

Review Article

Arbuscular Mycorrhizal Symbiosis and Water Stress: A Critical Review

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ABSTRACT

Through evolutionary time, the ever changing environmental conditions have been faced by plants among which water stress is the most common. Nevertheless, a great deal of variations in responses of plants to water deficit and their sensitivity to water scarcity has been noticed. For perception, signalling and response to water stress, plants are supposed to have programmed capability. Under the conditions of water scarcity, improved resistance to drought has been provided by AM fungi by enhancing efficiency of water absorption, uptake of mineral nutrients, especially phosphorus, accumulation of osmoprotectants like proline and sugars, activity of antioxidant enzymes like SOD, CAT and POD, production of isoprenoids, stomatal conductance, chlorophyll contents, photosynthesis and decline in ABA content. Expression of drought related plant genes like *p5cs* genes, aquaporin genes, as well as *nced* genes, brings about the physiological response of mycorrhizal plants to drought stress. Moreover, the efficacy of AM in reducing the use of phosphorus fertilisers and enhancement of soil stability increase the value of mycorrhizae for sustainability and ecosystem services. Their appropriate management has prospective to ameliorate the effectiveness and sustainability of drought tolerance.

Keywords: Arbuscular mycorrhizal fungi, water stress, osmoprotectants, aquaporin genes, stomatal conductance

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INTRODUCTION

Water scarcity is one of the major abiotic stresses having detrimental effects on crop productivity throughout the world (Kramer & Boyer, 1995). On earth, 45% of agricultural lands are subjected to

recurrent water deprivation leading to an average grain yield loss of 50% (Singh *et al.*, 2012). During growing season, insufficient soil water and rainfall results in agricultural water deficit (Vadez *et al.*, 2012). Estimates have shown an increase in intense rain events simultaneously decrease in the number of rain days. This has led to increased drought risk (Trenberth, 2011). Therefore, water deficit is a major limitation to crop production under rainfed conditions.

A period of dry weather which is harmful to crops is called drought. Drought stress is experienced when ambient temperature is high and relative humidity of air and soil humidity are low. During drought, plants predispose themselves in order to keep the water potential high in their tissues. This is termed as dehydration avoidance and the avoidance which determines plant predisposition is called drought resistance (Blum, 2005). In plants, a series of biochemical, physiological and morphological injuries occur due to water stress (Gong *et al.*, 2013). Different factors like duration of exposure of plants to the drought, genetic resistance and stage of growth determine the effect of water stress on plant growth (Song *et al.*, 2011). Nevertheless, several anti-stress mechanisms like accumulation of osmolytes have been used by plants in order to reduce osmotic pressure through enrichment of antioxidant enzyme activities for scavenging free radicals and increase in length of roots to absorb much water (Huang *et al.*, 2011).

Due to population explosion, the greatest challenge faced by agricultural

community is to satisfy the demands placed on agriculture for food and fibre supply. In order to meet the challenge, a wide variety of efforts focusing on agro ecosystem and soil biological system as a whole is required to understand the stability of process. Keeping in view the concept of sustainability, a vehicle for sustainable agriculture has been hiding secretly for decades in the rhizosphere in the form of plant growth enhancing microbes. Arbuscular Mycorrhizal Fungi (AMF) is one of the ancient, diverse and beneficial groups of such soil microbes (Smith & Read, 2008). Nearly 250,000 plant species form Arbuscular mycorrhizal associations. The AMF are susceptible to alteration in plant and soil conditions and form an interface between plant roots and soil (Power & Mills, 1995).

Molecular sequencing and palaeobotanical data implies that glomalean fungi belonging to glomeromycota formed associations with the first land plants nearly 460 million years ago. On the basis of morphology, 150 - 200 species of AM fungi have been well known so far. Highly branched fungal structures called arbuscules characterise the symbiosis, which grows intracellularly without piercing the host cell membrane (Brundrett, 2004). The intra-radical mycelium of these soil fungi proliferates in the root cortex of the host plant. Meanwhile, extra-radical AM hyphae provides increased surface area by extending into the soil around the root for absorption of nutritional elements like phosphorus, nitrogen, copper, zinc, etc. and convey them

to host (Smith & Read, 2008). Plants native to arid and semi-arid ecosystems have their roots highly colonised with AMF, which indicates the significance of AM symbiosis for performance under scarcity of water (Chaudhry *et al.*, 2005). Studies have shown the transfer of water to host plant by extra-radical mycelium under low moisture conditions (Khalvati *et al.*, 2005).

As AMF species richness and AM hyphal length increase, nutrient capture, productivity in microcosms and plant biodiversity increases considerably (Vander Heijden *et al.*, 1998). The use of AMF inoculums in agriculture, site remediation, horticulture or landscape restoration dated back to almost two decades. Thus, the idea of exploiting AMF as biofertiliser is not new (Hamel, 1996). For maintaining soil health, nutrient uptake, fertility, plant community development and above ground productivity under phosphorus limitation conditions, AMF is extremely important (Smith & Read, 1997).

Different ways through which AMF management could be helpful for sustainable ecosystems including restoration and agro ecosystems had been described by researchers during the early 1990s (Pfleger & Linderman, 1994). Although AMF has several utilities, practical application of AMF has not yet been able to reach main stream markets. Even *Rhizobium* is more familiar to farmers for its practical applications while AMF is almost unknown. The reasons are (1) production limitations and (2) knowledge gaps. Being obligate symbionts, they are difficult to produce.

Modern production systems are dependent on soil based systems (plots or pots), where contamination by other AMF or other microbes is unavoidable (Gianninazzi & Vosatka, 2004). Undoubtedly, production is a limitation for the current use of AMF. Therefore, discovery and development are still awaited for its large scale production and use.

DROUGHT TYPES AND CAUSES

Being a natural hazard, the effects of drought differ from one region to another. Frequently, it is referred to as a creeping phenomenon which can be classified as:

1. Meteorological drought
2. Hydrologic drought
3. Agricultural drought

Meteorological drought occurs when if precipitation is less than the seasonally normal or climatologically accepted for a long period of time over a wide area. In particular, drought affects the economy rigorously but it may affect only a few farmers or a small community if it occurs in a small region. A method of computing numerical drought index and index number was developed by Palmer (1964, 1965) for the assessment of severity of meteorological drought.

