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Effects of VAM on host plant in the condition of drought stress and its Mechanisms

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Abstract

Most of the experiments have indicated that *vesicular-arbuscular mycorrhiza* (VAM) was able to alter water relation of its host plants. This paper summarizes effects of VAM on morphology, metabolism and protective adaptation of host plants in the condition of drought stress. Mechanism that VAM can enhance resistance of drought stress in host plant may include many possible aspects: (1) VAM improves the properties of soil in rhisophere; (2) VAM enlarges root areas of host plants, and improves its efficiency of water absorption; (3) VAM enhances the absorption of P and other nutritional elements, and then improves nutritional status of host plant; (4) VAM activates defence system of host plant quickly; (5) VAM protects against oxidative damage generated by drought; (6) VAM affects the expression of genetic material.

Keywords: *Vesicular-arbuscular mycorrhiza*; Fungi; Host plant; Drought stress; Resistance of drought stress

1. Introduction

Throughout evolutionary time, plants have been confronted with changing environmental conditions, among which drought is considered as the most important abiotic factor limiting plant growth and yield in many areas. Although different plant species can vary in their sensitivity and responses to the decreased water potential caused by water deficit, it is assumed that all plants have an encoded capability for stress perception, signaling and response [1]. Plants can respond to drought stress at morphological, metabolic and cellular levels with modifications that allow the plants to avoid the stress or to increase its tolerance [2].

In addition to the intrinsic protective system of plants against stress, a number of soil microorganisms have been proved to be able to alleviate the stress symptoms. Mycorrhiza is an association or symbiosis between the roots of most land plants and many soil fungi that colonize the cortical tissue of roots during periods of active plant growth, from which both partners benefit; *vesicular-arbuscular mycorrhiza* (VAM) is the most common and universal mycorrhiza. More and more experiments have indicated that VAM was able to alter water relations and played a great role in the growth of host plant in the condition of drought stress. Augé compiled the existing literature on plant water relations, drought and VAM symbiosis [3]. The aim of the present review is to have further exploitation to the effects of VAM on host plant and its mechanism based on previous works.

2. Effects of VAM on host plants

2.1 Effects on morphology

The effects of VAM on morphology of host plants during drought can be shown by comparing VAM plants with non-mycorrhizal (NM) plants. VAM *Acacia* and rose were found more leaf abscission during drought than NM plants by Osonubi and Henderson separately, while VAM wheat had less leaf drop and necrosis [4, 5]. Relatively VAM maize had more green leaf area than NM maize after drought and VAM symbiosis delayed leaf senescence in droughted alfalfa. VAM soybeans had less drought-induced pod abortion than NM ones [3]. It was also reported that VAM plants would recover from wilting more quickly than NM plants upon relief of drought [6]. In addition, it was found VAM symbiosis has generally not affected stomatal density and guard cell size when comparing VAM and NM plants with similar leaf areas, even when transpiration or stomatal conductance differed [5].

2.2 Effects on metabolism

2.2.1 Effects on metabolism of water

Plant tissue water status is generally quantified by measuring its water content. Water contents of non-stressed plants were usually not different in VAM and NM plants [7-10]. In the condition of drought stress, VAM symbiosis usually postponed declines in leaf water potential [11-14]. VAM plants were also reported to return to the control level more quickly than NM plants after relief of drought stress [13]. VAM and NM plants often show different transpiration rates and stomatal conductances. It was proved in more than three times that VAM symbiosis induced alterations of stomatal conductance or transpiration in blue grama, cowpea, lettuce, rose, safflower, soybean and wheat, and VAM plants usually increased stomatal opening relative to NM plants [3]. However, several cases have been founded that there were no differences between VAM and NM plants in stomatal conductance. For example, the stomatal conductance of *Citrus taxa* generally was not affected by VA fungi colonization, while sorghum was only sometimes sensitive to VA fungi colonization.

2.2.2 Effects on photosynthesis

VAM plants often display higher rate of photosynthesis than NM counterparts do, which is consistent with VAM effects on stomatal conductance. Most of the researchers suggested that VAM symbiosis increased the units of photosynthesis, and so as to increase the rates of photosynthetic storage and export at the same time [3]. It has been proved that concentration of chlorophyll in VAM plants was higher than their control NM plants [6,15,16]. And higher concentration of chlorophyll is associated with higher photosynthesis rate [15].

Different VAM fungi have different effects on photosynthesis in the condition of drought stress [11]. Ruiz-Lozano and Azcón found that in comparison with NM plants one species of Glomus increased photosynthetic P-use efficiency of its host, while another *Glomus spp*. decreased these efficiency [17]. This illustrates the variable influence of mycobionts on host photosynthesis.

