minerals from the soil solution to tree roots (Harley and Smith 1983). Effects of acid precipitation and gaseous pollutants have been shown to reduce root growth and mycorrhizal development. Indirect effects of pollutants in reducing photosynthesis and hence carbon allocation to the root system, may also inhibit mycorrhizal developments. Effect of elevated CO_2 (Rillig and Allen 1999) and other gaseous pollutants have recently been reviewed by Dighton and Jansen (1991), but most of the work was based on researches with ectomycorrhizae. Shaw et al. (1992a, b) studied the effects of SO_2 and O_3 on the mycorrhizae of Scots pine These were fumigation experiment based on collecting data of fruit bodies above-ground and taking root harvests below ground. Toermorshuizen and Shaffers (1987) observed that under Scots pine in the Netherlands mycorrhizal fruit bodies were not depressed by air pollution in young stands than they were in mature stands. Studies by Brown and Roberts (1988) discussed the effects of ozone on foliar leaching in Norway spruce *Picea abies* confounding effects due to N_2O_5 production during ozone generation in fumigation experiments. Shafer and Schoeneberger (1994) have indicated the mycorrhizal connection in the relationship of air pollution and ecosystem health.

The term "mycobioindication" was first of all coined by Kraigher et al. (1996). In their discussion of mycobioindication of forest site pollution, they employed a supposedly pollution sensitive (*Hydnum rufescens*) and supposedly insensitive (*Paxillus involutus*) fungal species of ectomycorrhizae. However, they emphasized that further screening of comparable forest sites differently influenced by pollution was needed to confirm the choice of species. The literature is wanting as regards the role of VA mycorrhizal fungal species as indicators of air pollution (Nasim et al. 2007). There are, however, sporadic reports of some fumigation studies employing AM. During a pioneer study, McCool et al. (1979) investigated the effects of ozone and HCl gases on the development of mycorrhizal fungus, *Glomus fasciculatum* and growth of Citrus sp. He noticed that higher concentration than the normal ones inhibited the growth and spread of *G. fasciculatum*. In subsequent studies, and Heath et al. (1982) concluded that the air containing higher concentration of ozone affects the rate of photosynthesis by reducing the photosynthetic capacity of the chloroplast and inhibits mycorrhiza formation in return. In another preliminary study, the effect of ozone exposure on mycorrhiza formation and growth of a forage grass, *Festuca arundinacea*, were studied (Ho and Trappe 1984). This grass usually forms abundant mycorrhizae (Ambler and Young 1977) but when exposed to 0.1 ppm ozone for three months a significant decrease in root weight and intensity of mycorrhizae formation was observed. In 1983, Brewer and Heagle, exposed soybean plants to ozone in open-top chambers in sterilized and unsterilized soil inoculated with AM and Rhizobium. Their results indicated that soybean infected with *Glomus geosporum* was less sensitive to adverse growth and yield effects of ozone.

3.1 Drought Stress

Stress is defined an external factor that exerts a disadvantageous influence on the plant. In most, cases stress is measured in relation to growth or to the primary assimilation processes (CO_2 and mineral uptake) which are related to overall growth. Under both natural and agricultural conditions, plants are constantly exposed to stress. Some environmental factors (such as air temperature) can become stressful in just a few minutes, whereas others may take days to weeks (soil water) or even months (some mineral nutrients) to become stressful (Taiz and Zeiger 2006). In this section we would focus our discussion on drought stress and role of arbuscular mycorrhiza in alleviating this stress (Table 6.1).

Table 6.1 Impacts caused by drought on plants

Drought resistant strategies vary with climatic or soil conditions:
Water stress has several effects on growth. Of particular importance is a specific limitation to leaf expansion or otherwise plants have to complete their life cycles to avoid the onset of drought and rapid depletion of water through much expanded leaves.

Decreased leaf area is an early response to water stress:
As water content of the plant decreases the cell shrinks and the cell walls relax. This decrease in cell volume results in lower hydrostatic pressure. The plasma membrane becomes thicker and compresses as it occupies a smaller area than before. Inhibition of cell expansion results in a slowing of leaf expansion.

Water deficit stimulates leaf abscission:
In response to water stressed conditions the leaves will undergo senescence and will fall off. This leaf area adjustment is an important long-term change that improves the fitness for water-limited environment.

Water deficit enhances root extension into deeper, moist soil:
Inhibition of leaf expansion reduces the consumption of carbon and energy during photosynthesis, and a greater proportion of the plant's assimilates can be distributed to the root system, where they can support further growth.