If meteorological drought occurs for a long time, it may lead to hydrologic drought, which is a step ahead of meteorological drought and is usually marked by a shrinkage of above ground water bodies like drying up of rivers, streams, etc., as well as a decline in ground water levels. As compared

to meteorological drought, hydrologic drought is far more reaching as it affects industry, agriculture and hydroelectric power generation and if it persists, irrigable lands have to be deserted. Another category of drought is agricultural drought, which occurs at the time of growing season when rainfall and soil moisture are not sufficient to sustain healthy crop production that causes severe wilt and crop stress. Agricultural drought is independent of meteorological drought; it may subsist even if there is no meteorological drought (<http://drought.unl.edu>).

PLANTS' STRATEGIES TO SURVIVE WATER DEFICIT

To survive water scarcity, different mechanisms have been developed by plants like avoidance, escape and tolerance to cell or tissue dehydration (Ludlow & Muchow, 1990).

Drought Escape

Drought escape involves the accomplishment of life cycle prior to the adverse effects of drought (Wu *et al.*, 2010). In arid regions, annual plants escape against water deficit by producing seeds at the time of water availability followed by intermittent rainfall.

Drought Avoidance

Plants avoid drought through changes in their anatomy, orientation and area of leaves or by increasing resistance towards stomata and cuticle to transpiration (Jones & Corlett, 1992). Despite water scarcity, plants can maintain their normal growth to

avoid drought. This is generally achieved by increasing water use efficiency (WUE), which is measured as photosynthetic carbon gain over transpirational water loss, while high WUE may decrease development and growth rate (Arntz & Delph, 2001).

Drought Tolerance

The strategy of drought tolerance of primitive terrestrial plants, including bryophytes and lichens, which remain conserved all through the evolution of angiosperms is by restricting intense levels to resurrection plants (Ingram & Bartels, 1996). The main mechanism to sustain cell turgor is osmotic adjustment which enables water uptake, and thus helps in maintenance of plant metabolism (Gunasekera & Berkowitz, 1992).

MYCORRHIZAE AMELIORATING WATER STRESS IN PLANTS

In terrestrial ecosystems, mycorrhizae are the most important symbiosis between AM fungi and 80% of terrestrial plants (Brundrett, 2009). It is a mutualistic association in which a biochemical communication between two symbionts helps the spores to recognise the presence of host plant. After recognising the host, hyphae is produced into the apoplastic space of cortical cells inside the host root to form arbuscules which are highly branched structures meant for exchanges of carbon and nutrients between two partners, whereas the bulbous structures that arise as terminal or intercalary swelling of hyphae (called vesicles) are meant for storage (Miransari, 2010). Arbuscules have been

considered as the only structures which define the features of arbuscular mycorrhizal fungus (Gianinazzi *et al.*, 1979). They are temporary structures having turnover rate of up to 2 weeks, varying in their morphology according to the species of AM fungi (Morton, 2000). However, vesicles are not formed by all genera of AM fungi as the members of *Scutellospora* and *Gigaspora* are devoid of vesicles. When they mature, vesicles may act as reproductive structures. Besides arbuscules and vesicles, a variety of structures have been seen to be produced by AM fungi, like:

- **Appressoria:** These are the first fungal structures (Tawaraya *et al.*, 2007) formed on epidermal cell wall after the first contact with host (Garriock, 1989).
- **Auxillary cells:** They are the swollen structures produced by extra-radical hyphae terminally. They are a morphological distinguishing feature between the members of Glomeromycetes and Gigasporaceae (Morton & Benny, 1990).
- **Intra-radical mycelium:** Morphologically, the mycelium may be straight, coiled and show a Y or H shaped branching having the function of transportation of the substances which have been absorbed by extra-radical hyphae.
- **Extra-radical mycelium:** It performs the functions of absorption and translocation of nutrients, propagation, spore production and production of other structures, as well as to look for

new roots of different or same plant for infection (Smith & Smith, 2011).

- **Sporocarps:** They are meant for accommodation of spores and specialised hyphae or they may sometimes be found enclosed in an outer layer called Peridium.
- **Spores:** These are unicellular, multinucleate structures formed at the tip of sporocarp sometimes inside or outside the root and on decaying plant material or on the plant itself. They may be produced singly called azygospores or chlamyospores or may be grouped in the sporocarps.

Occupying a protected ecological niche, AMF constitutes an approach to minimise the use of chemical fertilisers mainly in phosphorus nutrition, thus improve nutritional status of both associates (Almagrabi & Abdelmoneim, 2012). Plants get the benefits of increased nutrient uptake and AMF gets carbohydrates from plants in turn. It is now well known that AMF protects the plants from the detrimental effects of biotic and abiotic stresses and enhances plant production and growth (Song *et al.*, 2011). Under drought stress conditions, mycorrhizae help the plants to perform well through direct uptake and transport of water with the help of external hyphae (Auge, 2004), stomatal conductance regulation (Goicoechea *et al.*, 1997) and osmotic adjustment (Wu & Xia, 2006). Protection of plants from the detrimental effects of

drought by AM is well documented (Auge, 2001; Zhang *et al.*, 2014).

IMPACTS OF WATER STRESS ON AMF COLONISATION

As compared to other climates, spore production and species richness of AM fungi in arid climates are lower and found to decrease with the increase in aridity (Pond *et al.*, 1984). However, comparable species richness of arid climates to that of other communities has been revealed by using different sophisticated culture techniques (Morton *et al.*, 1995). In response to declining soil moisture, production of resilient spores and opportunistic rapid growth of mycelium may be the feature which allows AM fungal communities to perform under dry conditions (Jacobson, 1997).

