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Full Length Article

Efficiencies of Five Arbuscular Mycorrhizal Fungi in Alleviating Salt Stress of Trifoliate Orange

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ABSTRACT

Arbuscular mycorrhizal fungi (AMF) can enhance plant tolerance to salinity, while effects of dissimilar AMF on salt-stressed plants are unclear. This study was carried out to evaluate the efficiencies of five AMF species viz. *Diversispora spurca* (Preiff, Walker & Bloss) Walker and Schüssler, *Glomus etunicatum* Becker and Gerdemann, *G. mosseae* (Nicol. & Gerde.) Gerdemann and Trappe, *G. versiforme* (Karsten) Berch and *Paraglomus occultum* (Walker) Morton and Redecker on growth, leaf relative water content (RWC), root architecture and sugar content of trifoliate orange [*Poncirus trifoliata* (L.) Raf.] seedlings subject to 100 mM NaCl. In saline soils, root mycorrhizal colonization and numbers of entry points, vesicles and arbuscules were as follows: *G. versiforme* > *D. spurca* > *G. mosseae* > *P. occultum* > *G. etunicatum*. All the fungi except *G. etunicatum* notably enhanced plant height, stem diameter, shoot, root and total dry weights and also partly or markedly improved root architecture, including number of root tip, length, surface area, projected area and volume. *D. spurca*, *G. versiforme*, *G. mosseae* and *P. occultum* abviously increased root sucrose, leaf and root glucose and allocation of sucrose to root, but decreased allocation of glucose to root. Leaf RWC was higher in mycorrhizal (except *G. etunicatum*) than in non-mycorrhizal seedlings. The results of the present study suggest that *G. versiforme* is the best effective mycorrhizal fungus in alleviating salt stress of trifoliate orange and *G. etunicatum* is the lowest effective mycorrhizal fungus.

Key Words: Arbuscular mycorrhiza; *Glomus versiforme*; Root architecture; Salt stress; Sugar; Trifoliate orange

INTRODUCTION

Citrus (*Citrus* spp.) is widely distributed and produced all around the world, including the southern and southwestern regions of China. In citrus cultivation, the desired cultivars usually graft onto rootstocks selected for disease resistance and hardiness. Herein, trifoliate orange [*Poncirus trifoliata* (L.) Raf.], a closed related to *Citrus*, has been used as a rootstock for *Citrus* in China. Trifoliate orange is very sensitive to salt, because relatively low levels of salinity are able to reduce tree vigor and cause leaf damage (Cerda *et al*., 1990). Therefore, enhancing salt tolerance of trifoliate orange is an important task.

Arbuscular mycorrhizal fungi (AMF), the widely distributed soil microorganisms in the Phylum Glomeromycota, can form the arbuscular mycorrhizal (AM) symbiosis with around 80% of plant species (Helgason & Fitter, 2009). Arbuscular mycorrhizas are based on the reciprocal exchange of resources: the fungi provide water and nutrients to host plants in return for plant assimilates (Van der Heijden & Horton, 2009). It is well documented that AMF can enhance plant tolerance to salinity (Nasim, 2010) by induction of antioxidant enzymes (Kohler *et al*., 2009), improving plant nutrient uptake (Asghari *et al*., 2005) and ion balance (Giri *et al*., 2007), facilitating water uptake (Colla *et al*., 2008) and increasing the capacity of osmotic adjustment (Kumar *et al*., 2010). Although the positive effects of AMF on alleviating salt stress have been reported, the beneficial roles are absolutely dependent on fungal behaviour and efficiency. The isolate of *Glomus deserticola* from non-saline soils was a more efficient AM fungus under saline conditions than the autochthonous fungus from a saline soil (Ruiz-Lozano & Azcon, 2000). The AM salt-tolerant species can alleviate plant growth under salinity stress through increasing carbohydrates concentrations and enhancing leaf respiration and transpiration, while the non-resistant AM species mainly improve nutrient (N & P) uptake of host plants (Tian *et al*., 2004; Miransari, 2010). Therefore, selecting an efficient mycorrhizal fungus and evaluating AMF functionality are important for successful utilization of AMF under salinity stress. To date, nothing is known about different efficiencies of AMF in alleviating salt stress of trifoliate orange.

The objective of the present study was to evaluate the symbiotic efficiencies of five AMF in alleviating salt stress on trifoliate orange, in terms of plant growth performance, root architecture and carbohydrates production.

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MATERIALS AND METHODS

Mycorrhizal inocula: The five AMF species used were *Diversispora spurca* (Preiff, Walker & Bloss) Walker and Schüssler [No.: BGC SD03A], *Glomus etunicatum* Becker and Gerdemann [No.: BGC HEB07A], *G. mosseae* (Nicol. & Gerde.) Gerdemann and Trappe [No.: BGC XZ02A], *G. versiforme* (Karsten) Berch [No.: BGC NM04B] and *Paraglomus occultum* (Walker) Morton and Redecker [No.: BGC BJ04B], which were commercially provided by the Institute of Plant Nutrition and Resources, Beijing Academy of Agriculture and Forestry Sciences. Hereinto, *D. spurca* was isolated from the rhizosphere of *Lycopersicon esculentum* in Shouguang, Shandong, *G etunicatum* from the rhizosphere of *Lycopersicon esculentum* in Langfang, Hebei, *G. mosseae* from the rhizosphere of *Incarvillea younghusbandii* in Dangxiong, Sitsang, *G. versiforme* from the rhizosphere of *Astragalus adsurgens* in Ejin Horo Banner, Inner Mongolia Autonomous Region, and *P. occultum* from the rhizosphere of *Prunus persica* in Pinggu, Beijing, respectively. All the fungal species were propagated using the identified spores by pot culture utilizing *Sorghum vulgare* as the host plant for 16 weeks, and the inocula contained the infected roots, spores, extraradical hyphae and growth substrates.