Mid-noon Stomatal closure due to stress induced ABA synthesis:
Stomata may close during the peak hours of the day in response to severe water stress. This is also facilitated by the production of excess amount of ABA and translocation of the same in the transpiration stream initiating the closure of stomata.

Water stress limits the photosynthesis within the chloroplast:
Rate of photosynthesis is less sensitive to turgor as compared to leaf expansion. However, Mg^{2+} concentration in chloroplast may influence photosynthesis during water stress.

Osmotic adjustment of cells helps maintain plant water balance:
As soil dries up, its matric potential becomes more negative. Plants are able to take up water as long as their water potential is more negative than the water potential of the soil. Osmotic adjustment, or accumulation of solutes by cells is a process by which water potential can be decreased without an accompanying decrease in turgor. These solutes which are generally accumulated are called compatible solutes or osmolytes.

Water deficit alters energy dissipation from leaves:
The evaporative cooling lowers leaf temperature and is highly effective for the survival of plants in arid environments. When transpiration slows down, the leaf temperature increases. Under these circumstances reduced leaf surface area, oreientation of leaves away from sunlight, wilting, leaf rolling, presence of hair or pubescence on the leaf surface, by layer of reflective epicuticular wax, or grey-white appearance are effective strategies adopted by the plants.

Table 6.1 (continued)

Water deficit increases resistance to liquid-phase water flow:
With and increasing development of water stress the resistance to the flow of water in the plant increases sharply (Blizzard and Boyer 1980). As plant cells lose water, they shrink. When root shrinkage during the day is pronounced, the root surface moves away from the soil particles that hold the water, as a results the delicate root hairs are damaged. Another reason may be the deposition of suberin, a water impermeable lipid increasing the resistance to water flow. Another reason may be cavitation, or breakage of water column under tension.

Water deficit increases wax deposition on leaves:
During water stress, production of a thicker cuticle that reduces water loss from the cuticle (cuticular transpiration) is a common observation.

Water deficit may induce Crassulacean Acid metabolism:
Crassulacean Acid Metabolism (CAM) is a plant adaptation in which stomata open at night and remain closed during the day. Therefore the water use efficiencies of CAM plants are among the highest measured in all higher plants. The phenomenon of CAM is characteristic of succulent plants such as *Bryophyllum* or cacti. A few succulent species display facultative CAM, switching to CAM when subjected to water deficit or saline conditions (Hanson and Ting 1978).

Drought as a cause of Dieback and decline of trees:
The decline is a general loss of vitality throughout the entire tree caused by a systemic disease or by a sequence of stressing events that causes, the tree to deplete its energy reserves. Twig and branch dieback is initiated in the tree as a response to poor growing conditions, physical injury to the tree and/or pest attack. Usually a combination of physical, climatic and pest problems lead to decline and dieback of trees (Clatterbuck 2001, 2006). Drought is a primary contributing factor to tree decline. Extended drought can influence the health of shade trees by the loss of absorbing roots. Most of the roots occur in the top 6–12 inches of the soil. Once the upper soil becomes dry, many absorbing roots dry out and die. Leaves and stems can also be damaged by drought conditions, especially when there is little water available for evaporative cooling and for photosynthesis and food production. Trees that occur on these soils or convex surfaces (ridges and ridge crests) where soil does not have much water holding capacity are more susceptible to drought that others. Some species of trees are more drought tolerant than others (Clatterbuck 2001). Trees may not readily show initial drought symptoms (curling of leaves, gradual loss of leaves, thinning of the crown) because of stored food reserves that reside in the woody tissues. However, as these stored food is depleted, drought symptoms become more prevalent. Drought symptoms can be delayed for two or more years as food reserves slowly deplete and imbalance between the aboveground and belowground tissue occur, making it difficult for many to believe that drought was actually the problem.

Drought is an evocative term. It comes with connotation of severe financial hardship among farmers in rich countries, to malnutrition, even famine, among farmers in poor countries. If prolonged it can lead to major social upheaval, mass migration, and desertification, not only in the sense that the affected region is deserted by its former inhabitants but also because over-farmed land may become so degraded that it can no longer support human habitatition even when the prolonged drought is over (Passioura 2007).

'Drought' has many meanings in relation to crop production. These range from: statistical, to a meteorological; through yield being limited by too little water to an agronomist; to sudden severe water deficits to many molecular biologists (Passioura 2007). Laboratory scientists typically work at short time scales. One area that has

attracted much attention is desiccation tolerance, the ability of plants to survive severe water deficit. Work with transgenic involving CBF/DREB transcription factors is proceeding apace. This is covered by 300 patents that also refer to drought tolerance (Passioura 2007).