Being obligate biotrophs, hyphal spread after spore germination occurs at slow pace or is inhibited by water scarcity which makes clear the adverse effects of drought on AM colonisation. Inhibition of AM colonisation due to water stress has been seen in foxtail millet roots (Gong *et al.*, 2014) which has been attributed to reduced availability of carbon from host plants (Subramanian & Charest, 1995). Other pot-based experiments have confirmed the same in *Triticum aestivum* (Al-Karaki *et al.*, 2004). Nevertheless, some reports have shown the promotion of colonisation in drought conditions. Under field conditions, persistent drought may promote more extensive colonisation as examined by Kuhn (1991) and Kuhn *et al.* (1991) on a

fallow agricultural site in Germany, whereas some workers have also examined the promotion in spore production under short-term temporary decline in soil moisture (Jacobson, 1997).

AMF INDUCED METABOLOMIC AND BIOCHEMICAL RESPONSES TO WATER DEFICIT

Under the condition of water scarcity, water potential may increase as a result of less stomatal conductance and more diffusive resistance to carbon dioxide. Therefore, water potential is required to be reduced in order to maintain uptake of water from the soil, which in turn is achieved by different mechanisms of osmoregulation. The mechanism of osmoregulation causes a decrease in osmotic potential due to accumulation of compatible solutes (Munns, 1988), as discussed below:

Proline

It is the most commonly distributed non-protein amino acid, N-storage compound, osmosolute and a hydrophobic protectant for cellular structures and enzymes in higher plants accumulated as a universal metabolic response to osmotic adjustment under water stress (Szabados & Savoure, 2009). Proline is commonly synthesised in chloroplasts or mitochondria of plants by glutamate synthetic pathway. A key enzyme, n1-pyrroline-5-carboxylate synthetase converts glutamate firstly into n1-pyrroline-5-carboxylate and then another enzyme n1-pyrroline-5-carboxylate reductase (P5CR) transforms n1-pyrroline-5-carboxylate into

proline (Szabados & Savoure, 2009). An alternate pathway for proline synthesis is ornithine synthetic pathway, where proline is synthesised in mitochondria from ornithine. Enzyme ornithine-d-aminotransferase (OAT) causes transamination of ornithine to form glutamate semialdehyde and δ^1 -pyrroline-5-carboxylate which is converted into proline (Szabados & Savoure, 2009). In mitochondria, proline dehydrogenase causes catabolism of proline into δ^1 -pyrroline-5 carboxylate. Hence, the net proline accumulation in plants involves one proline catabolic enzyme and two proline synthetic enzymes.

There is a positive correlation between proline accumulation and AMF induced drought tolerance in plants. During the period of inhibited growth, proline serves as nitrogen and energy source (Kala & Godara, 2011). As compared to non-AM plants, higher proline accumulation in AM plants has been seen in *Allium sativum* (Borde *et al.*, 2012) and *Oryza sativa* (Ruiz-Sanchez *et al.*, 2011). Some studies have also shown a decrease in proline content in *Cyclobalanopsis glauca* (Zhang *et al.*, 2014) and *Zea mays* (Abdelmoneim *et al.*, 2014) as compared to their non-AM counterparts. Building up of lower proline in AM plants has been ascribed to less injury by water deficit (Auge & Moore, 2005). Furthermore, underwater stress mycorrhization in soybean causes more proline accumulation in roots as compared to shoots (Porcel *et al.*, 2004).

Sugars as Osmoprotectants

Among osmotic solutes, sugars are equally important as they play an important role in stabilising cell turgor pressure. Higher photosynthetic rates in AM plants may cause increased building up of carbohydrates which act as excellent osmoprotectants to lower osmotic potential (Khalvati *et al.*, 2005). AM symbiosis increases plant growth which in turn causes increased transport to the organs for consumption to meet the growth demands. Furthermore, AM fungi also utilise carbohydrates produced by the plant. Therefore, the overall increased utilisation rates do not point toward accumulation of carbohydrates. Studies have shown an increase in sugars in mycorrhizal plants exposed to drought in *Cyclobalanopsis glauca* (Zhang *et al.*, 2014) and in *Poncirus trifoliata* (Qiangsheng *et al.*, 2006). High sugar content of *Poncirus trifoliata* confirms a high natural physiological metabolism of AM plants under water stress and well watered conditions leading to accumulation of carbohydrates resulting in decrease of osmotic potential of host cells. In contrast, less sugar content has been noticed in water stress exposed mycorrhizal plants as in *Casuarina equisetifolia* (Zhang *et al.*, 2010) and *Glycine max* (Porcel *et al.*, 2004). In case of *Glycine max*, lower accumulation of sugars may be due to utilisation of photosynthates by fungus and their non-availability for storage (Schellembaum *et al.*, 1998). Successful avoidance of drought stress due to AM may also be responsible for lower sugar accumulation as stated by Auge (2001).

Defense against Oxidative Stress

Oxygen generated during photosynthesis in chloroplasts can accept the electrons passing through photosystems forming superoxide radicals, which are scavenged by various antioxidant defense mechanisms under steady state conditions (Foyer & Noctor, 2005). Different abiotic stresses including drought, salinity, heavy metals, UV radiations, high temperature, herbicides, pathogen attacks, air pollution, heavy metals, nutrient deficiency cause disturbance in equilibrium between scavenging and production of ROS leading to increase in intracellular levels of ROS that suddenly cause damage to cell structures. Antioxidant defense system including enzymatic systems like superoxide dismutase (SOD) which breaks down H_2O_2 and O_2^- to O_2 , with different substrates at the cost of H_2O_2 are detoxified by peroxidase (POD), whereas H_2O_2 is detoxified by catalase (CAT) (Mohammadi *et al.*, 2011) and non-enzymatic defense system including flavonoids, glutathione and ascorbate (Mohammadi *et al.*, 2011). Different studies have shown increases in the activities of antioxidant enzymes in plants inoculated with mycorrhizae during drought conditions. Increases in CAT and peroxidase activities have been seen in mycorrhizal *Plukenetia volubilis* during water stress conditions (Tian *et al.*, 2013). The SOD and CAT of leaf and POD activities of root were higher in mycorrhizal *Allium sativum* plants as compared to non-mycorrhizal ones when exposed to drought (Borde *et al.*, 2012). In addition, an increase in non-enzymatic

molecules like glutathione and ascorbate has been noticed in *Avena nuda* seedlings subjected to SO_2 (Huang *et al.*, 2008) when exposed to drought stress.

