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Mycorrhizas in citrus : Beyond soil fertility and plant nutrition

QIANG-SHENG WU¹, A K SRIVASTAVA², YING-NING ZOU³ and S K MALHOTRA⁴

College of Horticulture and Gardening/Institute of Root Biology, Yangtze University, Jingzhou, Hubei 434025, China, and

Department of Chemistry, Faculty of Science, University of Hradec Kralove, Hradec Kralove 50003, Czech Republic

Received: 27 August 2016; Accepted: 30 September 2016

ABSTRACT

Citrus, one of the important fruit trees grown in tropical and subtropical regions of the world, has less and shorter root hairs in the field, thus, highly dependent on arbuscular mycorrhizas. Citrus rhizosphere inhabits 45 species of arbuscular mycorrhizal fungi (AMF), belonging to seven genera like *Acaulospora*, *Entrophospora*, *Gigaspora*, *Glomus*, *Pacispora*, *Sclerocystis* and *Scutellospora*. These AMF can be associated with the roots for the formation of arbuscular mycorrhizal symbiosis, who would enlarge the contacted areas of roots to soil and be regarded as a potential soil biofertilizer, thereby promoting citrus nutrients. In addition to the vital function, mycorrhizas in citrus display other roles in soils and plants. Most AMF species usually significantly increase plant growth and fruit quality of citrus plants, but occasionally inhibit or did not impact plant growth. The inoculation with AMF obviously improved root system architecture of citrus, thereby conferring greater ability of the host plant to obtain soil resources. Mycorrhizas can develop an extensive common mycorrhizal network to colonize neighbouring citrus or other plants for underground communication. AMF release a special glycoprotein, glomalin, into the soils, which can improve soil structure and contribute soil carbon pools, thus, providing better soil fertility and soil physical-chemical traits. Mycorrhizas enhance tolerance of citrus plants to drought stress, salt stress, high temperature but not low temperature, flooding, elevated [CO₂], diseases, and insect pests in terms of various physiological and molecular approaches. Based on the mycorrhizal functionings, citrus production will consider mycorrhizal management of citrus orchard and new perspectives are also outlined.

Key words : Citrus, Glomalin, Mycorrhiza, Nutrient uptake, Root system architecture, Soil structure

Citrus is one of the world's major fruit trees grown in more than 140 countries, whilst China, Brazil, USA, India, Mexico, and Spain are the world's dominant countries in citrus fruit-producing, occupying approximately two-thirds of global production (Srivastava and Singh 2008, Liu *et al.* 2012). Citrus is mainly used for the fresh fruits, which are either eaten alone, processed into juice, or added into dishes, beverages, and teas, thereby providing commercial export markets around the world.

Arbuscular mycorrhizal fungi (AMF), belonging to the order Glomales, are a kind of ancient soil microorganism and have existed for almost 400 million years old (Miransari 2010). These fungi can form mutualistic relationships with

over 80% of land's plants, namely, arbuscular mycorrhizas (AMs). This symbiosis is the most common mycorrhizal association in natural ecosystems (Brundrett 2002), and partly undertakes the absorption and delivery of mineral nutrients and water from the soil to the host plant by mycorrhizal hyphae (Srivastava *et al.* 2015, Smith and Smith 2011). Additionally, AM benefits include enhancement of tolerance to abiotic and biotic stresses (Sikes *et al.* 2010, Wu *et al.* 2013b), growth improvement (Smith and Smith 2011), modulation of ecosystem resilience (Garrido *et al.* 2010, Barea *et al.* 2011), and maintaining and improvement of soil structure (Rillig 2004, Rillig and Mummey 2006, Kreditsu and Srivastava 2014). Therefore, AMs are critical for plant health, survival, and restoration in native ecosystems and good soil structure.

Given the beneficial roles of AMs on plant growth and health, mycorrhizal biotechnology has used in horticultural plants, especially citrus (Azcón-Aguilar and Barea 1997). Citrus plants are easy to infection by AMF in roots, afterwards forming typical AM structures (Wu *et al.* 2009, 2013b), such as intraradical and extraradical hyphae, entry points, vesicles, and arbuscules. Such extraradical hyphae are able to develop and then colonize neighbouring plants for

^{1,2}Professor (e mail: wuqiangsh@163.com), College of Horticulture and Gardening/Institute of Root Biology, Yangtze University, Jingzhou, Hubei 434025, China. ³Principal Scientist, Soil Science (e mail: aksrivastava2001@gmail.com), ICAR-Central Citrus Research Institute, Nagpur, Maharashtra 440033. ⁴Agriculture Commissioner (e mail: malhotraskraj@yahoo.com), Ministry of Agriculture and Farmers Welfare, Government of India, New Delhi 110012.

the establishment of common mycorrhizal network, which can exchange nutrients and signalings between plants for resource sharing and as a part of warning system associated with herbivore's attack (Walder *et al.* 2012, Song *et al.* 2014). On the other hand, citrus plants possess shallow root systems and less root hairs in field, thereby, strongly dependent on AM-symbiosis to help roots nutrient absorption. Moreover, AMF can induce greater root system architecture in poor soils (Wu *et al.* 2011b, 2016). As a result, mycorrhizas are a vital factor in growth of citrus trees.

Citrus rhizosphere inhabits many native AMF species involving 45 species of seven genera like *Acaulospora*, *Entrophospora*, *Gigaspora*, *Glomus*, *Pacispora*, *Sclerocystis*, and *Scutellospora* (Wu and Srivastava 2012, Wu *et al.* 2013b). These AMF communities are often considered as the critical component of soil and functional links between soil and plants and thereby involve in nutrient and water cycling, soil structural stabilization, organic matter transformation and accumulation, and turnover of soil organic residues (Yang *et al.* 2010). In general, host plant species are more important than the soil P level to determine the AM fungal community (Gusling *et al.* 2013). Although like, most citrus trees from different countries often exhibit different dominant AMF species. *G. caledonium*, *G. clarum*, and *G. mosseae* were commonly found in citrus orchards in Italy (Palazzo *et al.* 1992), *G. intraradices* and *G. mosseae* in citrus soils of eastern Spain (Camprubi and Calvet 1996), *G. etunicatum* and *Acaulospora tuberculata* in Thailand (Watanarojanaporn *et al.* 2011), and *G. aggregatum*, *G. claroideum*, and *G. intraradices* in covering grass of soil management, *G. aggregatum* and *G. claroideum* in grass cultivation and *G. etunicatum* in no-tillage soil management in southern region of China (Srivastava and Ngullie 2009, Zhang 2010). Therefore, it concludes that *Glomus* species are the most common and dominant AMF species in citrus rhizosphere. On the other hand, it suggests the diversity of AMF community in various ecosystems. It is clear that AMF are the important component of terrestrial ecosystems and strongly affect ecosystem processes via altering plant community composition, directly and indirectly influencing soil microbial communities, mediating changes in host physiology and resource capture to regulate ecosystems, and directly effects of soil mycorrhizal mycelium and its products (Rillig 2004). Sharma *et al.* (2010) proposed that microbial community diversity has been considered as an indicator for evaluating soil quality. Thus, analyzing AMF community diversity is important for soil quality in citrus orchards. It is reported that spore density of AMF was considerably higher in no-tillage citrus orchards than in tillage orchards (Wang *et al.* 2010). AMF community diversity varied severely between trifoliate orange and red tangerine (Wang and Wang 2014). In general, dominant AM fungal species may be not the best efficient fungal species using in citriculture. These AMF species can strongly infect roots of citrus plants in the field from 42 to 83% in Brazil (de Souza Nunes *et al.* 2006) and from 13 to 28% in China (Wu *et al.* 2004).

In recent past, Srivastava *et al.* (2002) reviewed the mycorrhizal contribution to soil fertility and plant nutrients in organic citriculture. They proposed that mycorrhizas were highly effective in stimulating plant growth and nutrient uptake in low fertility, coarse textured soil. As time goes on, mycorrhizas in citrus also have other potential benefits for plant growth, soil structure, root system architecture, and stressed tolerance in citrus. For example, Wu *et al.* (2008) first found that AMF were able to release a special glycoprotein, glomalin, into the citrus rhizosphere, which can help to stabilize soil water-stable aggregates, thereby, improving soil structure, irrespective of ample water or soil water deficit. Studies also reported a positive effect of AMF on root hair and root system development (Wu *et al.* 2011b, 2016). Such changes in roots, correspondingly, improve fruit quality of citrus (Sui *et al.* 2007). In addition, a number of studies had confirmed that AM presence could enhance tolerance of adversity in drought, salt stress, high temperature, flooding, diseases, and insect pests. Such an advance will provide more chances to understand AMF roles in citrus, beyond soil fertility and plant nutrition.