3.1.1 Morphological and Anatomical Effects

Plants facing the problem of drought or continued water stress may respond in terms of exhibiting certain changes in morphological or anatomical features. Of particular importance in this connection are surface area, shape and arrangement of leaves and their internal structure. Small changes in leaf water status can have relatively large effects on critical physiological processes such as photosynthesis and water transport (Franks 2006; Taiz and Zeiger 2006). Because of this, leaves appear to be designed to maintain a certain degree of hydraulic homeostasis, both across species and across environments (Cowan and Farquhar 1977; Farquhar et al. 2002; Franks 2006).

3.1.2 Metabolic Effects

Continued episodes of water stress lead to inhibition of plant growth and photosynthesis, as well as to other effects. The process that is most affected by water deficit is cell growth. More severe water stress leads to inhibition of wall and protein synthesis, accumulation of solutes, closing of stomata and inhibition of photosynthesis.

3.1.3 Drought Resistance

Drought resistance mechanisms have been divided into several types. At the first level the phenomenon may be distinguished into desiccation postponement (ability to maintain tissue hydration) and desiccation tolerance (ability to function when dehydrated) which are sometimes referred to as drought tolerance at high and low water potentials respectively. A third category is drought escape which comprises plants that complete their lifecycles during the wet season, before the onset of drought. These are the only true drought avoiders. Among the desiccation postponers are water savers and water spenders. The water savers use water conservatively saving some in the soil for use late in the life cycle, whereas the water spenders aggressively absorb water, often using prodigious quantities (MacMahon and Schimpf 1981; Levitt 1972) (Table 6.2).

3.1.4 Mycorrhiza and Plant Water Relations

Water is one of the major global problems facing humankind at the moment and that is likely to be ever increasing in the future. Furthermore, there would be an increased competition for water resources available for agriculture in the future, despite the fact that there will be an ever increasing demand for water resources

Table 6.2 List of impacts caused by arbuscular mycorrhiza on plants exposed to drought

An immense magnitude of work has been published in the form of 200 peer reviewed papers on the influence of AM fungi on water relations, photosynthetic rates and drought responses of 90 host species representing 69 genera.

Stomatal conductance and transpiration:
AM and Non-AM plants often display different transpiration rate and stomatal conductances to water vapour being higher in the case of AM plants. AM effects on stomatal conductance have been observed with similar frequency under amply watered and drought conditions. AM symbiosis has also affected stomatal sensitivity to atmospheric water status (humidity). AM induced increases in transpiration and stomatal conductance in non-stressed plants are often stable but have been found to be three times that of P-limited NM controls. Stomatal conductance and leaf Ψ are linked functionally: changes in one usually derive changes in other. Thus when AM symbiosis hastens or postpones leaf dehydration, this would naturally be associated with altered stomatal behaviour. The extent of this alteration, however, may vary with different combinations of host plants and AM fungi (Augé et al. 2008).

Photosynthesis:
AM plants often show higher photosynthetic rates than their experimental non-AM counterparts, which is consistent with AM effects on stomatal conductance. Like stomatal conductance and transpiration, photosynthesis is stimulated by AM symbiosis about as frequently under non-stresses as under drought conditions. As with stomatal conductance, different AM fungi have different effects on photosynthesis during drought (Dixon et al. 1994).

Leaf hydration:
Tissue hydration or water status is typically quantified by measuring Ψ or its components or water content. Leaf Ψ of non-stressesd plants has usually not been affected by AM symbiosis. However, leaf osmotic potential may differ in AM and Non-AM plants during drought. Osmotic potential tends to be higher in leaves of AM plants than non-AM plants which means that AM plants are not as strained by the water stress as non-AM plants.

Root hydration:
Root Ψ components and water contents are more difficult to measure than corresponding leaf parameters and root water relations of AM and NM plants have seldom been compared. Nodule water content was higher in AM than in Non-AM alfalfa plants. Symplastic water fractions were increased by AM symbiosis in droughted rose roots.

Hydraulic conductivity and hyphal water transport:
Root hydraulic conductivity is generally not improved by AM symbiosis in the absence of AM-induced growth or P effects. In fact it was lower in AM plants. The hyphae of various AM fungi differ in their influence on water uptake, despite similar intra- and extra-radical hyphal extensions.

Soil drying rates and moisture relations:
AM root systems can dry soil more quickly and thoroughly than NM root systems, signified by larger declines in soil water contents or soil Ψ over time. This is probably because the shoots of the AM plants were larger (more evaporative leaf surface area) or the root systems of AM plants were larger or more finely divided (more water absorptive surface area) than those of non-AM plants (Okon et al. 1996).