Isoprenoids

Isoprenoids represent a large group of plant compounds which have highly diverse and complex chemical structures. They are synthesised from isopentenyl diphosphate (IPP) and dimethylallyl diphosphate (DMAPP). Isoprenoids may be non-volatile like carotenoids, which are terpene pigments in the plants helpful in dissipation of excess of energy during photosynthesis (Demming-Adams & Adams, 2006). Carotenoids act as precursor for the synthesis of ABA and strigolactones. It has been investigated that plant abscissic acid content is related to water deficit tolerance, while strigolactones help to promote AM colonisation in roots and are secreted by the host itself (Bouwmeester *et al.*, 2007). Volatile isoprenoids including sesquiterpenes, isoprenes, monoterpenes produced in response to abiotic factors like oxidative stress, irradiation or temperature, as well as biotic factors like pathogens, pests, insects or herbivores, may provide protection against abiotic stress (Penuelas & Munne-Bosch, 2005). Different workers have reported induction of high levels of ABA (Meixner *et al.*, 2005) and apocarotenoids in host roots by mycorrhizae (Walter & Strack, 2011). Thus, AM induces synthesis of isoprenes in roots as both are isoprene derived compounds. In addition, it has been seen that production of essential isoprenoids by leaf has been favoured by

AM symbiosis under water stress but a decrease in volatile isoprenoids of roots has also been noticed. This has been attributed to more carbon demand by AM fungi which affect the amount of carbon allocation and carbon partitioning among various classes of isoprenoids (Asensio *et al.*, 2012).

IMPACTS OF AMF ON GROWTH AND YIELD

Under drought stress, AM induced improvement in morphology, growth and yield has been reported in different plants. Improved plant growth and enhanced yield have been attributed to better uptakes of Cu and P under drought stress conditions (Al-Karaki & Clark, 1998). After relief from drought, it has been found that AM plants recovered from wilting more quickly than non-AM plants (Gemma *et al.*, 1997). In case of wheat, leaf drop and necrosis (Bryla & Duniway, 1997) due to drought was reduced in AM plants. Biomass, panicle number per plant, grain number per panicle, grain yield and weight increased in AM inoculated wheat under water stress (Al-Karaki *et al.*, 2004). In *Citrus tangerine* and *Poncirus trifoliata*, plant height, stem diameter, leaf number, leaf area, root and shoot dry weights increased due to mycorrhizal colonisation under water stress and well watered conditions than corresponding plants without AM (Qiangsheng *et al.*, 2006; Wu & Xia, 2006). In rice, AM inoculation causes increase in root and shoot fresh weights after a drought stress period of 15 days (Ruiz-Sanchez *et al.*, 2010). Stimulation of plant height,

stem diameter and root fresh weight of *Cucumis melo* under drought conditions has been confirmed by Huang *et al.* (2011). In marigold, flower parameters and growth criteria have been stimulated by mycorrhizal fungus under drought stress (Asrar *et al.*, 2011) due to increased phosphorus nutrition (Bethlenfalvay *et al.*, 1988) and water uptake (Faber *et al.*, 1991). Increases in growth parameters and grain yield due to inoculation with AM have been observed in foxtail millet under water stress (Gong *et al.*, 2014).

IMPACTS OF AMF ON PHYSIOLOGICAL PARAMETERS

Arbuscular Mycorrhizal fungi affect shoot physiology and tissue water content by altering influx and efflux rates of water. The AM fungal symbiosis has impact on stomatal conductance, leaf water potential, abscisic acid content, photosynthetic pigments and photosynthesis. Enhancement in the gas exchange rates including stomatal conductance, transpiration and CO₂ assimilation in mycorrhizal plants as compared to their non-AM counterparts has been investigated by different researchers (Khalvati *et al.*, 2005). The AM that induced changes in different physiological parameters is discussed below:

Abscisic Acid

Arbuscular Mycorrhizal symbiosis influences stomatal conductance and other physiological traits during drought stress by some non-nutritional chemical signals like phytohormone abscisic acid (ABA)

(Ludwig-Muller, 2010). Among the different responses of plants to drought stress, abscisic acid is the most significant stress signal transduction pathway (Zhang *et al.*, 2006) as it regulates root hydraulic conductivity (Aroca, 2006), expression of different aquaporins (Aroca *et al.*, 2006), as well as transpiration rate (Zhang *et al.*, 2006). In response to water deficit causing stresses, endogenous level of abscisic acid increases in vegetative tissues of plants (Zhang *et al.*, 2006). The relationship between abscisic acid content and water stress tolerance has been clearly demonstrated by Kulkarni *et al.* (2000). Abscisic acid minimises water loss through transpiration by promoting stomatal closure and then causes alleviation of damage due to stress by activation of many stress responsive genes leading to more stress tolerance by plants (Zhang *et al.*, 2006). Drought stress inducible genes can be categorised into functional and regulatory genes. Functional genes help in acquiring drought tolerance through late embryogenesis abundant proteins, proteases, enzymes for biosynthesis of osmolytes, detoxification enzymes and water channels or other transporters.

Expression of functional genes is regulated by regulatory genes which involve protein kinases, phosphatases, transcription factors and also those involved in biosynthesis of abscisic acid (Shinozaki & Yamaguchi-Shinozaki, 2007). Abscisic Acid regulates transcription of genes with the help of cis and trans-acting factors, as well as MYC-like and MYB-like deoxyribonucleic acid elements. It has been reported that

abscisic acid levels increased in mycorrhizal maize (Danneberg *et al.*, 1992) and soyabean (Meixner *et al.*, 2005) as compared to non-AM plants under normal conditions. It has been reported that when subjected to drought stress, AM plants showed lower levels of abscisic acid than non-AMF ones revealing that AM plants experience less intense water stress (Doubkova *et al.*, 2013). When subjected to osmotic stress by polyethylene glycol mycorrhizal larch plants had lower abscisic acid as compared to non-AM plants (Rincon *et al.*, 2005). Adequate balance between root water movement and transpiration during drought and its recovery are maintained by AM plants as compared to non-AM plants due to better and faster regulation of abscisic acid levels by AM plants (Aroca *et al.*, 2008).