The objective of this review is to discuss the AM contribution to growth, nutrient absorption and fruit quality, in combination with the AM-mediated soil structure, root morphology, and adverse tolerance in citrus (Fig 1). It is expected that the new insights on mycorrhizas in citrus will

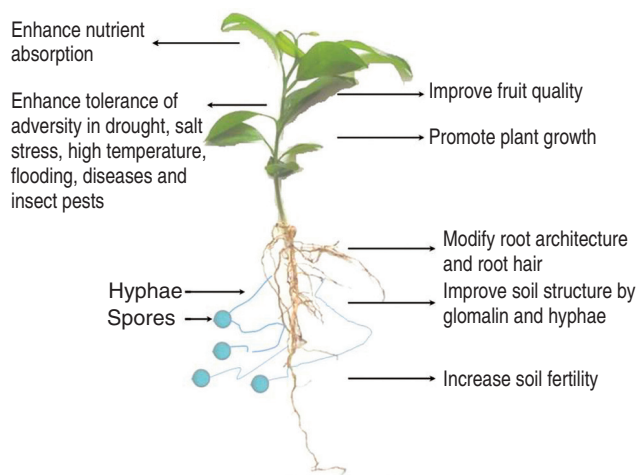


Fig. 1 Mycorrhizal functionings on citrus plants

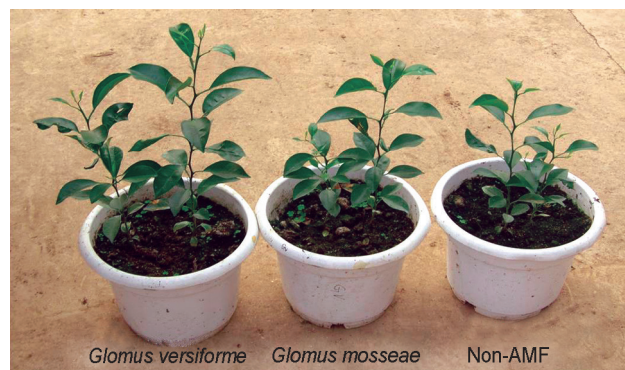


Fig 2 Growth of micropropagated red tangerine (*Citrus tangerina*) infected by *Glomus mosseae*, *G. versiforme* and non-AMF

be concerned, and an appropriate management of AMs in the citrus orchard provides the reduction of chemical fertilizer and pesticide inputs for sustainable citrus production.

Relationship between mycorrhizas and plant growth

Enhancement of AMF on plant growth including citrus plants has been demonstrated. Ortas (2012) reported that mycorrhizal citrus seedlings grown healthy on sterile soil after 18 months, but non-mycorrhizal plants were stunted. Moreover, AMF has also played beneficial role in their post-transplanting performance of micropropagated citrus plantlets (Kapoor *et al.* 2008). After 300 days of inoculation with *Glomus mosseae* and *G. versiforme*, the stem diameter, leaf area, leaf number, root volume, and shoot and root dry weights in mycorrhizal plants of micropropagated trifoliolate orange were notably higher than those in non-mycorrhizal plants, and the effect of *G. mosseae* was better than *G. versiforme* (Wu *et al.* 2006c). AM symbiosis is well known to increase the vigour of plants by improving water use and nutrient uptake, such as P, particularly in soils with low P contents (Graham 2000). In addition, AMF exhibited a notable impact on root growth of citrus plants (Wu *et al.* 2011b, 2012b). Optimization of root morphology caused by mycorrhization is beneficial for greater absorption of water and mineral nutrition, thereby, promoting growth performance of AM plants. The growth promotion was also observed under abiotic stress conditions. AMF colonization significantly stimulated growth traits of trifoliolate orange and red tangerine seedlings growth exposed to drought stress and NaCl stress (Wu and Xia 2006, Srivastava *et al.* 2008, Wu *et al.* 2008, 2010b, 2011a). Since soils from citrus orchard commonly contain the communities of AMF rather than a single species, further studies still need to be conducted to compare the different communities of AMF on plant growth (Fidelibus *et al.* 2000).

In addition to alone AMF application, integration of both AMF and plant growth-promoting rhizobacteria (PGPR) is used to test the effect on citrus growth (Wang *et al.* 2016b). In this study, an arbuscular mycorrhizal fungus, *Rhizophagus intraradices*, and a PGPR *Paenibacillus mucilaginosus*, were applied into trifoliolate orange under three P conditions by adding 0, 73.41, 220.23 mg/kg Ca₃(PO₄)₂. Plant height, stem diameter, and shoot and root biomass were the greatest under *R. intraradices*+*P. mucilaginosus* than under *R. intraradices* and under *P. mucilaginosus* conditions. It suggests that AMF can joint PGPR to enlarge the stimulated plant growth in citrus.

Studies also showed that inoculation with AMF inhibited the growth of citrus plants. *G. intraradices* did not affect growth of sour orange (*Citrus aurantium*) but significantly depressed by 18% in sweet orange (*C. sinensis*) under a high CO₂ level (Jifon *et al.* 2002). This indicated differential responses of citrus genotypes to AMF treatment. A severe growth depression was observed in micropropagated lemon plants (*Citrus limon* (L.) Burm. 'Zagara Bianca') inoculated with *Glomus mosseae* (Quatrini *et al.* 2003). Wu *et al.* (2011c) reported that inoculation

with *G. versiforme* significantly decreased the plant height and stem diameter of micropropagated red tangerine, but inoculation with *G. mosseae* notably increased plant height and stem diameter (Fig 2), indicating that AM-promoted growth would depend on AMF species. Growth depression often coincided with increased rhizosphere respiration, reduced root starch concentration and lower relative growth rates, and carbon expenditure on mycorrhizas might cause the growth depression (Jifon *et al.* 2002). At a high P level (250 mg/kg), *G. intraradices* significantly decreased the dry matter and plant height of *Citrus reshni* Hort. ex Tanaka, cv. Cleópatra, which may be related to a strong carbon sink in mycorrhizal roots (Sena *et al.* 2004).

Besides growth promotion and depression by mycorrhization, AMs did not significantly alter plant performance of citrus plants (Ngullie *et al.* 2015). *Glomus clarum* did not show any effects on plant height, stem diameter, and shoot and root dry weight of trifoliolate orange seedling in three different growing media [soil + sand (1:1); soil + sand + carbonated rice husks (1:1:1); soil + sand + decomposed Acacia bark (*Acacia mearnsii*) after tannin extraction (1:1:1)] at the alveolated styrofoam trays (Schmitz *et al.* 2001). Wu and Zou (2010) reported that *G. mosseae* did not significantly impact the stem diameter, plant height, leaf area, and shoot and root dry weight of trifoliolate orange at 15°C but markedly increased these growth traits at 25°C. In sour orange, a commercial AM inoculum, in combination with 90 mg/kg KH₂PO₄, did not significantly affect plant dry weight and stem diameter than uninoculated plants (Al-Karaki 2013).

As stated above, the dramatic effects of AMF on citrus growth might be associated with the compatibility between AMF and the host plants. If the nutrient consumption of AMs is less than the benefits for the host plants, AMs could provide the symbiosis for the host plants. However, if the AM consumption exceeded the benefits for the host plants, AMs can transform from symbiosis to parasitism, and consequently AMs would depress plant growth.