Growth and nutrient uptake during drought:
AM symbiosis usually increases host growth rates during drought by affecting nutrient acquisition and possibly hydration. It has also typically increases water use efficiency and colonization by different fungi affects water use efficiency differently. As soil first begins drying, shoot growth can be inhibited before any leaf dehydration occurs through a root-to shoot non-hydraulic signaling mechanism. AM effects on host growth during drought are often related to improved P acquisition, as the available P in the soil is reduced by soil drying. It has been observed that copper and zinc concentration were higher in leaves of droughted AM than non-AM plants. While manganese and boron concentration was lower in leaves of AM than non-AM plants. Shoot concentration of nitrogen, potassium, calcium, magnesium, iron, sodium and molybdenum appear to be affected little by AM symbiosis in drought conditions.

Table 6.2 (continued)

Metabolic effects during drought:
AM plants respond more quickly to the onset of drought than non-AM plants. This is also reflected in their metabolism. A plant more strained by water stress would be expected to be more metabolically perturbed. AM plants of tobacco accumulated less glucose and fructose in leaves and roots than non-AM ones in drought conditions. While a fungal disaccharide trehalose greatly increased in AM plants during drought. Concentration of amino acids in drought stressed AM plants have been reported to increase along with an increase in the activities of several enzymes. While during drought the concentration of ABA in xylem sap is reported to be low in AM plants. Chlorophyll concentration is high in leaves of AM than non-AM plants.

Morphological effects during drought:
AM effects on plant water relations and metabolism during drought have been associated with morphological and phenological effects. In some plants early and enhanced leaf abscission were recorded during drought in AM plants, while in some the leaf drop decreased in AM plants under stress. AM soybean had less drought-induced pod abortion. Leaf movements were greater in AM plants under stress. AM rose leaves had less epicuticular wax and lower cutical weight than non-AM plants. AM plants show reduced wilting under water stress and recover more quickly from wilting when provided with ample water. However, stomatal density is not significantly affected in AM plants during drought.

Mechanisms:
The best understood mechanism of AM mediated responses under water stress conditions involves AM effects on plant size. The size of a plant can affect its water relations and drought responses. Enhanced P uptake is the most dramatic means by which AM fungi affect overall plant biomass, but AM effects on carbon and nitrogen relations can also influence host size. Both overall plant size and within-pant relationship, such as root-to-shoot ratios, can influence plant behaviour, particularly when soil water becomes limiting.

Modified from Augé (2001)

available for agriculture to meet the needs of the increasing world population. A range of strategies have been proposed to cope with global water scarcity which include desalinization, virtual water and food trade, increasing agriculture yields, and improving the efficiency of water use in agriculture.

Biotechnology can play a significant role to address the last two possibilities. Through a number of investigations innumerable attempts have been made to genetically modify the plants so that they are able to withstand water stress conditions either through drought tolerance or drought avoidance. Here the specific application of symbiotic soil fungi has been discussed in relevance to water use in agriculture. This is regarding the inoculation of crops with arbuscular mycorrhizal fungi.

The extensive amount of research literature on the subject indicates that mycorrhizae often have a substantive impact on water movement into, through and out of host plants, with consequent effects on plant tissue hydration and leaf physiology. They usually increase host growth rates during drought, by affecting nutrient acquisition and possibly hydration, and typically water use efficiency, which are influenced by the kind of fungi involved (Augé 2001)

Mycorrhizal fungi can therefore be applied as biofertilizer with the aim of increasing growth potential and reducing water and fertilizer use and are used in

crop production, horticulture, habitat restoration, bioremediation and forestry. The mycorrhizal fungal innoculum may be applied in a number of ways e.g., by simply applying soils known to contain the desirable mycorrhizal fungi to areas lacking the fungi or using one of the many commercially available products available world-wide (Schwartz et al. 2006). Benefits, however, are not granted and a number of factors have to be considered when assessing their potential application, such as competition with other soil microorganisms as well as the dependence of the plant species on mycorrhizae, the nutrient status of the soil and the inoculum potential of the mycorrhizal fungi already present in the soil (Sylvia et al. 2005).