Leaf Water Potential and Stomatal Conductance

The index of water status of the entire plant is known as leaf water potential, which corresponds to a major trait showing improved resistance of plants to water stress through better hydration. Higher water use efficiency due to mycorrhization has been reported by many workers (Ruiz-Lozano & Aroca, 2010). During water stress, an increase in water use efficiency due to mycorrhizae has been seen in *Allium sativum* (Borde *et al.*, 2012). At the same time, a lack of constructive effect of mycorrhizae on water use efficiency in *Knautia arvensis* (Doubkova *et al.*, 2013) has also been found. Higher relative water content and water use efficiency help in the movement

of water to the evaporating surfaces so that stomata in leaves can be maintained in open state (Nelsen & Safir, 1982). During lethal periods of water stress, osmotic adjustment in the leaves of mycorrhizal basil plants was found to be more as compared to non-mycorrhizal plants (Kubikova *et al.*, 2001). Similarly, during water stress, a decline in leaf water potential has been postponed by AM in plants (Subramanian *et al.*, 1997) and after relief from water stress, leaf water potential returns back to its normal level much faster in mycorrhizal than non-mycorrhizal maize plants (Subramanian *et al.*, 1997).

Often water status of AM plants is found related to gas exchanges including stomatal behaviour and transpiration fluxes (Zhu *et al.*, 2012). As pointed by Auge (2001), leaf water potential and stomatal conductance are functionally linked with each other. Stomatal conductance during water stress remains unchanged for a longer time in mycorrhizal plants as compared to non-mycorrhizal plants (Duan *et al.*, 1996). Different rates of stomatal conductance and transpiration have been shown by AM and non-AM plants during water stress. It has been confirmed many times that altered rates of stomatal conductance and transpiration have been observed in mycorrhizal lettuce, rose, soybean and wheat. Stomatal opening increased in AM plants as compared to their non-AM counterparts (Auge, 2001). Increased stomatal conductance has also been found in mycorrhizal maize (Zhu *et al.*, 2012).

Photosynthetic Pigments

A decrease in chlorophyll content due to water stress is a typical symptom of oxidative stress in water stressed plants. It has been observed by different researchers as in *Tagetes erecta* (Asrar & Elhindi, 2011), *Citrus* (Wu & Xia, 2006) and *Zea mays* (Zhu *et al.*, 2012; Abdelmoneim *et al.*, 2014). The chlorophyll content of mycorrhizal plants has found to be more as compared to non-AM plants (Mathur & Vyas, 1995; Gemma *et al.*, 1997). Moreover, the rise in photosynthetic pigments due to mycorrhizae has been confirmed by Abdelmoneim *et al.* (2014). During water stress, mycorrhization resisted the reduction of chlorophyll (Asrar & Elhindi, 2011; Zhu *et al.*, 2012; Abdelmoneim *et al.*, 2014). It has been well recognised that chlorophyll concentration is related to photosynthetic rate and chlorophyll fluorescence. Thus, in AM plants, an increased rate of chlorophyll has been associated with the increased rate of photosynthesis or with higher Mg and N which are major constituents of chlorophyll (Mathur & Vyas, 1995). Meanwhile, application of AM helps the plants to overcome photodestruction and photoinhibition of pigments under the conditions of water stress by increasing the content of carotenoids, as they help in protection of photosynthetic apparatus against the harm caused by single oxygen. Therefore, quenching and deactivation of excited triplet state of chlorophyll can be brought about by carotenoids (Foyer & Harbinson, 1994).

Photosynthesis

Higher rates of photosynthesis have often been shown by AM plants in comparison to their non-AM counterparts, which are consistent with the effects of mycorrhizae on chlorophyll content and stomatal conductance, as discussed earlier. In AM colonised *Bouteloua gracilis*, higher photosynthesis was related to a decrease in both liquid phase and gas phase resistance to CO₂ transported in leaves (Allen *et al.*, 1981). An increase in the number of photosynthetic units by AM symbiosis has been suggested by some researchers. AM fungi are also known to increase the rate of photosynthetic export and storage. During drought, different effects have been shown by different AM fungi on photosynthesis, as confirmed by Ruiz-Lozano and Azcon (1995). When comparing different *Glomus* species, it was found that one species decreased the photosynthetic phosphorus use efficiency while the other increased it (Ruiz-Lozano & Azcon, 1995). During drought stress, different mycobionts influence host photosynthesis differently (Dixon *et al.*, 1994). With the help of chlorophyll fluorescence, it has been found that water stress interrupts transport of electrons in photosynthetic apparatus and causes the destruction in structure and function of PSII reaction centre (Baker, 2008). Reduced availability of CO₂, which results in inefficient use of CO₂ and high susceptibility of photo damage (Powles, 1984), poor ability to manage excess of radiation is one of the main photosynthetic limitations imposed by water stress (Chaves *et al.*, 2003). Photo

protective mechanisms help in regulation of excitation energy reaching reaction centre of photosystem by dissipation of thermal energy (Demmig-Adams & Adams, 2006). These photoprotective mechanisms also help in repair of oxidative damage by scavenging oxidative molecules (Fernandez-Marin *et al.*, 2009). Drought stress decreases the quantum efficiency or photochemical efficiency of PSII, which is given by the ratio of (Fv/Fm) (Borkowska, 2002). This ratio also provides a way to monitor environmental stress (Krause & Weis, 1991). Mycorrhizal symbiosis has been shown to alleviate the undesirable effects of drought stress on photochemical efficiency and PSII reaction centre (Baker, 2008) in maize (Zhu *et al.*, 2012).