Soil fertility and plant nutrition

Highly significant effects of AMF colonization on citrus nutrition have been observed. An early study showed that native *Glomus caledonium*, *G. macrocarpum*, *G. monosporum*, *G. velum*, and *Gigaspora margarita* isolated from Troyer citrange significantly increased shoot and root P, Cu, and Zn concentrations (Vinayak and Bgyaraj 1990). In trifoliolate orange seedlings, inoculation with *Gigaspora margarita*, *G. mosseae*, and *G. versiforme* provided higher N, P, K, Ca, Mg, Zn, Cu and Mn concentrations, whilst the efficiency on nutrient uptake ranked as *G. mosseae* > *Gigaspora margarita* > *G. versiforme* (Wang *et al.* 2006). In orange (*C. sinensis*) seedlings, *Glomus mosseae* (UK), *G. mosseae* (USA), *G. clarium*, *G. caledonium* and *G. etunicatum* generally increased shoot P, Zn, and Cu levels compared with non-AMF control, and *G. clarium* showed the best effects (Ortas *et al.* 2002a). Therefore, Marschner and Dell (1994) proposed that extraradical hyphae of

mycorrhizas could confer up to 80% of plant P, 25% of plant N, 10% of plant K, 25% of plant Zn, and 60% of plant Cu. In addition, AMF-inoculated trifoliolate orange seedlings possessed higher activities of functional hyphae, active hyphae and total hyphae under drought stress condition, thus stimulating more absorption of P and water (Wu *et al.* 2011a). On the other hand, under sand culture, inoculation with *G. mosseae* and *G. versiforme* significantly increased P levels of trifoliolate orange seedlings, which may be due to the acid and neutral phosphatase release of extraradical hyphae into rhizosphere to dissolve insoluble phosphates (Liu *et al.* 2008). The presence of AMs could help the host plants to dissolve the nutrients in soil under poor soil nutrient condition or slow release fertilizer application (Ortas 2012). The AM contribution to citrus P is absolutely dependent on substrate P level. Under 25, 300, and 1 000 mg/kg P as triple superphosphate, mycorrhizal P contribution ranged from 4 to 818% in Rangpur lime (*C. limonia*) at 30–150 days after transplanting under 25 mg/kg P, from 2 to 157% under 200 mg/kg P, and from -23 to 21% under 1 000 mg/kg P (Nogueira and Cardoso 2006). Correlation analysis also revealed that root AM colonization and substrate hyphal length was highly positively correlated with shoot P concentration of Rangpur lime exposed to 25 and 200 mg/kg P. Moreover, the AM contribution of P increased with the increase of transplanting days and was generally highest under 25 mg/kg P, higher under 200 mg/kg P, and lowest under 1 000 mg/kg P. Another greenhouse study indicated that mycorrhizal dependency was gradually decreased with increasing P (0, 100, and 200 mg/kg) and Zn (0, 2.5, and 5 mg/kg) supply, and the decrease was more pronounced for P requirement rather than Zn requirement (Ortas *et al.* 2002b). It seems that under no-excessive P availability, the AM functioning on P uptake was more effective than roots alone, whereas under excessive P availability, AM functioning on P uptake was ignored and plant P uptake mainly depended on roots alone. In addition, owing to poor root hairs, citrus plants are highly dependent on AMs for P uptake in soil with low available P.

Apart from P absorption, Fe absorption was also concerned. Treeby (1992) reported that AMF might increase the supply of Fe for rough lemon and trifoliolate orange in an acid soil, but not in an alkaline soil. In a sand culture, *G. versiforme* notably increased Fe content of leaves in trifoliolate orange seedlings grown in pH 5.0, 6.0, 7.0, and 8.0, whereas the colonization by the AM fungus only significantly increased leaf Fe levels of *C. reticulata* seedlings in pH 5.2 and 6.2 but not in pH 7.2 and 8.2 (Wang *et al.* 2008). These results strongly suggest that the AM contribution to Fe absorption lies on the combination of citrus genotype and substrate pH. The mechanism has been clarified, namely, both the enhancement of root ferric chelate reductase and the well-developed extraradical hyphae would help the citrus host plants to absorb more Fe from the substrate (Wang *et al.* 2008). In addition, mycorrhiza-inoculated sour orange seedlings tended to have a higher content of zinc (Zn) than non-inoculated seedlings (Ortas and Ustuner 2014). In a

Zn deficient soil condition, *Glomus intraradices*-colonized 'Newhall' navel orange and 'Ponkan' tangerine grafted on trifoliolate orange had greater Zn concentration in leaves and roots, as well higher Zn percentages in the leaves but lower Zn ratios in roots (Chen *et al.* 2014).

Recently, a non-invasive micro-test technique was used to measure the net fluxes of Ca^{2+} , H^+ , and NO_3^- in AM and non-AM roots of 9-months-old trifoliolate orange (Xiao *et al.* 2012). The results showed that AM seedlings recorded significantly higher net Ca^{2+} efflux at 0 and 600 μm , net H^+ influx at 600 μm , and net NO_3^- influx at 2400 μm from root tip than non-AM control. It appears that Ca^{2+} -ATPase, $\text{Ca}^{2+}/\text{H}^+$ antiporters and NO_3^-/H^+ symporters may be more induced by mycorrhization in root plasma membranes and thus synergistically take part in nutrient absorption.

In addition, molecular technique revealed that expression of *PiT* genes commonly was down-regulated or even suppressed by mycorrhization (Glassop *et al.* 2005). However, in seven *Ph1* phosphate transporter genes cloned from the combination of five *Glomus* species (*G. diaphanum*, *G. etunicatum*, *G. geosporum*, *G. mosseae*, and *G. versiforme*) and trifoliolate orange, *PtaPT4* and *PtaPT5* were still up-regulated by root AM colonization, and *PtaPT1*, *PtaPT2*, *PtaPT3* and *PtaPT7* were down-regulated in mycorrhizal roots, suggesting that the *PtaPT4* and *PtaPT5* transporters involve in mycorrhizal uptake of P in trifoliolate orange (Shu *et al.* 2012).

Mycorrhizas alter root system architecture

Plant roots involve in a wide variety of biological processes, such as nutrient and water uptake, nutrient storage, anchoring, and mechanical support (Smith and Smet 2012). In general, root system architecture (RSA) is used to describe the shape and structure of root systems in spatial concept in soil (de Dorlodot *et al.* 2007). RSA status in plants can potentially determine the ability of a plant to obtain soil resources. However, plants often grow in various environments and thereby also possess high plastic characteristics of RSA, which is dependent on the plant species, soil composition, soil microorganisms, and water and nutrient availability (Hodge *et al.* 2009). Most of the citrus species such as sour orange, trifoliolate orange, cleopara mandarin, swingle citrumelo and carrizo citrange have short or even rare root hairs, and are thus dependent on AM-colonization (Wu and Xia 2006). Root architectural alteration in AM-colonized citrus could increase root functioning to explore more water and nutrients under salt stressed conditions (Wu *et al.* 2010a,b).

Arbuscular mycorrhizal fungi as one of the soil inhabitant fungi have shown the functions on root longevity and architecture in strawberry, rice, and citrus (Fig 3) (Norman *et al.* 1996, Gutjahr *et al.* 2009, Wu *et al.* 2011b, b). In a citrus study, inoculation with *G. mosseae*, *G. versiforme* and *Paraglomus occultum* significantly increased root total length, total projected area, surface areas, and total volume and decreased root average diameter of 6-month-old trifoliolate orange seedlings (Wu *et al.* 2011b). Meanwhile,

better RSA traits of trifoliolate orange ranked as colonization by *G. mosseae* \approx *Paraglomus occultum* $>$ *G. versiforme*. Similar results also were found in red tangerine inoculated with *G. mosseae* (Wu *et al.* 2012b). In addition, for root total length, AMs mainly induced notably increased 0–1 cm classified root length, other than 1–2, 2–3, 3–4, $>$ 4 cm classified root length (Wu *et al.* 2012b). Accordingly, the proportion of 1–2 cm classified root length was decreased by AMF colonization. Interestingly, mycorrhizal inoculation in combination with exogenous putrescine (Put) but not spermidine (Spd) and spermine (Spm) more significantly increased these RSA traits of 4-months-old trifoliolate orange seedlings (Wu *et al.* 2010c). The AMF-induced alteration of RSA in citrus plants might be due to the fact that the RSA traits were highly correlated with root Put synthetases through arginine decarboxylase and ornithine decarboxylase, thus resulting in an increase of root Put, which indirectly improved root average diameter and proportion of fine roots (Wu *et al.* 2012b). On the other hand, AMF themselves mainly contained Put and Spd, which involved in spore germination and hyphal growth and also in control of the root cell division and differentiation, thereby participating in RSA alteration through lateral and adventitious root formation (Couée *et al.* 2004). Apart from polyamine regulation, altering both the allocation of carbohydrates to root (Wu *et al.* 2010f) and the balance of endogenous cytokinins and gibberellins by mycorrhization (Berta *et al.* 1993) led to the improvement of RSA in AM plants.