3.1.5 Mycorrhiza and Soil Water Relations

The contributions of AM fungal hyphae in terms of improving soil structure and its water holding capacity are substantial (Miller and Jastrow 2000). Not only can mycorrhizal fungi influence plant growth overall (and hence soil water regimes), but mycorrhizal plants exhibit different water relations from their non-mycorrhizal counterparts (Augé 2001, 2004). AM symbiosis has been reported to result in altered rates of water movement into, through and out of host plant, with consequent effects of tissue hydration and leaf physiology. For example, higher stomatal conductance and transpiration can occur in the mycorrhizal situations (Ebel et al. 1997; Augé et al. 2004). More efficient exploration of water by mycorrhizal fungi may lead to more extreme wet/dry cycles, which could have very strong consequences for soil aggregation (Six et al. 2004). Additionally, because the symbiosis can allow leaves to fix more carbon during water stress (Duan et al. 1996), carbon inputs into the soil would be expected to be increased, which might be especially important in more arid environment. Hyphae and roots can be viewed as a "sticky string bag" from a mechanistic point of view. Basically, the hyphae of AM fungi contribute to the entanglement and enmeshment of soil particles to form aggregates, the basic building blocks of soil structure. Furthermore, the glycoprotein, glomalin, deposited on the cell wall of the AM fungus is rather stable hydrophobic glue that might enable the fungus to cope with gas-water interfaces during aerial growth. In addition, the hydrophobicity of the deposited glomalin may reduce macro-aggregate disruption during wetting and drying events (Miller and Jastrow 2000).

3.1.6 Molecular Basis for Drought Resistance

Of all the abiotic stresses that curtail crop productivity, drought is the most dev-astating one and the most recalcitrant to breeder's efforts. In the past, breeding efforts to improve drought tolerance have been hindered by its quantitative genetic basis and our poor understanding of the physiological basis of yield in water lim-ited conditions (Passioura 2002; Blum 1988). Further complexity derives from the occurrence of other abiotic stresses that often amplify the negative impact of drought on growth and metabolism (Mittler 2002, 2005). From an application point of view, it is crucially important to select genotypes able to optimize water harvest and water

use efficiency while maximizing yield in relation to the dynamics of the drought episodes prevailing in each target environment (Bacon 2004).

The genetic basis of the molecular, cellular and developmental responses to drought involves many gene functions regulated by water availability. Genomics based approaches provide access to agronomically desirable alleles present at quantitative trait loci (QTLs), that affect such responses, thus enabling us to improve the drought tolerance and yield of crops under water limited conditions more effectively. Marker-assisted selection is already helping breeders to improve drought related traits. Analysis of sequence data and gene products should facilitate the identification and cloning of genes at target QTLs. Based on such ideas, we envision a quick broadening of our understanding of the genetic and functional basis of drought tolerance. Novel opportunities will be generated for tailoring new genotypes "by design". Harnessing the full potential of genomics-assisted breeding will require a multidisciplinary approach and an integrated knowledge of the molecular and physiological processes influencing tolerance to drought (Tuberosa and Salvi 2006).

Among a seemingly endless list of morpho-physiological characters, the roots traits seem to be of much significance due to the crucial role of roots in harvesting water from the soil. Roots show a high degree of plasticity as regards water and nutrient uptake. Although this plasticity is under genetic control to a varying degree and several QTLs have been identified for in rice and maize, most recently, QTLs for the response of leaf elongation rate to soil moisture, temperature and evaporative demand have been identified. Remarkably, a model based on the combined effects of the major QTLs was able to predict 74% of the variability for leaf elongation rate measured among recombinant inbred lines of the mapping populations. Applying this modeling approach to root elongation rate sould provide valuable insight onto the role of root plasticity in the 'Genotype x Environment' (GxE) interaction under different water regimes and allow MAS to be used more effectively to tailor drought-tolerant genotypes by improving the root architecture.

During the past decade, an increase in QTL studies for drought-related traits and the first encouraging results in QTL cloning (Salvi and Tuberosa 2005) has lead us to a better understanding and to be able to effectively manipulate the traits influencing drought tolerance. This molecular assisted breeding will help us to face the challenges posed by the decreasing availability and escalating price of irrigation water. The successful exploitation of genomics to enhance drought tolerance will only be possible within a coherent, interdisciplinary context able to provide a thorough understanding of the factors limiting crop yield in drought-prone environment.

3.2 Nutrient Stress

Arbuscular mycorrhiza (AM) having a great influence on overall plant physiology contributes to improved plant health and growth, particularly under suboptimal conditions (Peuss 1958; Hirrel and Gerdemann 1980; Sharma et al. 1992). AM can

improve the uptake of water (Augé 2001) and nutrients (George 2000). Carbon assimilation and export from leaves may also be increased in mycorrhizal plants (Douds et al. 2000; Gernns et al. 2001).

