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Review

AMF-induced tolerance to drought stress in citrus: A review

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ABSTRACT

Citrus is one of the most widely cultivated fruit crops, whose rhizosphere inhabits a class of beneficial fungi, popularly known as arbuscular mycorrhizal fungi (AMF). Different species of AMF viz., *Acaulospora*, *Entrophospora*, *Gigaspora*, *Glomus*, *Pacispora*, *Sclerocystis*, and *Scutellospora* have been observed to colonize citrus roots for the formation of arbuscular mycorrhizal (AM) symbiosis, where both the symbiotic partners are mutually benefited (up to 20% of photosynthetic carbohydrates from the host plant is diverted toward the growth of AM, in the exchange of water and nutrient uptake from the fungal partner to the host plant). AM symbiosis can usually confer better plant growth, higher nutrient uptake, greater tolerance to abiotic and biotic stresses, and soil structure improvement in the host plant. Meanwhile, AM-inoculated citrus plants have shown greater tolerance to drought stress (DS). Drought stress strongly restricted both the development of non-AM-citrus and the mycorrhizal development of AM-citrus, but AM colonization produced a positive effect on plant growth and photosynthesis, even under DS. This review provides an overview of possible mechanisms involved in DS tolerance through improved water and nutrient uptake (especially P nutrition) using extraradical hyphal growth; effective spatial configuration of root system; elevated concentration of tetramine spermine; osmotic adjustment through non-structural carbohydrates, K^+, Ca^{2+}, and Mg^{2+}, but not proline; scavenging reactive oxygen species through antioxidant enzymes and antioxidants; and glomalin-bound soil structural improvements, besides, some new exciting perspectives including water transport by mycorrhizal hyphae and molecular analysis are suggested.

Contents

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1. Introduction

Drought stress (DS) as one of the most ominous abiotic factors limiting the productivity of horticultural crops, is increasingly growing in dimension of severity in many regions of the world (Shukla et al., 2012). Citrus, a perennial crop with a long orchard life, is likewise a globally important fruit crop responsible for world trade and tariff, and often exposed to the vagaries of soil and atmospheric DS (Molinari et al., 2004). Drought stress is known to restrict the vegetative growth and yield of citrus, in addition to adversely affecting fruit quality and incurring huge economic loss to the citrus growers (Rodriguez-Gamir et al., 2010).

Citrus rhizosphere inhabits many soil microorganisms, such as bacteria, fungi, nematodes, protozoa, algae, and microarthrops, which are affected by root exudates, plant species, plant developmental stage, and soil properties (Srivastava, 2013; Wu and Srivastava, 2012). These soil microorganisms not only control ecosystem function through decomposition and nutrient cycling, but also serve as an indicator of ecosystem health (Balser et al., 2010). In addition, these microorganisms play multiple roles in regulating growth and ecological fitness of their hosts (Nihorimbere et al., 2011). Arbuscular mycorrhizal fungi (AMF), a kind of useful soil microorganism, can colonize roots of ~80% land plants to establish the symbiotic association. Such symbiosis helps the host plant to take water and nutrients from the soil, and in return, the AMF obtains up to ~20% of photosynthetic carbohydrates from the host plant (Parniske, 2008). In recent years, many studies have been conducted to evaluate the essential roles of AMF in many horticultural plants, such as vine, citrus, apple, peach, strawberry, lettuce, and pepper (Ruiz-Lozano et al., 2001; Borowicz, 2010; Krishna et al., 2010; Ortas et al., 2011; Wu et al., 2011a, 2012). Meanwhile, due to the less root hairs and high AM dependency (Wu and Xia, 2006a), citrus plants are well concerned by mycorrhizal workers and horticulturist. Studies have shown that infection by AMF can stimulate citrus growth, increase the absorption of nutrient and water, maintain citrus yield and quality at low inputs of nutrients; helps the host plant to enhance the resistance against disease and pathogenic organisms, in addition to the formation and stabilization of soil water-stable aggregates, contributing toward soil health resilience (Ortas, 2012). The mycorrhizal effects on citrus are significant differences between species of AMF (Ortas et al., 2002).

Inoculation with AMF also increased tolerance against DS in host plants including citrus (Augé, 2001). Mycorrhizal research on the DS in citrus began more than 30 years ago, when Levy and Krikun (1980) firstly reported the effects of AMF on stomatal conductance, photosynthesis, and proline content of rough lemon (*Citrus jambhiri* Lush) seedlings during development and recovery from soil water deficit. Since then, many interesting results have emerged through a number of field and potted experiments. This review is aimed to analyze the work done on mycorrhizal colonization of citrus roots, changes in mycorrhizal development affected by DS, and potential mechanisms involved in ameliorating effect of mycorrhiza toward DS tolerance in citrus. The current state of knowledge on this important subject area is highly fragmental.