Recently, Wu *et al.* (2016) evaluated effects of AMF on root hair development of trifoliolate orange. Four tested AMF species, *Claroideoglossum etunicatum*, *Diversispora versiformis*, *Funneliformis mosseae*, and *Rhizophagus intraradices* substantially stimulated root hair density, while decreased root hair length. These AMF-modulated modification in root hair is closely related to P, nitric oxide, carbohydrates, IAA and MeJA levels in roots.

In short, AMF-altered root hair and root system architecture will potentially increase fruit yields or decrease fertilizer inputs in citriculture.

Improvement in fruit quality

It is well documented that AMF can stimulate nutrient absorption, enhance plant and tree growth, and improve root development, which are the important fact affecting fruit quality in citrus. Earlier studies showed that, in a *Citrus iyo* orchard, an AM fungus, *Funneliformis mosseae*, with the dosage of 100 spores/m², was applied into soils in March. The results indicated the greater carotenoid content in flavedo, the greater soluble solid content, and solid acid ratio in fruit juice under the condition of decreased P application plus charcoal treatment, as compared with both decreased P treatment and normal P application (Yao *et al.* 1997, 1999). Subsequently, Sui *et al.* (2007) also designed five treatments to confirm AMF roles in fruit quality in 6-yr-old *Citrus sinensis* grafted on trifoliolate orange, namely, (1) conventional fertilization and inoculation with *Funneliformis mosseae*, (2) conventional fertilization and inoculation without *F. mosseae*, (3) reduced fertilization and inoculation with *F. mosseae*, (4) reduced fertilization in combination with both charcoal and inoculation with *F. mosseae*, and (5) reduced fertilization and inoculation without *F. mosseae*. The results indicated relatively greater weight of single fruit, fruit shape index, and soluble solid content, as well considerably lower titratable acid concentration in fruit juice, as compared with other treatments. As a result, in citrus orchards, AMF presence could decrease the input of P fertilizer, whilst greater fruit quality occurs in such conditions.

Improvement in soil properties

Soil structure can be described from the form and stability. Hereinto, form of soil structure refers to a three-dimensional arrangement of soil aggregates and pores in soils (Juarez *et al.* 2013), and stability of soil structure is the ability of a soil to maintain its arrangement of solid after being exposed to the kinds of environmental stresses. Well-aggregated soil structure is highly important in soil tillage, water relations, root penetration, organic matter accumulation and soil erosion, and consequently affects soil sustainability and crop production (Miller and Jastrow

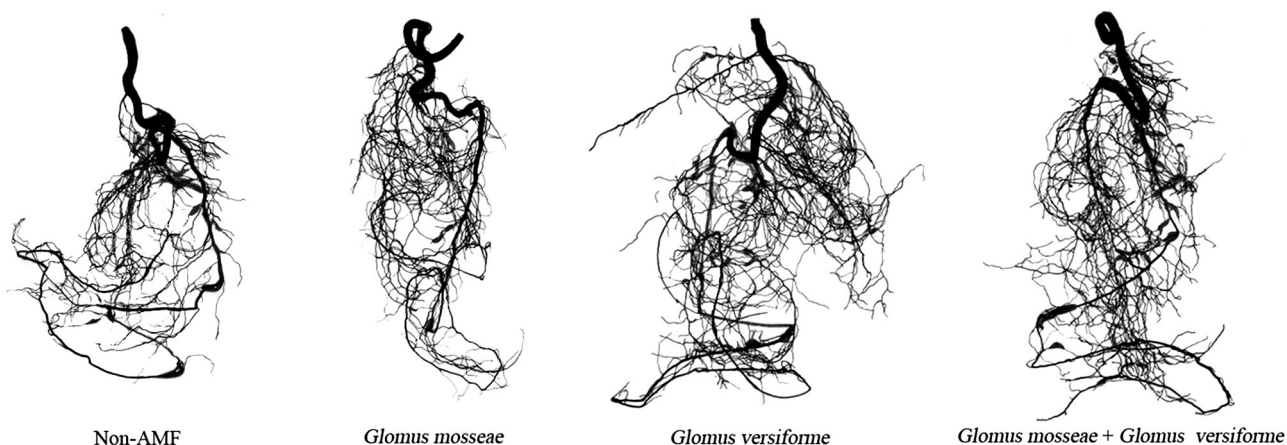


Fig 3 Root system morphology of trifoliolate orange (*Poncirus trifoliata*) infected by *Glomus mosseae*, *G. versiforme*, mixture of *G. mosseae* and *G. versiforme*, and non-AMF

2000). The size distribution and the stability of aggregates are often used as an indicator of soil structure (Rillig and Mummey 2006). Therefore, formation and stabilization of soil aggregates, especially water-stable aggregate, are vital to maintain soil structure stability (Barea *et al.* 2005). Meanwhile, macroaggregate (> 250 μm diameter) formation mainly depends on temporary (i.e. fungal hyphae and roots) and transient (i.e. polysaccharides) binding agents.

Studies have demonstrated the beneficial role of AMF in the formation and stabilization of aggregate stability via mycorrhizal hyphae and glomalin (Rillig 2004, Rillig *et al.* 2010, Peng *et al.* 2013, Wu *et al.* 2014). Glomalin, an insoluble N-linked glycoprotein, was first found by Wright and Upadhyaya (1996) and originated from hyphae and spore walls of AMF (Driver *et al.* 2005). Glomalin extracted from the soil is defined as glomalin-related soil protein (GRSP) (Rillig 2004). GRSP is insoluble and hydrophobic in the native state (Rillig 2004) and contains 3–5% N and nearly 37% C (Lovelock *et al.* 2004). In addition, glomalin is a putative homolog of heat shock protein 60 (Gadkar and Rillig 2006), and may be not a typical glycoprotein (Schindler *et al.* 2007). AMF inoculation could enhance the production of both EE-GRSP and T-GRSP in citrus rhizosphere, which may not depend on external P concentrations (Wu *et al.* 2015a). Many studies had shown that glomalin were significantly positive correlated with aggregate stability (Wilson *et al.* 2009, Fokom *et al.* 2013). Some studies have shown AM benefit on soil structure of citrus rhizosphere. In the field, easily extractable-GRSP (EE-GRSP) ranged from 0.45 to 0.62 mg/g and total-GRSP (T-GRSP) from 0.6 to 1.07 mg/g in rhizosphere of a 23-year-old *Citrus unshiu* grafted on *Poncirus trifoliata* (Wu *et al.* 2013a), which is lower than other plant rhizosphere (Lovelock *et al.* 2004, Violi *et al.* 2008). Lower GRSP levels in citrus rhizosphere may be due to that citrus rhizosphere mainly inhabits a high proportion of *Glomus* species. On the other hand, GRSP exhibited a certain distributive characteristic in water-stable aggregate fractions: EE-GRSP in $\text{WSA}_{0.25-1\text{mm}}$ and T-GRSP

in $\text{WSA}_{2-4\text{mm}}$ (Wu *et al.* 2013a). In addition, both EE-GRSP and T-GRSP were significantly positively correlated with water-stable aggregate at 0.25–0.50 mm size (Wu *et al.* 2012a). Using a controlled potted experiment, Wu *et al.* (2008) found that trifoliolate orange seedlings inoculated with *G. mosseae*, *G. versiforme* and *G. diaphanum* displayed significantly higher GRSP concentrations, soil hyphal length, and proportion of water-stable aggregates, regardless of soil water status, and GRSP concentrations and soil hyphal length were highly positively correlated with percentage of water-stable aggregates. In *G. mosseae*-colonized *C. junos*, in GRSP fractions only EE-GRSP ($r = 0.89$, $P < 0.05$) but not T-GRSP ($r = 0.77$, $P > 0.05$) represented a significantly positive correlation with aggregate stability (Huang *et al.* 2013). However, another study revealed the significantly positive correlation of aggregate stability with EE-GRSP and T-GRSP (Fig 4) in *G. mosseae*-colonized *Citrus tangerina*, *Fortunella margarita* and *Poncirus trifoliata* (Wu *et al.* 2014). GRSP contained ~60% carbohydrates and showed 3–10 times adhering soil aggregate ability than hot-water-extractable carbohydrates (Wright and Upadhyaya 1998). It appears that GRSP contribution to aggregate stability may depend on its concentrations in water-stable aggregates (WSA) fractions (Wright *et al.* 2007; Wu *et al.* 2013a).