ROLE OF VAM IN MINERAL NUTRITION

Drought stress and the nutritional status of plants are correlated to each other. It has been confirmed that AM plays an important role in improving nutritional status of host plants. The concentration of phosphorus may influence host water balance but it is not easily accessible to the plants as it cannot flow freely in soil. In addition to phosphorus, zinc and copper are the other elements which are also fixed in the soils. In a study on clover plants planted on five compartments having an air gap, Li *et al.* (1991) observed that more than a half of the overall copper and zinc content was absorbed by extension hyphae. The AM symbiosis has been reported to improve the absorption of silicon, nickel, copper

and calcium (Gong *et al.*, 2000). Enhanced phosphorus and nitrogen nutrition is the most recognizable benefit of AM fungi for plants. Further details of this are discussed below:

Phosphorus Nutrition

Phosphorus deficiency can greatly limit plant growth as it is extremely important for plant growth. From the reserves in the soil, the most important way of assuring adequate supply of phosphorus to the land plants is through mycorrhizal associations (Al-Amri *et al.*, 2013). In the phosphorus deficient soils, the principal role of AM symbiosis in efficiently absorbing phosphorus has been shown (Smith *et al.*, 1986). Using gel electrophoresis (Abdel-Fattah, 2001) and ultra-cytochemistry (Gianinazzi-Pearson & Gianinazzi, 1978), an active enzyme alkaline phosphatase has been identified in arbuscular mycorrhizae (Abdel-Fattah, 2001). Localisation of alkaline phosphatase in the vacuoles of mature arbuscules (Gianinazzi *et al.*, 1979) reveals the involvement of this enzyme in acquisition of phosphorus in mycorrhizal plants. The AMF can be of great benefit to the plants growing in tropical soil having high capacity to immobilise phosphorus, as well as having low phosphates (George *et al.*, 1995). High content of phosphorus may lead to inhibition of AM colonisation in roots and can decrease vesicle and entry point formation (Amijee *et al.*, 1989), as well as the length of AM associated external hyphae (Abbott *et al.*, 1984). Symbiotic efficiency of AM fungi reduces

in the concentration of soil phosphorus suboptimal for functioning of mycorrhizae and competition occurs between mycobiont and host for scarce phosphorus. Meanwhile, low mobility of phosphorus in the soil and quick uptake of phosphate into the roots results in the formation of phosphate depletion zone (Abdel-Fattah, 1997). This phosphate depletion zone in the roots of non-mycorrhizal plants goes beyond root hair cylinder which points towards the unavailability of phosphate to plants directly. The absorption and transportation of phosphorus beyond the depletion zones into root tissues can be brought about by external hyphae of AMF (Wu *et al.*, 2010).

Improved hydraulic conductivity and quick recovery from water stress confirm the water stress tolerance of the plants which has been attributed to better phosphorus nutrition (Bryla & Duniway, 1997). As compared to amply watered plants, significant reduction in the phosphorus levels has been noticed in mycorrhizal and non-mycorrhizal plants and the rate of decrease was found to be higher in non-mycorrhizal plants as compared to the AM plants in wheat (Al-Karaki *et al.*, 2004), citrus (Wu & Xia, 2006) and marigold (Asrar & Elhindi, 2011). Despite water stress, increased phosphorus uptakes in both the roots and shoots of mycorrhizal tomato plants have been noticed by Subramanian *et al.* (2006). Host water balance is also influenced by phosphorus concentration as phosphorus starvation affects stomatal conductance. It has been suggested that enhancement in photosynthetic capacity due to phosphorus leads to high stomatal

conductance and transpiration (Koide, 2000). The concentration of phosphorus in the leaves may have impact on the response of stomata to environmental disturbances possibly by affecting energy involved in osmotic potential of guard cells leading to opening of stomata (Weyers & Meidner, 1990). Under drought stress, different inorganic ions and organic solutes are accumulated by higher plants, whose accumulation in AM seedlings results in higher biomass due to better accumulation of carbohydrates and better osmotic adjustment (Wu & Xia, 2006).

Nitrogen Nutrition

Although the role of mycorrhiza in phosphorus nutrition of plants has been well documented, only a few studies on the importance of mycorrhizae in nitrogen nutrition under drought stress conditions have been carried out. An increase in the utilisation and absorption of nitrogen in plant shoots due to mycorrhizal inoculation has been confirmed by Zhao and Yan (2006). It has been well recognised that ammonium is taken by external hyphae (Rains & Bledsoe, 2007), while nitrate is made available to mycorrhizal roots directly by external mycelium under water stress (Subramanian & Charest, 1999). Improved uptake of nitrogen causes key nitrogen assimilating enzymes to increase their activities (Subramanian & Charest, 1998), which in turn cause increases in amino acid and protein concentrations (Subramanian & Charest, 1995). It has been

recommended that the increased activities of enzymes like nitrate reductase (NR) and glutamine synthetase (GS) (Subramanian & Charest, 1999) can be associated with enhanced nutrition of phosphorus. In mycorrhizal plants, increased root hydraulic conductivity, as a result of enhanced phosphorus nutrition, results in improved tolerance to water stress (Bryla & Duniway, 1997). On the other hand, no variation in root hydraulic conductivity has been noticed in non-mycorrhizal phosphorus fertilised and mycorrhizal plants having similar size as well as phosphorus status (Davies *et al.*, 1993). Other studies on AM plants have shown that despite the phosphorus content, the activities of GS (Azcon & Tobar, 1998) and NR (Ruiz-Lozano & Azcon, 1996) have increased. Studies on the role of N uptake and assimilation in perennial rye grass have shown that AM symbiosis improves uptake of nitrogen, water and also activities of N-assimilating enzymes, leading to higher amounts of amino acids and proteins (Subramanian & Charest, 1999).