2.2.3 Effects on growth and absorption capacity

VAM symbiosis improved absorption capacity, and increased the growth of its host plant, which was proved in sugarcane, mung bean, apple, orange, wheat, tomato and wild jujube [18]. When water content of soil was 12%, biomass of mung bean colonized with *Glomus mosseae*, *Glomus spp*. or *Glomus caledonium* were found 1.99, 1.95, and 1.80 times that of their control NM partners [19]. In the condition of drought stress, biomass of shoot and root in VAM maize decreased by 12%, 31%, while in NM plants they decreased by 23% and 55% individually [13]. This means that the VAM symbiosis plays a positive role in growth of host plant, which may be caused by melioration of nutritional status in host plant, especially melioration of P status. Capacity of P in soil was decreased by drought, but VAM plants were found to have different concentration of P in many researches. This difference was also found in other elements. Concentration of Cu and Zn in VAM plants have been suggested higher than that of NM plants in more than one half of researches, while concentration of Mn in leaf of VAM plant was lower than that of NM one [20-23]. VAM plants also appear to absorb less boron than NM plants during drought. Shoot concentrations of nitrogen, potassium, calcium, magnesium, iron, sodium and molybdenum appear to be little affected by VAM symbiosis in drought conditions [3].

2.3 Effects on protective adaptation

Changes of protective adaptation can also reflect the effects of VAM on host plants. Soluble carbohydrate accumulation, amino and imino acids and protective enzyme activity are typically biochemical parameters used in studies on plant protective adaptation. Investigators have usually suggested that the differences of these biochemical parameters between VAM and NM plants reflect greater drought resistance in the VAM plants. For example, lower accumulation of soluble sugars indicates that plants avoid drought more successfully and so have less need to osmotically adjust symplasm or osmoprotect enzymes, or shows less strain or injury.

Schellenbaum et al. observed that VAM symbiosis significantly affected tobacco plants during drought in terms of soluble carbohydrate accumulation and partitioning [24]. Their VAM plants accumulated less glucose and fructose in leaves and roots than NM plants in drought conditions. Similar findings were reported for rose and pepper after drought [15,25,26]. Higher foliar concentrations of soluble sugars in VAM than in NM maize plants after drought was reported, suggesting the positive role of VAM in enhancing drought resistance of host plants [12,13]. In drought conditions, concentrations of amino and imino acids in plants with VAM symbiosis have been reported to increase [12,24], and opposite results were also found [12,25]. Viewing in conjunction with other parameters in the same study, all the authors suggested this indicated greater drought resistance in the VAM plants. Levels of proline and other compounds such as free polyamine have also been compared in VAM and NM plants, as a measure of resistance capacity or injury. The results are in consistent with studies on soluble sugars.

The activities of several protective enzymes have been studied in VAM and NM plants during drought and found to be typically higher in VAM plants. For example, VAM lettuce had higher root and shoot superoxide dismutase activity than NM lettuce [27] and VAM alfalfa higher acid phosphatase activity than NM alfalfa [8]. Other similar reports include glutamate-ammonia ligase in maize, glutamine and glutamate synthase activity in soybean [28]. Nitrate reductase activity in leaves and roots was also increased by VAM symbiosis in numerous studies [29-31]. Where reported, total protein concentrations have been consistently higher in VAM than NM plants during drought, considered by the authors to be a beneficial VAM effect [3, 12, 27].

3. Mechanism of drought resistance

Mechanism of VAM symbiosis enhancing drought resistance is of environmental and agronomic importance. Safir et al. suggested that VAM symbiosis probably affected the water relations of plants indirectly by improving P nutrition in the early age. Recently several reports considered that VAM symbiosis could modify host water relations in a way entirely unrelated to improved P acquisition. Studies carried out so far have suggested several mechanisms by which VAM can alleviate drought stress in host plants. Some of important ones are mentioned in the following section.

3.1 Properties of soil in rhisophere

VA fungi are concerned with metabolic physiology of host plant in the formation of VA symbiosis, which affects the characteristic of root exudation, and in turn affects properties of soil in rhisophere. Barea et al. proved that VAM extension hyphae grow into the soil matrix to create the skeletal structure holding primary soil particles to steady aggregates [32]. Tisdall considered the function of VAM on soil was to create conditions conducive to formation of these macroaggregate structures [33]. Augé et al. proposed that VAM and NM plants might behave differently during drought. They found that soil colonized with Glomus intraradices changed its moisture characteristic curve, relative to non-mycorrhizal soils having similar root densities [26]. This means hyphae and secretion of roots affect soil water retention properties. In rhisophere of maize, clover and Populus ussuriensis, phosphatase activity of soil changed when colonized by VA fungi. In addition, the amount and species of other fungi, bacteria, wireworm in rhisophere will change when root is colonized by VA fungi, which in turn affects properties of soil indirectly. But studies on this subject are still limited.

3.2 Enlargment of root areas and its efficiency of water absorption

The main absorption apparatus of mycorrhiza extension hyphae with a diameter of 2-5µm can penetrate soil pore inaccessible to root hairs (10-20µm) and so absorb water that is not available to non-mycorrhizal plants [34]. Because the number of extension hyphae is far more than that of root hairs, the area of surface where VAM plant and soil interacted was increased greatly. In addition, Colonized with VA fungi might change the architecture of root, which may be used to increase the interaction of root and soil [35]. Li et al. proved that VAM hyphae were able to absorb phosphorus from the dense soil location where the host roots could not access [36]. Paxfitt considered the resistance of transport was low because hyphae of VA fungi are nonseptate. Faber et al. measured rates of water transport by hyphae ranging from 375 to 760 ml H_2O h^{-1} [37]. All those discussed above suggested VAM enlarged root absorption areas, and improved its efficiency of water absorption.