3.3 Salinity Stress

Soil Salinization is an ever-present threat to crop yield. It is a widespread problem. Approximately, 7% of the global land surface is covered with saline soils (Ruiz-Lazano et al. 1996). Out of 1.5 billion ha cultivated land, about 77 million ha (5%) are affected by excess salt content mainly induced by irrigation with ground water of high salt content (Munns et al. 1999). It is well known that crop production is low in saline soil, mainly due to salt toxicity to plants leading to a decrease in plant water holding capacity, the imbalance of nutrient uptake, and toxicity of ions towards plant photosynthesis (Katerji et al. 1998; van Hoorn et al. 2001). The responses to salt stress comprise an array of changes at the molecular, biochemical and physiological levels (Garg and Manchanda 2008).

Mycorrhizal symbiosis is a key component in helping plants survive under adverse environmental conditions (Augé et al. 1992). Arbuscular mycorrhizal fungi widely occur in salt stressed environment (Wang and Liu 2001). Recently, many researchers reported that AM fungi could enhance the ability of the plants to cope with salt stress (Yano-melo et al. 2003; Rabie 2005; Jahromi et al. 2008) by improving plant nutrient uptake (Canterall and Linderman 2001; Asghari et al. 2005), and ion balance (Zandavalli et al. 2004; Giri et al. 2007), protecting enzyme activity (Rabie and Almadini 2005; Giri and Mukerji 2004, and facilitating water uptake (Berta et al. 1990; Ruiz-Lazano and Azcon 1995). Shi et al. (2002) and Shi and Guo (2006) found that salt stress could decrease photosynthetic ability and induce physiological drought in plants which leads to a decrease in crop production. There are few reports which indicate that AM colonization could enhance relative water content in *Zuchhini* leaves Colla et al. (2008), water potential of maize plants (Feng et al. 2000a; b) and chlorophyll concentration in the leaves of several plant species like *Sesbania aegyptica*, *S. grandiflora*, and *Lotus glaber* (Giri and Mukerji 2004; Sannazzaro et al. 2006; Colla et al. 2008). Sheng et al. (2008) evaluated the influence of arbuscular mycorrhizal fungus *Glomus mosseae* on characteristics of the growth, water status, chlorophyll concentration, gas exchange, and chlorophyll fluorescence of maize plants under salt stress. Maize plants were subjected to five levels of NaCl for 55 days. The results of this experiment by Sheng et al. (2008) that mycorrhizal maize plants had higher shoot and root dry weights than non-mycorrhizal plants when being exposed to salt stress, which means that mycorrhizal plants grow better than non-mycorrhizal plants under saline conditions. This is in line with many greenhouse studies on tomato (Al-Karaki and Hammad 2001), cotton (Feng and Zhang 2003), barley (Mohammed et al. 2003), and maize (Feng et al. 2000a, b).

In an experiment while evaluating the effect of AM inoculation on salt-induced nodule senescence in *Cajanus cajan* (Pigeon pea) it was reported that many of the

physiological and biochemical plant processes were affected by salt stress as a result of triggering premature nodule senescence along with a reduction in N-fixing ability of the nodules. In an experiment of 80 days, the plants were exposed to fairly high salinity regimes of 4, 6, 8 dS m^{-1} with and without mycorrhizal inoculation. Various parameters linked to nodule senescence were assessed like nodulation, leghemoglobin content, and nitrogenase enzyme activity measured as acetylene reduction activity (ARA). Two groups of antioxidant enzymes were studied: (1) enzyme involved in detoxification of O^{2-} radicals and H$_2$O$_2$ namely, superoxide dismutase, catalase and peroxidase, and (2) enzymes that are important components of the ascorbate glutathione pathway responsible for the removal of H$_2$O$_2$, namely, glutathione reductase and ascorbate peroxidase. The results of the experiment showed that AM significantly improved nodulation, leghemoglobin content and nitrogenase activity under salt stress. Activities of the rest of the enzymes mentioned above increased markedly in mycorrhizal-stressed plants. In some of the previous studies by Alguacil and others (2003) it was reported that increased antioxidative enzyme activities could be involved in the beneficial effects of mycorrhizal colonization on the performance of plants grown under semiarid conditions. Similar observation as those of Garg and Manchanda (2008) were noticed by Ruiz-Lozano and others (2001) and Porcel and others (2003) in soybean under drought stress (Table 6.3).

Arbuscualr mycorrhizal symbiosis is often alleged to improve plant resistance to drought stress (Cho et al. 2006) and AM plants often far batter during drought than their non –AM counterparts (Augé and Moore 2005; Augé et al. 2007). The intensity of mycorrhizal effect can increase with the intensity of drought (Subramanian and Charest 1998).