EXPRESSION OF AQUAPORIN GENES AND GENES ENCODING DEHYDRIN PROTEINS

Mycorrhizae improve drought tolerance by enhancing plant activities like proline or ABA synthesis (Ruiz-Sanchez *et al.*, 2011) and altering the flow of water through networks of hyphae or higher nutrient uptake and photosynthesis. The regulation of the physiological response of mycorrhizal plants to drought stress is brought about by expression of drought related plant genes

like *p5cs* genes encoding rate-limiting enzyme in proline biosynthesis (Porcel *et al.*, 2004), aquaporin genes (Porcel *et al.*, 2006), as well as *nced* genes encoding key enzyme in ABA biosynthesis (Aroca *et al.*, 2008).

Furthermore, in order to improve water deficiency, water may be absorbed and transported directly from the soil in vicinity or even distant places from the root tip to the host plants with the help of fungal extraradical mycelium (Egerton-Warburton *et al.*, 2007). In plants, water balance is maintained by diffusion or through water channels across the biomembranes known as aquaporins (Ruiz-Lozano *et al.*, 2009). Aquaporins are the proteins encoded by aquaporin genes, which are an important component of cellular transport system. It is considered that aquaporins are generally concerned with the process of symbiotic exchange at fungus-plant interface determining the transport properties of plant and fungus (Maurel & Plassard, 2011). In comparison to diffusion, water movement through aquaporins is 10-100 times higher. Seven classes of aquaporins have been found in plants which include plasma membrane intrinsic proteins (PIPs), NOD 26-like intrinsic proteins (NIPs), small basic intrinsic proteins (SIPs), tonoplast intrinsic proteins (TIPs), GlpF-like intrinsic proteins (GIPs), X-intrinsic proteins (XIPs) and hybrid intrinsic proteins (HIPs) (Danielson & Johanson, 2008). To decrease transpiration rate or to increase leaf water potential and root hydraulic conductivity, AMF may downregulate or upregulate aquaporin genes in leaves or

roots (Aroca *et al.*, 2008; Ruiz-Lozano *et al.*, 2009). The regulation of expression of aquaporin genes by AMF improves water stress tolerance by improving plant water status (Li *et al.*, 2012). Gene silencing and overexpression have verified the functions of aquaporins (Yu *et al.*, 2005). Meanwhile, expression of aquaporin encoding genes has also been demonstrated by Uehlein *et al.* (2007). In AM fungal structures, including extraradical mycelia and periarbuscular membrane (Li *et al.*, 2012), an aquaporin has also been identified. Drought stress affects both fungal and plant aquaporins (Uehlein *et al.*, 2007; Li *et al.*, 2012). Compared to non-AM plants, mycorrhizal plants have shown reduced expression of aquaporin genes during water stress but overall plant water relations in AM plants are influenced by other properties of aquaporins during drought stress (Aroca *et al.*, 2007).

When maize plants were subjected to drought stress, enhanced expression of two functional genes encoding aquaporins were identified in fungi and maize roots. As this pattern is related to enhanced root water content and accumulation of proteins, it is evident that water status has been improved by regulation of expression of aquaporins by AM fungi (Li *et al.*, 2012). In mycorrhizal plants, enhanced apoplastic flow of water in roots competitive to cell to cell pathway has been reported during water stress by using an inhibitor of aquaporin activity and apoplastic tracer dye (Barzana *et al.*, 2012).

Arbuscular mycorrhizal (AM) symbiosis can help plants to cope with the detrimental effects of soil water deficit

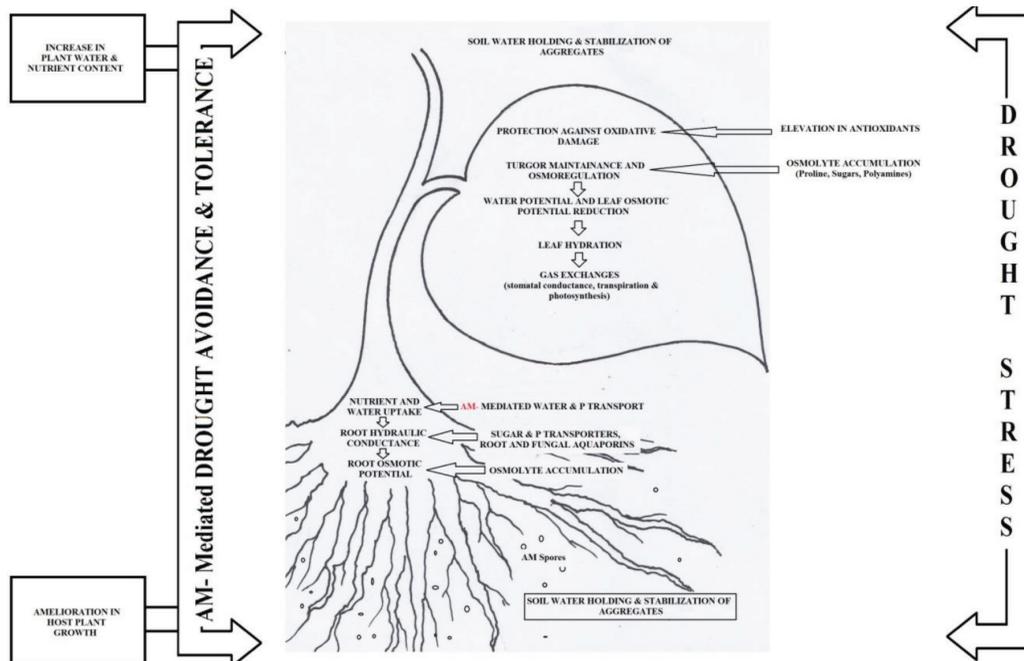


Fig.1 Arbuscular mycorrhizal (AM) symbiosis can help plants to cope with the detrimental effects of soil water deficit.