To confirm the GRSP roles, exogenous EE-GRSP was applied into potted trifoliolate orange and cultured Satsuma mandarin in field (Wang *et al.* 2015, 2015b). The results showed the positive effects of EE-GRSP on soil fertility and soil structure, and thus EE-GRSP could be considered as an effective regulator in soils, at least within citrus rhizosphere.

Apart from GRSP, AMF inoculation can develop an extensive common hyphae network of AMs, which could entangle and enmesh soil particles (Miller and Jastrow 2000, Peng *et al.* 2013), increase soil water repellency (Rillig *et al.* 2010), and mediate wet/dry cycles (Rillig and Mummey 2006), thereby improving soil structure. Wu *et al.* (2016) recently simulated an extraradical hyphae disturbance, and found that hyphal disruption inhibited the production of

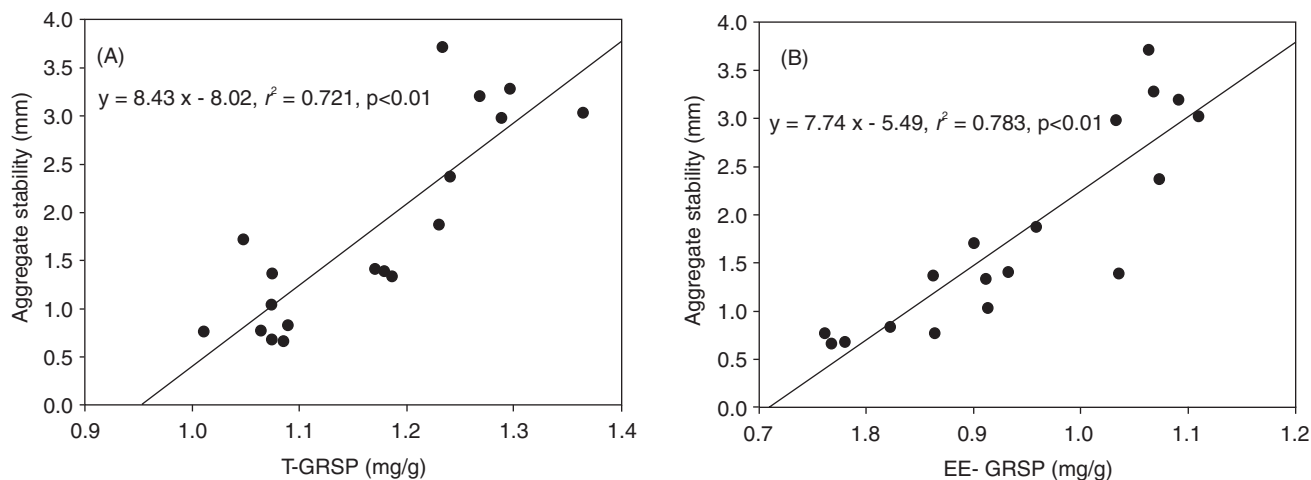


Fig 4 Correlation between T-GRSP (A) or EE-GRSP (B) and aggregate stability in rhizosphere of *Glomus mosseae*-infected *Citrus tangerina*, *Fortunella margarita* and *Poncirus trifoliata* seedlings ($n = 18$). Aggregate stability was expressed by mean weight diameter. Adapt from Wu *et al.* (2014) with minor modifications

EE-GRSP and T-GRSP, resulting in bad aggregate stability in rhizosphere of trifoliolate orange. It also proposed that soil tillage disrupted hyphal network, which adversely influenced GRSP production, subsequently weakening the GRSP functioning on aggregate stabilization. AMF could also improve RSA of citrus (Wu *et al.* 2011b, 2012b), which has a profound effect on soil aggregate stability (Rillig and Mummey 2006). More information about the beneficial role of mycorrhiza on soil structure of citrus orchard will be detailed clarified.

Mycorrhiza-mediated tolerance to abiotic and biotic stresses

During citrus growth, a number of stresses can occur, such as drought stress, salinity, temperature stress, and pathogenic microorganisms. These abiotic and biotic stresses adversely affect fruit production and decrease tree growth. Therefore, it is critical for the enhancement of tolerance to abiotic and biotic stresses in citrus plants. Here, AMF-mediated tolerance to various stresses is described and discussed as follows.

Drought stress: Citrus plants are highly sensitive to soil drought and are also subjected to seasonal drought during summer and autumn. Wu *et al.* (2009, 2013b) have summarized the AMF-induced tolerance to drought stress in citrus in detail. The present review simply discussed the AMF-induced potential mechanisms in citrus, though direct evidence is not clarified now. A two-chamber rootbox was utilized to evaluate the functioning of mycorrhizal hyphae on water absorption in trifoliolate orange (Zou *et al.* 2015b). After periodical disruption of hyphae in the hyphae chamber, leaf water potential and leaf relative water content were pronouncedly decreased, suggesting that mycorrhizal hyphae participate in water uptake, since the hydrophilic nature of mycorrhizal hyphae facilitated the absorption of water.

In drought-stressed trifoliolate orange seedlings, red tangerine seedlings, and grafted citrus trees, inoculation with AMF commonly increased tissue antioxidant enzyme activities (i.e. superoxidase, ascorbate peroxidase, catalase, guaiacol peroxidase, and glutathione reductase) and non-enzymatic antioxidant contents (soluble protein, reduced ascorbate, and reduced glutathione), thereby accelerating the cycle of the ascorbate–glutathione to eliminate excessive reactive oxygen species (i.e. hydrogen peroxide and superoxide anion free radical) (Wu *et al.* 2006b, 2007b, Wu and Zou 2009a). Moreover, AMF-modulated CaM change in trifoliolate orange can upregulate the antioxidant defense system in the whole process of signal transduction, thus, repairing the possible oxidative damage under drought stress conditions (Huang *et al.* 2014). In the study of Zou *et al.* (2015a), a noninvasive microtest technology was firstly used to analyze the net fluxes of root H_2O_2 and Ca^{2+} in trifoliolate orange under drought stress. They observed an influx of root Ca^{2+} and an efflux of root H_2O_2 , and AMF inoculation induced significantly higher net H_2O_2 effluxes and Ca^{2+} influxes in the root meristem zone. Such results from this study showed that AM-induced lower oxidative

burst is related with higher root net H_2O_2 effluxes and Ca^{2+} influxes under drought stress. In AM structures, root AM colonization and arbuscules but not entry points and vesicles have a direct effect on antioxidant defense systems (Wu and Zou 2009a), suggesting that the two morphological structures may accumulate reactive oxygen species (Fester and Hause 2005) and possess *SOD* genes (Corradi *et al.* 2009), thereby partly alleviating oxidative burst in AM plants. Molecular level revealed that the mRNA abundance of four genes encoded in antioxidant enzymes was significantly higher in the *G. mosseae*-colonized trifoliolate orange than in the non-AMF control during drought stress, indicating that transcriptional activation of these responsive genes was promoted by colonization by AMF in citrus plants (Fan and Liu 2011). Based on these results, AM citrus plants kept lower oxidative damage under drought stress, which is related to the enhancement of antioxidant defense system, CaM, net H_2O_2 effluxes and Ca^{2+} influxes, and arbuscules.

On the basis of the analysis of osmotic adjustment in citrus plants such as trifoliolate orange and red tangerine, AMF prominently increased the capacity of osmotic adjustment, which is related to glucose, fructose, sucrose, K^+ , Ca^{2+} , and Mg^{2+} accumulation and without proline accumulation (Wu and Xia 2006, Wu *et al.* 2007a). A lower proline accumulation in AM trifoliolate orange seedlings under drought stress derived from the integration of an inhibition of proline synthesis with an enhancement of proline degradation (Zou *et al.* 2013). A greater osmotic adjustment in AM citrus plants would confer lower tissue osmotic potential and maintenance of turgor potential, thus enhancing tolerance to drought stress.