AM symbiosis has also been reported to increase resilience of host plants to salinity stress, perhaps with greater consistency than to drought stress (Cho et al. 2006). Growth in saline soils was increased by inoculation with *Glomus* spp. with AM plants having increased phosphate and decreased Na$^+$ concentrations in shoots compared to uninoculated controls (Giri and Mukerji 2004). Salt resistance was improved by AM colonization in maize (Feng et al. 2002), mung bean (Jindal et al. 1993) and clover (Ben Khaled et al. 2003), with the AM effect correlated with improved osmoregulation or proline accumulation. AM colonization also improved NaCl resistance in tomato, with extent of improvement related to salt sensitivity of the cultivar (Al-Karaki 2000; Al-Karaki et al. 2001). AM improvement of salt resistance has usually been associated with AM-induced increase in P acquisition and plant growth, although two of three AM fungi tested were able to protect cucumber plants from NaCl stress compared to similarly sized non-AM plants (Rosendahl and Rosendahl 1991). Alfalfa was also more effectively protected against salinity stress by AM symbiosis than by P-supplementation (Azcon and El-Atrash 1997), and the improvement of NaCl resistance in lettuce induced by several AM fungi was not attributed to nutrition (Ruiz-Lozano et al. 1996).

Since solutes can concentrate in the soil solution just outside roots as soil dries (Stirzaker and Passioura 1996), and since AM symbiosis often increases plant resistance to salinity stress, one can speculate that the amount of salts in drying soil may

Table 6.3 Impacts of salinity on plants

A highly complex and extensive problem in agriculture is the accumulation of salts from irrigation water. Evaporation and transpiration remove pure water (as vapor) from the soil and this water loss concentrates solutes in the soil. When the quality of irrigation water is poor and when there is no opportunity to flush out accumulated salts to a drainage system with an occasional excess irrigation, salts can quickly reach levels that are injurious to salt sensitive species (Taiz and Zeiger 2006).

Soil Salinization impairs plant function and soil structure:
High concentration of Na^+ results into sodicity while the increase in total salt concentration is called as salinity. The high Na^+ concentration of the sodic soils cannot only injure plants directly but also degrade the soil structure, decreasing porosity and water permeability. A sodic clay soil is very hard and impermeable.

Salinity depresses growth and photosynthesis in sensitive species:
Plants are divided into two broad groups on the basis of their response to high concentration of salts. *Halophytes* are native to saline soils and complete their life cycle in that environment. *Glycophytes* (sweet plants), or non-halophytes are not able to resist salts to the same degree as halophytes. Usually there is a threshold concentration of salts above which glycophytes begin to show signs of growth inhibition, leaf discolouration, and loss of dry weight. Among crops, date palm and sugar beet are highly tolerant crops (Greenway and Munns 1980). Species like *Suaeda maritima* and *Atriplex nummularia*, which are highly tolerant to salt show growth stimulation at Cl^- concentration many times greater than the lethal level of sensitive species.

Salt injury involves both osmotic effects and specific ion effects:
The increase in salt concentration is just similar to that of sol water deficit. Some plants can adjust osmotically when growing in saline soil and in this way prevent loss of turgor, which would slow extension growth of cells while generating a lower (more negative) water potential. Specific ion effect occurs when injurious concentration of Na^+, Cl^-, or SO_4^{2-} accumulates in the cells. A high Na^+ to K^+ ratio and high ratio of total salts inactivate enzymes and inhibit protein synthesis resulting into an inhibition of photosynthesis.

Plants use different strategies to avoid salt injury:
Plants avoid salt injury by exclusion of ions from the leaves or by compartmentation of ions in vacuoles. The salts may be excluded at the level of roots or may be secreted through salt glands and crystallize in the form of harmless crystals.

Salt stress induces synthesis of new proteins:
Exposure to NaCl induces synthesis of proteins associated with improved tolerance to NaCl. In tissue culture, cells of *Citrus* species or tobacco (*Nicotiana tobaccum*) have been acclimated to tolerate unusually high concentration of salts.

be one experimental factor that can explain why AM fungi increased drought resistance in some studies but not in others i.e., perhaps AM effects on drought resistance are linked to AM effects on salt resistance; in those reports where AM symbiosis did improve drought resistance, AM fungi may have helped to overcome plant susceptibility to an osmotic or NaCl stress that developed as soil dried (Cho et al. 2006). Cho et al. (2006) found that in *Sorghum bicolor* plants, salinity stress tended to nullify an AM-induced change in drought response. In another experiment, Augé at al. (2008) observed that in the case of squash leaves, across all AM and NaCl treatments, the leaf hydraulic conductance change in synchrony with stomatal conductance corroborating leaf tendency towards hydraulic homeostasis under varying rates of transpirational water loss.