acting, directly or indirectly, on plant functionality both above and below ground (Fig.1). At the levels of both leaves and roots, the osmotic stress which is usually caused by drought is counteracted by mycorrhizal plants through biochemical changes that mostly include increased biosynthesis of metabolites (mainly proline and sugars) that act as osmolytes. These compounds contribute to the lowering of osmotic potential, and in turn, of the leaf water potential. These lower potentials allow the plants to maintain high organ hydration and turgor that sustain overall cell physiological activity that is mainly related to the photosynthetic machinery. The AM plants withstand drought-induced oxidative stress by increasing their production of

antioxidant compounds that scavenge ROS and enhancing the activities of antioxidant enzymes. The AM root colonisation can enhance root growth, architecture and hydraulic properties and thus induce the formation of a highly functional root system for nutrient/water uptake. At the same time, AM fungal hyphae in the soil provides an efficient pathway for nutrient/water uptake and transport, allowing a more efficient exploitation of the water and nutrient reservoirs in the soil where only fungal hyphae can grow, thereby bypassing the zones of water and nutrient depletion around the roots. Molecular mechanisms activated by AM symbiosis to counteract drought include gene activation of functional proteins such as the membrane

transporter aquaporins, and potentially, ion and sugar transporters, in both roots and fungi. Improved nutrient/water uptake and transport in roots translate into enhanced hydration of the aboveground organs that in turn affects physiological and biochemical processes. In addition, AM symbiosis can increase the resistance of plants to drought through secondary actions such as the improvement of soil structural stability that in turn increases the retention of soil water.

AMF AND ECOSYSTEM SERVICES

Global environment is being changed by human at an unprecedented rate. Thus, to predict the path of future ecosystems and communities in a changing world, a sound understanding of mycorrhizal reaction to anthropogenic environmental changes is helpful. Due to the higher interference of landscape by humans, it is important to understand the effects of land use changes on AMF activity, their abundance and influence on ecosystem services. Meanwhile, loss of AMF propagules due to tilling, liberal fertilisation and use of pesticides (Helgason *et al.*, 1998) may threaten ecosystem stability by lowering the soil fertility and nutrient uptake capacity of plants (Jeffries *et al.*, 2003). Among major impacts of AMF are elaborated in the subsequent sections.

Reduction in the Use of Phosphorus Fertilisers

Diffusion capacity of inorganic phosphate (Pi) is limited in soil and Pi depletion zones are generated at root surface due to its rapid absorption from the soil solution leading to a

decline in concentration of Pi (Marschner & Dell, 1994). In a given cropland, phosphate requirements are difficult to predict, whereas recommendations of phosphorus fertilisers are often vague as these recommendations are based on only soil tests (Olsen, 1954). Organic fraction of soil phosphorus pool is ignored and this results in application of phosphorus in a wasteful manner (Gilbert, 2009). Considering the different adverse effects of phosphates like algal blooms, eutrophication, etc., a main step towards sustainable agriculture is to reduce huge amounts of phosphate applied to croplands. Excess fertilisation causes phosphorus build up in the soils, runoff losses, pollution hazards and increased dependence of crops on fertilisers (Vance *et al.*, 2002). Moreover, phosphorus fertilisers have negative impacts on AM fungi even though AMF strains have shown tolerance to high phosphorus levels (Ndiaye *et al.*, 2009).

Benefits derived from mycorrhizae are reduced due to excess of P fertilisation (Plenchette *et al.*, 2005). Also in soil, phosphate ions get rapidly bound to cations leading to the formation of insoluble complexes which can not be used by plants, whereas existence of mycorrhizae in soil increases solubility of phosphate (Vance *et al.*, 2002; Smith & Read, 2008). It is still unknown whether or not the fungus releases the enzymes itself for degrading insoluble P complexes. Yet, it is definite that mycorrhizal fungi cooperate with rhizosphere microorganisms and increase the establishment of bacteria which in turn release enzymes for phosphate

solubilization (Barea *et al.*, 2002). The processes of nutrient mobilisation explained above are significant in nutrition of plants and provide a reason for high soil fertility requirements of non-mycorrhizal plants for their maintenance.

AMF Enhances Soil Stability

During mycorrhizal development, a complex ramifying network of mycelium grows from the mycorrhizal roots into surrounding soil reaching up to 30 meters per gram of soil (Cavagnaro *et al.*, 2005). The network forms up to 50% of mycelium in soil and contributes significantly to soil aggregation and formation of macroporous structure in soil that allow air and water to penetrate (Rillig *et al.*, 2002). This enhances soil quality and stability and prevents soil erosion (Jeffries *et al.*, 2003). The AMF retains soil aggregates physically with the mycelium and also secretes a hydrophobic, non-proteinaceous glue-like fungal substance called glomalin which binds the soil particles to other soil particles and hyphae (Rillig *et al.*, 2002). Even after the death of their host, AMF are known to stabilise the soils up to 5 months (Tisdall & Oades, 1980). Agronomic practices including ploughing, monoculture cropping or fertilisation affect the diversity and quantity of AMF adversely (Helgason *et al.*, 1998). The decrease in fungal biomass reduces soil stability, and thus the risk of soil erosion also increases. As soil is a non-renewable resource, the effect of soil erosion is increasing and it is irreversible in most cases.

CONCLUSION

The utmost importance of mycorrhizal symbiosis lies in establishing a connection between heterogeneously distributed nutrients especially nitrogen and phosphorus to plant systems. Mycorrhizae are valuable for sustainability and ecosystem services as they help in shaping plant communities and terrestrial ecosystems. Their appropriate management in nutrient deficient soils will allow a greater sustainable management of production without productivity loss. A variety of protective mechanisms are employed by mycorrhizal plants to neutralise the adverse effects of drought. In all aspects, it is obvious that AM symbiosis causes altered water movement rates into, through and out of plants affecting physiology and morphology of plants. Unlike mycorrhizal effect on phosphate uptake and growth, the influence of mycorrhizae on plant water relations is not dramatic and reliable. The effect of mycorrhizae on gas exchange and tissue hydration is often subtle, temporary and specific to symbiont. The mechanisms increasing drought resistance in plants due to mycorrhizae are still a matter of debate. Two characteristics are important for mycorrhizal symbiosis to increase drought resistance, one being activation of defense system rapidly and the other is the synthesis of some biochemicals which are able to resist water stress. Significant progress has been made in understanding the role of AM symbiosis in conferring drought resistance to plants; however, more attention is required to unravel hidden metabolic pathways and metabolites.

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