Another study indicated that colonization by *G. mosseae*, *G. versiforme* and *G. diaphanum* significantly increased the levels of T-GRSP in drought-stressed trifoliolate orange rhizosphere, and this increment was consistent with the change of soil hyphal length (Wu *et al.* 2008). GRSP itself carries water as well as the “super glue” role, which further improved the distribution of water-stable aggregates in > 2 cm, 1–2 cm, and >0.25 cm size fractions, resulting in the enhancement of aggregate stability under drought stress. Moreover, in GRSP fractions, only T-GRSP, but not EE-GRSP, was significantly negatively correlated with leaf and soil water potential (Zou *et al.* 2014). This change of aggregate stability is advantageous for maintaining higher soil porosity and soil water holding capacity (Augé 2004, Smith *et al.* 2010). Once the soil moisture changes, mycorrhizal soils would be able to delay the flow of soil water to the soil pores, so that mycorrhizal citrus plants obtain more water and thus lead to the enhancement of drought tolerance (Augé 2004, Wu *et al.* 2013b). Hence, Zou *et al.* (2014) concluded that T-GRSP had a glue function on aggregate stability, thereby aiding toward prevention of soil water loss for improving soil-plant water relations. Further study will need to clarify the functioning of GRSP on water relations of soil and plants in terms of the fluorescence localization and to evaluate how many GRSP contributes to drought tolerance and water relations.

Mycorrhizas showed a vital role in the absorption of mineral nutrients from the soil to the fungal partner under drought stress or not conditions (Srivastava *et al.* 2002). *G. versiforme*-infected trifoliolate orange seedlings exhibited higher concentration of P, K, and Ca in leaves and higher concentration of P, Ca, and Fe in roots under well-watered and drought stress conditions, respectively (Wu and Zou 2009b). On the other hand, there are higher mycorrhizal contribution of N, P, K, Ca, Fe, Mn, and Zn under drought stress than under well-watered conditions (Table 1). It seems that mycorrhizas conferred a higher effect on mineral nutrients of citrus for plant survival under drought stress. **Salt stress:** As stated by Miransari (2016), AMF inoculation can increase the plant survive under salt stress through phytohormone production, enhancement of chlorophyll and its fluorescence, improvement of water, and maintenance of cell permeability. Studies showed the increase of salt tolerance in citrus plants inoculated with AMF. Wu and Zou (2011) summarized the effects of salt stress on mycorrhizal colonization and found that salt stress obviously decreased or did not affect AM colonization, but the decrease of root AM colonization was more often than unchangeable. In general, hyphal growth process is more sensitive to salinity than spore germination process (Talaat and Shawky 2014). Under salt stress, AMF colonization has significantly shown the positive promotion for citrus growth (Duke *et al.* 1986, Ezz and Nawar 1994, Wu *et al.* 2010b, 2013c; Wu and Zou 2013). Moreover, growth promotion of Carrizo citrange seedlings was more obviously under salt stress than under no-salt stress (Duke *et al.* 1986). The growth promotion was due to the three explanations: (i) Better root system architecture in AM plants to uptake mineral and water from soil to the host partner (Wu *et al.* 2010b); (ii) AM citrus plants would release more H⁺ effluxes in rhizosphere, resulting in more acidified rhizosphere (Wu and Zou 2013), which is important to secondary active transporter of organic and inorganic nutrients, turgor regulation, and in the regulation of cell wall plasticity, as suggested in “Acid-Growth Theory” (Ramos *et al.* 2008); and (iii) AM citrus represented higher levels of K⁺, Ca²⁺, and Mg²⁺ and lower level of Na⁺, thereby maintaining greater ionic balance, which is related with selective absorption but not selective transport of K⁺ over

Na⁺ in trifoliolate orange (Wu *et al.* 2013c).

In addition, inoculated red tangerine seedlings showed higher photosynthesis, stomatal conductance, and transpiration rate under salt stress and no-salt stress conditions, which is connected with the increase of chlorophyll concentration (Wu *et al.* 2010b). Inoculation with *G. mosseae* and *G. versiforme* significantly increased catalase activity and ascorbate, soluble protein, and glutathion contents in trifoliolate orange seedlings, thus enhancing the antioxidant protected systems and protecting the AM plants against damage of salt stress (Wu *et al.* 2010e).

Salinity stress reduced the hydraulic conductivity of roots, leaf water potential, stomatal conductance and not assimilation of CO₂ of mycorrhizal and non-mycorrhizal pineapple sweet orange, Carrizo citrange and sour orange seedlings inoculated with *Glomus intraradices* and salt stress of 150 mM NaCl for a period of 24 days (Hartmond *et al.* 1987). Zarei and Paymaneh (2013) observed that mycorrhizal (treated with *G. etunicatum* and *G. intraradices*) citrus (*Citrus jambhirilush*) exhibited greater tolerance to salt stress (up to 8 ds/m NaCl) than non-mycorrhizal seedlings and the enhanced proline content seems to be one of the mechanisms involved. Besides potted works, a small quantity of field works have been conducted in other plants (e.g., wheat). However, AMF effects on field citrus plants are not known and need to be further studied.

The mechanisms about AMF-enhanced salt tolerance of the host plant have been proposed: enhancing selective absorption K⁺ over Na⁺ (Wu *et al.* 2013c); enhancing antioxidant protected systems (Wu *et al.* 2010e); enhancing nutrient acquisition, such as N, P, Mg, etc. (Evelin *et al.* 2009); molecular changes in *PIP* genes, Na⁺/H⁺ antiporters, and *LsP5CS* (Evelin *et al.* 2009). Further works needs to highlight the expression of the different stressed genes, the activity of the H⁺ pumps, the activation of the stressed signaling pathway, and the allocation of Na⁺, K⁺, and Cl⁻ to cellular vacuole and apoplast (Miransari 2016).

Temperature stress : Studies indicated that inoculation with AMF did not affect the capacity on tolerance of low temperature but notably increased the capacity for tolerance of high temperature (Wu and Zou 2010, Wu 2011). Yang *et al.* (2005) reported that colonization by *G. mosseae*,

Table 1 Mycorrhizal contribution to nutrient concentration in trifoliolate orange seedlings inoculated with and without *Glomus versiforme* under amply water (AW) versus drought stress (DS) conditions

Tissues	Water treatments	Mycorrhizal contribution (%)								
		N	P	K	Ca	Mg	Fe	Cu	Mn	Zn
Leaf	AW	2.4	8.3	7.0	10.5	2.3	5.9	-0.3	-37.3	2.3
	DS	15.1	13.5	9.3	10.9	1.3	16.7	1.1	-7.9	1.3
Root	AW	-1.9	12.4	8.0	19.7	11.9	7.6	3.6	-28.2	11.9
	DS	10.0	23.0	31.7	23.6	15.0	8.8	-12.0	-13.2	15.0

Mycorrhizal contribution (%) = $(E_i - E_{ni})/E_i \times 100$, where E_i and E_{ni} are the values of nutrient elements of trifoliolate orange seedlings infected by AMF and non-AMF. Adapted from Wu and Zou (2009b) with minor modification.

G. versiforme, *Gigaspora margarita* and a mixture of each other markedly increased peroxidase and superoxide dismutase activity and soluble protein and soluble sugar contents in trifoliolate orange seedlings grown in 40°C for 30 days. Moreover, these increases would be dependent on AMF species, exhibiting *G. versiforme* < *G. mosseae* < *Gigaspora margarita* < Mixture. Other studies reported that inoculation with AMF did not alter growth performance, root system architecture, antioxidant enzymatic activity and mineral element contents in trifoliolate orange and red tangerine exposed to 15°C, but under 35°C these variables were notably increased by the AMF colonization (Wu and Zou 2010, Wu 2011). It suggests that AM symbiosis notably enhanced tolerance of citrus plants to high temperature, but the AM-mediated tolerance was absolutely lost under low temperature.

Elevated [CO₂] : Recent studies paid close attention to the relationship between elevated [CO₂] and mycorrhizas in citrus. A previous study indicated that the depressive effect of P on intraradical colonization and vesicle development was counteracted by elevated [CO₂] (Syvertsen and Graham 1999), suggesting that below-ground sink activity/strength in mycorrhizal plants was enhanced by elevated [CO₂] (Morgan *et al.* 1994). Until now, no evidence indicated a conclusive effect on higher sink strength in mycorrhizal than in non-mycorrhizal plants. On the basis of the increase of AM development, under elevated [CO₂] conditions, growth of the inoculated sour orange plants with *G. intraradices* was stimulated (Jifon *et al.* 2002), and thus growth depression of AM citrus seedlings grown at high P supply was mitigated by elevated [CO₂].