3.4 Heavy Metal Stress

An immense load of heavy metals such as Pb, Cr, As, Cu, Cd and Hg is being added to our soils through industrial, agricultural and domestic effluents. These elements can either be absorbed in soil particles or leached into ground water. Problems associated with the contamination of soil and water such as animal welfare, health, fatalities and disruption of natural ecosystems is well documented (He et al. 2005). Human exposure to these metals through ingestion of contaminated food or uptake of drinking water can lead to their accumulation in humans, plants and animals. Lead, copper, zinc and cadmium are also found naturally on soils and can cause significant damage to the environment and human health as a result of their mobility and solubilities (Shuman 1985; Khan 2006).

Heavy metals in the soil are associated with a number of soil components which determine their behavior in the soil and influence their bioavailability (Boruvka and Drabek 2004). The cell wall components such as free amino acids, hydroxyl, carboxyl and other groups of soil fungi can bind to potentially toxic elements such as Cu, Pb, Cd, etc., (Kapoor and Viraraghavan 1995). Many filamentous fungi can sorb these trace elements and are used in their commercial biosorbants (Morley and Gadd 1995). The proteins in the cell walls of AM fungi appear to have similar ability to sorb potentially toxic elements by sequestering them. There is evidence that AMF can withstand potentially toxic elements. Gonzalez-Chavez et al., (2004) pointed out that glomalin produced on hyphae of AMF can sequester them. AMF plays a significant ecological role in the phytostabilization of potentially toxic trace element polluted soils by sequesteration and, in turn, help mycorrhizal plants survive in polluted soils (Khan 2005). Glomalin, an iron-containing glycoprotein produced by the hyphae of AMF fungi (Wright and Upadhyaya 1998), is released into soil by AMF hyphae (Driver et al. 2005). These authors have shown in the case of Glomus intraradices that glomalin is tightly bound in AMF hyphae and spore walls. Small amounts were found to be adhered to soil via release into liquid medium from the hyphae and not through secretion. It has been hypothesized that glomalin has a role in the immobilization ('filtering') of heavy metals at the soil-hypha interface, i.e. before entry into fungal-plant system.

There has been few analytical studies of AM in polluted soils during which some workers observed that the external mycelium of AMF was the main site for trace element localization (Kaldorf et al. 1999; Turnau 1998), while others reported selective exclusion of toxic and non-toxic elements by adsorption onto chitinous cell walls (Zhou 1999), or onto glomalin, the extracellular glycoprotein (Wright and Upadhyaya 1998), or intracellular precipitation. All these mechanisms have implications in reducing a plant's exposure to potentially toxic elements. Gonzalez-Chavez et al. (2002) studied the form and localization of Cu accumulation on the extraradical mycelium of three AM fungi isolated form the Cu and As polluted soil. The authors reported differential capacity of AMF to absorb and accumulate Cu as determined by TEM and SEM. However, an insight into the nature of accumulation and mechanisms involved require further research (Khan 2006).

The AMF can be screened for their ability to produce maximum level of extra-radical mycelium in polluted soils (Joner et al. 2000), and to utilize adapted AM fungi to help accumulate heavy metals both within the plant roots (phytoaccumulation) and the extrametrical fungal mycelium (Khan 2006).

4   Conclusion

Mycorrhizae are symbiotic associations that form between the roots of most plant species and fungi. These symbioses are characterized by bi-directional movement of nutrients where carbon flows to the fungus and inorganic nutrients move to the plant, thereby providing a critical linkage between the plant root and soil. As a result, mycorrhizal plants are often more competitive and better able to tolerate environmental stresses than are nonmycorrhizal plants.

Mycorrhizal associations vary widely in form and function. Arbuscular mycorrhizal fungi belong to the order Glomales and form highly branched structures called arbuscules, within root cortical cells of many herbaceous and woody plant species. These structures are meant for bilateral transfer of growth factors.

Plant responses to colonization by mycorrhizal fungi can range from dramatic growth promotion to growth depression. Factors affecting this response include the mycorrhizal dependency of the host crop, the nutrient status of the soil, and the inoculum potential of the mycorrhizal fungi. Arbuscualr mycorrhiza confers resistance to water and salinity/nutrient stress in plants.

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