3.3 Absorption of P and other nutritional elements, and nutritional status of host plant

There is a great correlation between nutritional status of plant and its drought resistance, while VAM changed the nutritional status of its host plant. P concentrations themselves may affect host water balance, but it is often fixed in soil and not available to plant. Phosphatase produced by VA fungi play an important role in translating fixed or insoluble into soluble P, which can be used by plant freely. At the same time, hyphae are also important ways of P transported in soil. Other elements such as Zn and Cu can also not flow freely in soil. Li et al. measured contents of Cu and Zn in clover planted in five compartments with an air gap and found more than half of total were absorbed by extension hyphae [38]. The absorption of Ca, Si, Ni, Co etc. was also reported increased by VAM symbiosis [34]. It is still accepted by many that VAM enhance resistance of high stress of host plants by improving their nutritional status.

3.4 Activation of defense system

As soil dries out and soil water potential becomes more negative, plants must activate their defence system to be sure to absorb water as much as they can. It is not known the exact mechanism that defence system is activated. But plant hormone is thought an important factor. During drought, Duan et al. found concentrations of abscisic acid (ABA) in xylem sap were lower in VAM than in NM plants [39], which was also proved by Goicoechea et al. [7], suggesting that VAM plants were less strained. Cytokinin concentrations were similar in droughted VAM and NM plants, in leaves, roots and xylem sap [7, 39]. Liu et al. found the inoculation of VA fungi significantly increased the contents of zeatin, indole-acetic acid (IAA) and gibberellin (GA3), reduced ABA levels in leaves and roots of corn and cotton under drought conditions [40]. There was a correlation between ABA contents and stomatal resistance. It was suggested that endogenous hormone balance changed by VA fungi colonization contributed to the enhancement of plant drought resistance.

3.5 Protection against oxidative damage

Drought induces an oxidative stress in plants, but little attention was paid to studies on activity of antioxidant enzymes in the VAM symbiosis. Recently, the activity of superoxide dismutases (SODs) was studied time and time [28]. Several studies have shown that the VAM fungus G. mosseae possesses Cu Zn-SOD activity and that VAM clover roots exhibit 2 additional SOD isoforms

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as compared to NM plant roots [41]. In situation of drought, VAM lettuce had higher SOD activity than NM control, which was conformed at transcriptional level by molecular analyses. In legume plants, there are evidences showing VAM can alleviate drought-induced nodule senescence and reduce oxidative damage to lipids and proteins. Bartels proposed that both prevention of oxidative stress and the elimination of reactive oxygen species are the most effective approaches used by plants to gain tolerance against several abiotic stresses, including drought [42].

3.6 Effect on the expression of gene

Previous studies on mechanism focused on the effects on morphological and physiological levels. Recently, more and more researchers turn to elucidating it from DNA or molecular level. There is evidence showing that VAM affected the expression of host plant gene. Hanan Itzhaki et al. reported in talk session when expression of tobacco genes following early stages of Glomuse intraradix colonization were compared, thirty bands in total RNA and cDNA from both VAM and NM roots were found in mycorrhyzal tobacco roots but not in NM roots, and about 40 bands were found to be lighter or absent in the mycorhiazal roots as compared with NM roots. G. Berta et al. studied nuclear changes in roots of tomato and found that nuclei of mycorrhizal root cortex cells were larger and had more decondensed chromatin than those of control. Significant ploidy distribution differences were also observed between nuclei of VAM colonized and control roots, and a strong correlation between nuclear polyploidization and VA colonization was found [43]. Polyploidization and decondensation are usually associated with high metabolic activity. They even suggested the meaning of polyploidization is in relation to the structural and metabolic modification by VA fungi. In another study, gene expression patterns within leaf and root tissue of VAM and NM tomato plants were compared and differential regulation was observed [44].

4 Conclusion

On all accounts, it is clear that VAM symbiosis often results in altered rates of water movement into, through and out of host plants, with consequent effects on plant morphology and physiology. The mechanisms of VAM enhancing resistance of drought stress are still debated now. Two aspects are necessary when VAM symbiosis enhance resistance of high stress of host plants, one is VAM symbiosis activating defence system of host plant quickly; and the other is some biochemical compounds that can resist high stress are synthesized by VAM symbiosis. Although we do not understand clearly how VA fungi activated defence system of host plant, and whether there are other mechanisms concerned with the interaction of VA fungi and its host plants, it is just the case that VAM symbiosis enlarges absorption areas of host plant, and improves nutritional status of host plant. Therefore the conclusion that contribution of VAM symbiosis to plant drought tolerance is the result of accumulative physical, nutritional, physiological and cellular effects is available.

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