Flooding : Citrus plants are often exposed to flooding in a small amount of regions. Once damaged by flooding, root functions are impaired, resulting in wilt and death of leaves and shoots and reducing fruit yield. A 37-day waterlogging markedly restricted root AM colonization but increased the number of entry points and vesicles in *C. junos* seedlings infected by *Diversispora spurca* (Wu *et al.* 2013d). It seems that under soil waterlogging conditions, AM symbiosis would not obtain oxygen from the root aerenchyma of the host plant. However, when a mycorrhizal hyphal network was established between *Paspalum notatum* and *Gigaspora margarita*-infected trifoliolate orange, AM trifoliolate orange seedlings under root-zone waterlogging conditions would get oxygen from the root aerenchyma of *Paspalum notatum*, thus maintaining better growth performance of citrus (Matsumura *et al.* 2008). So, the well hyphal network is vital to tolerate soil waterlogging in citrus plants. In addition, part of AMF species can survive and grow at low O₂, or produce more vesicles to store O₂ (Tuheteru *et al.* 2015). As a result, mycorrhizal *C. junos* seedlings infected by *Diversispora spurca* recorded greater plant height, fresh mass production, root morphology (total length, projected area, surface area, and volume), soluble protein content in roots, and catalase activity in leaves under soil waterlogging conditions (Wu *et al.* 2013d), resulting in the enhancement of waterlogging stress in AM citrus. Flooding of roots zone

of three citrus seedlings (sweet orange, carrizo citrange and sour orange) for 3 weeks did not produce visible symptoms in the shoot but did influence the plant water relations and reduce A CO₂ of all three rootstocks, regardless of AMF or salt stress treatment (Hartmond *et al.* 1987). Enhancement of flooding by mycorrhization may be also due to the accumulation of proline accumulation and the decrease of ethanol. As reported by Tuo *et al.* (2015), AMF peach plants recorded more proline accumulation in leaves, in company with an increase of (Δ¹-pyrroline-5-carboxylate synthase and a decrease of orn-δ-aminotransferase and proline dehydrogenase activity. *Gigaspora margarita*-colonized peach and *Casuarina equisetifolia* plants under flooding condition represented lower ethanol level (Osundina 1998, Ruto *et al.* 2002)

Diseases and insect pests

Many soil fungal pathogens occur in citrus rhizosphere and seriously decrease growth vigor of citrus. In general, AM plants are less susceptible to pathogens but complete resistance is not provided. The responses of AM-pathogen relationship were summarized by Sharma *et al.* (1992) as follows: (i) AMF infection usually protected the host plant from soil-borne fungi (ii) Higher nutrient levels in AM plants would confer the host plant more susceptible to foliar pathogens (iii) There is no definite relationship reported between bacterial infection and mycorrhization (iv) Pre-inoculation with AMF could protect the transplanted crops against nematode infection.

Insect pests: Many positive effects of AMF on reducing disease severity have been reported within different combinations of host plants and fungal pathogens (Naqvi and Naqvi 2004). In soil nematodes, O'Bannon and Nemeč (1979) found that the inoculated *C. limon* with *G. etunicatus* showed higher tolerance to *Radopholus similis*. The infected *C. limon* seedlings by *G. mosseae* represented higher tolerance to *Tylenchulus semipenetrans* (O'Bannon *et al.* 1979). And Smith and Kaplan (1988) also reported the positive effect of *G. intraradices* on tolerance of *Radopholus citrophilus* in *C. limon*.

Diseases: In fungal pathogens, studies showed that inoculation with *G. intraradices* (8% of root colonization) markedly decreased root rot by *Phytophthora* on citrus in the field (Nemeč *et al.* 1996). Similarly, *G. fasciculatum* colonization exhibited a positive effect on tolerance of *Thielaviopsis basicola* in citrus (Davis and Menge 1980). Another study showed that root rot symptom and shoot die back symptoms were lower in *Phytophthora nicotianae* + AMF (*G. etunicatum* and *Acaulospora tuberculata*) *Citrus reticulata* Blanco cv. Shogun grafted on C-35 citrange than in *Phytophthora nicotianae*-AMF (*G. etunicatum* and *Acaulospora tuberculata*) control (Watanarojanaporn *et al.* 2011). Similar result was found in *Phytophthora parasitica*-colonized sweet orange seedlings inoculated with *G. fasciculatus* (Davis and Menge 1980). The decreasing root rot severity in AMF citrus plants caused by mycorrhization may be explained that in AM roots, AMF-colonized

and adjacent uncolonized root regions could restrict the *Phytophthora* development (Cordier *et al.* 1996). It seems that the AMF compete with *Phytophthora* pathogens for a same space and nutrients. If the AMF beforehand occupies the site and absorb the nutrients, the *Phytophthora* pathogens do not infect these sites and nutrients, which are invalid, resulting in the decrease of the *Phytophthora* infection.

In virus, *G. etunicatum* could alleviate the growth depression of *Citrus macrophylla* and Duncan grapefruit infected by tristeza virus T-3 and T-1, but AM infection did not minimize the T-3 and T-1 effects (Nemec and Myhre 1984), suggesting that AM contribution is dependent on citrus genotypes.

Mycorrhizal management in citrus orchards

Wu *et al.* (2013b) have summarized 45 species of AMF involved in citrus rhizosphere, which showed certain distributive characteristics in the soil depth. Soil spore density in rhizosphere of *C. satumn* grafted on trifoliolate orange was the highest in 10–20 cm soil depth and the lowest in >40 cm soil depth. And, spore numbers in 0–40 cm soil depth accounted for >90% in all investigated soil depth (Wu *et al.* 2005b). In different habitats, AM root colonization and soil spore density in adult citrus trees ranked as the terraced fields > slope field > bottomland (Tong *et al.* 2011). Meanwhile, grass cultivation management showed higher AM colonization and spore density than clean tillage management. Wu *et al.* (2006a) reported that in the process of dynamic in years, spore density and mycorrhizal infection in *C. satumn* grafted on trifoliolate orange were the lowest in February and December and highest in June and August. It appears that AM development is usually higher in summer or autumn but lower in winter or spring.

Azcón-Aguilar and Barea (1997) proposed that AM biotechnology can improve horticultural plant production, thereby emphasizing the mycorrhizal management. Here, we simply described the AM management in citrus orchard.

Chemical factors

Mycorrhizal development in the citrus orchard could be affected by many chemical factors. Zeng *et al.* (2004) reported that the growth of AMF and root mycorrhizal formation in *C. sinensis/Poncirus trifoliata* were significantly inhibited by the fungicides benomyl, iprodione and a herbicides glyphosate. Azcón-Aguilar and Barea (1997) proposed the application of metalaxyl or captan for no effect on AM development. Therefore, before inoculated with exogenous AMF, citrus orchard can allow to apply some high affinity binding fungicides.

After watered 0.5% carbamide into citrus orchard in four months, both root mycorrhizal colonization and spore density were notably decreased (Wu *et al.* 2005a). Yang *et al.* (2001) found that mixture of four kinds of weed fermentation broth (1%) with substance could promote the hyphal growth of trifoliolate orange but decreased root mycorrhizal infection.

In three polyamine species, exogenous putrescine but

not spermine and spermidine in 100 mg/l concentration could significantly increase the root AMF colonization on *G. versiforme*-infected trifoliolate orange seedlings (Wu *et al.* 2010c) and *G. mosseae*-infected red tangerine (Wu *et al.* 2010a). After combined with AMF and exogenous putrescine, better AM development in citrus would confer greater mineral element absorption (Wu and Zou 2009c). Therefore, the application of exogenous polyamines especially putrescine would improve the mycorrhizal development of citrus effectively.