2. Citrus mycorrhizas

Citrus was considered a highly mycorrhizal-dependent crop, since Peyronel (1922) observed mycorrhizal structures in citrus in Italy. Later, Rayner (1935) found mycorrhizal structures within the rhizosphere of citrus plants (*Citrus sinensis* Osbeck and *Citrus aurantium* L.) under cultivation in southern California. Unfortunately, these studies did not provide any meaningful headway toward the utility of such presence of mycorrhizal association with citrus. Recently, Wu and Xia (2010) reported in depth the morphological structures of AMs viz., entry points (Fig. 1a), arbuscules (the trunk hypha or hyphal coil from intercellular or intracellular hypha in the inner cortex adjacent to the endodermis and the vascular tissues) (Fig. 1b), intercellular or intracellular hyphae (Fig. 1c), extraradical hyphae (hyphae that develop to the outside of roots) (Fig. 1d), and spores formed in the extraradical mycelia in *Citrus unshiu* Marcovitch grafted on *Poncirus trifoliata* L. Raf. Interestingly, few intraradical vesicles but more arbuscules existed in mycorrhizal roots, which may be due to that in AMF species, the genera *Gigaspora* and *Scutellospora* do not form intraradical vesicles, and lots of vesicles occur in roots toward the end of the growing season (Peterson et al., 2004). A new insight that intraradical hypahe of AMs could infect root elongation and maturation zones, root cap, and meristematic zone in citrus roots, thus, was concerned (Wu and Xia, 2010).

Citrus rhizosphere has found the presence of as many as 45 species of AMF belonging to seven genera like *Acaulospora*, *Entrophospora*, *Gigaspora*, *Glomus*, *Pacispora*, *Sclerocystis*, and *Scutellospora* (Table 1). Species of genera such as *Acaulospora*, *Gigaspora*, and *Glomus* were dominantly observed in the citrus rhizosphere. *Glomus fasciculatus* was consistently associated with young citrus trees (0–30 yr) and *G. constrictus* with older trees (30–70 yr) (Nemec et al., 1981). The occurrence of AMF species was affected by various factors, such as soil P level and water content, citrus rootstock, soil type, soil depth, orchard altitute, and soil tillage management (Wang et al., 2011; Brito et al., 2012; Pagano et al., 2013; Shukla et al., 2013). The AMF may be systematically and functionally diverse with abundant ecological differentiation and specialization to environments (Pagano et al., 2013). In addition, high-input agricultural practices usually have adverse effects on AMF communities but low-input agricultural managements can increase the communities (Munyanziza et al., 1997). As a result, AMF communities are considered as a vital indicator of soil quality in citrus orchards.

3. Relationship between drought stress and mycorrhizal development of citrus

The spores of AMF in soil germinate and grow from a quiescent-like state in response to different edaphic and non-edaphic conditions (Giovannetti et al., 2010). However, soil water content can strongly affect spore germination, thereby, disturbing mycorrhizal formation and further development. It seems that soil wetting and drying cycles are the vital factors affecting spore survival and germination, and thus, the efficacy of mycorrhizal colonization. The effect of DS on AM fungal development in citrus plants (Table 2) clearly showed that DS strongly restricted the mycorrhizal development of citrus plants, irrespective of soil water. Meanwhile, some AMF species can quickly adapt to the DS conditions and thereby confer the beneficial effects on the host plant under DS (Nasim, 2010). Certainly, the soil water deficit is in company with the decrease of P availability, which may be a more direct effect on colonization (Augé, 2001). Although low soil moisture had a negative impact on the amount of extraradical hyphae of *Glomus intraradices*, the AMs still increased P uptake of host plant under partial rootzone drying (Neumann et al., 2009). In an experiment with spore storage in soils with different water potentials, more infectivity was in *Glomus mosseae* and *G. deserticola* after storage under −0.04 Mpa and in *Glomus fasciculatum* under −0.8 Mpa, implying that genetic characteristics and ecological adaptation of AMF species are related to the tolerated capacity of DS (Ruiz-Lozano and Azcón, 1996; Giovannetti et al., 2010). In saline soils of the Hungarian steppe, root AM colonization and arbuscule formation in halophytes were negatively correlated with the intensity of rainfall but without the soil water content (Füzy et al., 2008). It seems that