Culture substrate

Schmitz *et al.* (2001) inoculated *G. clarum* and *G. etunicatum* in trifoliolate orange seedlings grown in three planting substrates (soil: sand=1:1; soil: sand: corn husks=1:1:1; soil: sand: compost bark gum arabic=1:1:1) and found that mixed substrate of soil, sand and compost bark gum arabic could help the mycorrhizal development and plant growth. Wu *et al.* (2010d) planted *G. mosseae*-infected trifoliolate orange seedlings grown in four substrates and found that the mycorrhizal colonization, vesicles, entry points, and arbuscules were the highest in the mixture of soil and vermiculite (1:1). In short, when planted citrus plants, a substrate benefiting AM development and greater physical-chemical properties would be vital for citriculture.

Soil management system

In citrus orchard, root mycorrhizal infection and soil spore number were reduced significantly by soil tillage management, since soil tillage may destroy soil common mycorrhizal networks (CMNs) established between the citrus plants or between citrus and other plants (Zou *et al.* 2015). However, the AMF richness and diversity in an orange orchard in Brazil were notably higher under organic management than under conventional management (França *et al.* 2007). In general, CMNs exist as large, interconnected networks of fungal hyphae (Barto *et al.* 2012). These CMNs can connect a host plant such as a citrus tree and still remain high connection with multiple host plants, such as same citrus plant, intercropped plants, etc. The CMNs are responsible for substance uptake including nutrients and water and provide a pathway for systemic defense signals delivered to target plants or other animals (Barto *et al.* 2012). Furthermore, re-establishing the well CMNs in citrus orchard would consume lots of carbohydrates of the host plants (Wu *et al.* 2005a, Zhang *et al.* 2015). Zhang *et al.* (2015) confirmed the presence of CMNs between trifoliolate orange and white clover under potted and *Diversispora spurca* conditions. In four treatments of sand culture, straw coverage, fungicide treatment, and no-tillage management, citrus mycorrhizal colonization and soil hyphal length were the highest in sand culture and soil spore number was the highest under no-tillage cultivation (Wang *et al.* 2012). In another study, Wang *et al.* (2016a) further observed that sod culture strongly promoted mycorrhizal colonization in Satsuma mandarin, and natural grass cover stimulated AM fungal propagules. In a potted study, white clover

was planted around trifoliolate orange under mycorrhization, and the results showed that sod culture with white clover stimulated mycorrhizal development and potentially improved soil properties in citrus (Zou *et al.* 2016). So, it's necessary to minimize soil tillage for protecting the integrity of the CMNs in citriculture.

Zeng *et al.* (2005) intercropping bahia grass, white clover, alfalfa, and perennial ryegrass in orchard of *Citrus sinensis/Poncirus trifoliata* trees and found that the soil spore number and root AM colonization were significantly higher in the grassing region of bahia grass and white clover than in the region of clean tillage and other grasses during drought season. Interestingly, inoculation with exotic *G. intraradices*

around Red River orange in field obviously changed the community structure of the indigenous AMF, resulting in the decrease of community diversity of indigenous AMF (Gu *et al.* 2011). Therefore, it is very important to protect indigenous rhizosphere communities of AMF when exotic AMF species were applied in citrus orchards. The effect of all these factors has been further summarized (Table 2).

Future perspectives

Mycorrhizas are vital for the citrus growth and production, because of the less root hairs in roots of citrus. However, citrus rhizosphere often represents a population of low-effective propagules and low levels of indigenous

Table 2 Various roles of AMF in citrus beyond soil fertility and Plant Nutrition

AMF species	Response on plant	Reference
<i>Disease suppression</i>		
<i>Acaulospora tuberculata</i> , <i>Glomus etunicatum</i>	Tiogun and Tangerine produced highest mycorrhizal efficiency index, P- uptake, <i>Phytophthora</i> suppression.	Watanarojanaporn <i>et al.</i> (2011)
<i>Glomus fasciculatus</i>	Suppression in <i>Phytophthora</i> infestation.	Davis <i>et al.</i> (1980)
<i>Glomus mosseae</i>	Significant suppression of root rot of mandarin (<i>Citrus reticulatae</i>) caused by <i>Fusarium oxysporum</i> when co inoculated with <i>B. pumilus</i> .	Chakraborty <i>et al.</i> (2011)
<i>Root system architecture</i>		
<i>G. margarita</i> , <i>G. mosseae</i> <i>G. versiforme</i> , <i>G. caledonium</i>	Formation of lateral roots of high order, colonization of this fungus induced more fine roots and less coarse roots.	Yao <i>et al.</i> (2009)
<i>Glomus occultum</i>	Suppression of root growth of volkamer lemon, less root dry weight and total root length under continuously moist condition (- 0.01MPa) due to higher carbon costs to the plant.	Fidelius <i>et al.</i> (2000)
<i>Glomus</i> species	Stimulation in root growth of volkamer, lemon.	Fidelius <i>et al.</i> (2000)
<i>Abiotic stress tolerance</i>		
<i>G. mosseae</i>	Increased tolerance of citrus (<i>Citrus tangerina</i>) seedlings to soil water deficit through its higher root infection and antioxidant enzymatic activity in plants.	Ni <i>et al.</i> (2013)
<i>Glomus versiforme</i>	Enhance growth and Mg distribution in Newhall seedlings under low Mg concentration of soil.	Xiao <i>et al.</i> (2014)
<i>Glomus intraradices</i> , <i>Glomus mosseae</i>	Improved phosphorous nutrition of <i>Citrus volkameriana</i> .	Haghighatnia <i>et al.</i> (2011)
<i>Flooding tolerance</i>		
<i>Glomus intraradices</i>	Affecting root than hyphal nutrient uptake characterized by reduction in nitrogen and P content in Carrizo citrange and sour orange.	Hartmond <i>et al.</i> (1987)
<i>Salinity tolerance</i>		
<i>Glomus intraradices</i> , <i>G. versiforme</i> , <i>G. etunicatum</i>	EC of 162 ds/m with spore density of 100 spores/10 g soil due to stimulation of sporulation due to salt stress.	Aliasgharzadeh <i>et al.</i> (2001)
<i>Archaeospora</i> , <i>Acaulospora</i> , <i>Glomus</i>	Increased sporulation at soil EC of 40.2 ds/m	Wang <i>et al.</i> (2004)
<i>Rhizophagus irregularis</i> , <i>Funneliformis massaceae</i>	Seedlings of cleopatra mandarin better response due to higher accumulation of P, K, Fe and Cu in index values.	Navarro <i>et al.</i> (2014)
<i>Glomus intraradices</i>	Improved acquisition of P, K, Mg and Zn nutrients in leaves of sour orange and volkamer rootstocks.	Khalil <i>et al.</i> (2011)
<i>Glomus</i> , <i>Gigasopora</i> species	Karna khatta, Troyer citrange performed better due to proline accumulation and higher Ca and Mg in leaves.	Murkute <i>et al.</i> (2006)

AMF species. Therefore, mycorrhizal researches and optimization of mycorrhizal management appear very important. Mycorrhizal contribution to citrus has been outlined in this review as: i. promote plant growth, ii. improve fruit quality, iii. enhance nutrition absorption, iv. enhance tolerance of adversity in drought, salt stress, high temperature, flooding, diseases and insect pests, v. modify root architecture and root hair, vi. improve soil structure by glomalin and hyphae, and vii. increase soil fertility.

In the future, mycorrhizas in citrus need pay close attention some of the aspects including: i. clarify the possible mechanisms involved in nutrient (especially P) absorption by AMs in the molecule level; ii. clarify the signal recognition between AMF and citrus during formation of AMs; iii. analyse physiological and molecular mechanisms about AMF-induced tolerance of abiotic and biotic stresses in citrus, especially aquaporin and ion carrier; iv. identify the functions of GRSP in citrus rhizosphere, such as the contribution to aggregate stability and soil organic carbon pools, as well as the relationship between GRSP release and extraradical hyphae; v. survey diversity of AMF community under different soil managements by small subunit ribosomal RNA under the condition of HiSeq; vi. establish mycorrhization in citrus nurseries for vigour of growth; vii. apply mycorrhizal biotechnology to alleviate the damage of the citrus disease and insect pests.

ACKNOWLEDGEMENT

This work was supported by the Plan in Scientific and Technological Innovation Team of Outstanding Young, Hubei Provincial Department of Education (T201604), the National Natural Science Foundation of China (31372017; 31101513), the Key Project of Chinese Ministry of Education (211107), and the Natural Science Foundation of Hubei Province (2012FFA001).

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