Experimental design: The experiment was arrayed in a randomized block design of six treatments, including *D. spurca*, *G. etunicatum*, *G. mosseae*, *G. versiforme*, *P. occultum* and non-AMF control. Each treatment was replicated three times for a total of 18 pots (three seedlings per pot).

Plant culture, mycorrhizal inoculation and growth conditions: Six germinant trifoliate orange seeds were placed in one plastic pot (17.5 cm upper mouth diameter×13 cm bottom mouth diameter×16.5 cm height) supplied with 2.8 kg of autoclaved (121°C, 0.11 MPa, 1 h) growth substrate (soil/vermiculite/sphagnum, 5/1/1, v/v/v), whose characteristics were pH 6.3, 9.8 g/kg organic matter, and 17.71 mg/kg available phosphorus. The 15 g of mycorrhizal inoculum was placed 5 cm below the germinated seeds at the time of transplantation. The non-AMF control received an equal amount of autoclaved inoculum together with a 2 mL aliquot of a filtrate of mycorrhizal inoculum to provide a general microbial population free of mycorrhizal propagules. The mycorrhizal and non-mycorrhizal pots were arranged in a non-environmentally controlled plastic greenhouse from March 27 to July 4, 2010, where photo flux density is 576~869 μmol/m^2/s, average day/night temperature 24.6°C/16.7°C and relative humidity 70-95%, respectively.

Salinity stress began two months after the acclimation of the seedlings. The soil salinity was developed by 100 mM NaCl solution. The addition of NaCl was gradual, beginning with 25 mM and then increasing in 100 mM per day until reaching the desired 100 mM. All the mycorrhizal and non-mycorrhizal seedlings were irrigated every ten days to maintain the salt effects and the designed concentrations were maintained until the end of the experiment (38 days).

Parameter analysis: Leaf number per plant, stem diameter, and plant height were recorded before the end of the experiment. The shoots and roots were separated, oven-dried for 48 h at 80°C and ground as 0.5 mm powder for soluble sugar analysis.

These complete root systems were scanned using an Epson Perfection V700 Photo Dual Lens System (J221A, Indonesia) and then the acquired root images were analyzed with the WinRHIZO software (Regent Instruments Inc., Quebec, Canada). The parameters of root architecture, including length, projected area, surface area, average diameter, volume and number of tip were recorded. Mycorrhizal colonization was measured through the method of Phillips and Hayman (1970) and quantified using the following formula:

$$\text{AM colonization (\%)} = \frac{\text{root length infected}}{\text{root length observed}} \times 100$$

The entry points, vesicles and arbuscules were counted from the colonized roots at the time of microscopical observation and expressed the number per cm root. The concentrations of sucrose and glucose were determinated using the previous method decreased by Zhang and Zai (2004). Allocation of sugar to root was calculated as $S_{root}/(S_{leaf}+S_{root})$, where S_{leaf} and S_{root} are the amounts of sugar in leaf and root of citrus seedlings, respectively (Wu *et al*., 2010). Leaf relative water content (RWC) was determined by the procedure of Wu and Xia (2006) using the fifth full leaf from the apices of the mycorrhizal and non-mycorrhizal seedlings.

Statistical analysis: The data were statistically analyzed by analysis of variance (ANOVA) with SAS version 8.1. Fisher's protected least significant difference (LSD at $P<0.05$) was used to compare the significant difference among these treatments.

RESULTS AND DISCUSSION

Mycorrhizal development: The present study showed that the trifoliate orange seedlings inoculated with five AMF species exhibited different mycorrhizal developments (Table I). In the five mycorrhizal fungi, root mycorrhizal colonization ranged from 13.1% to 53.9%, arbuscules from 1.5 to 2.9 no/cm root, entry points from 0.6 to 1.9 no/cm root, and vesicles from 0.3 to 0.9 no/cm root (Table I). Generally, mycorrhizal development of the trifoliate orange seedlings was as follows: *G. versiforme* > *D. spurca* > *G. mosseae* > *P. occultum* > *G. etunicatum* > non-AMF. However, previous studies reported the highest root colonization of drought-stressed trifoliate orange or red tangerine (*C. tangerine*) seedlings inoculated with *G. mosseae* among *G. geosporum*, *G. mosseae*, *G. versiforme*, *G. etunicatum* and *G. diaphanum* (Wu *et al*., 2006; 2007). Although a mycorrhizal association is usually nonspecific, mycorrhizal characteristics in interacting with hosts exist

Table I: Mycorrhizal development of trifoliate orange (*Poncirus trifoliata*) seedlings inoculated with or without arbuscular mycorrhizal fungi (AMF) exposed to 100 mM NaCl

Mycorrhizal inoculation	Root colonization (%)	Arbuscules (num./cm root)	Entry points (num./cm root)	Vesicles (num./cm root)
Diversispora spurca	35.3±3.0b	2.3±0.3b	1.5±0.3b	0.7±0.0ab
Glomus etunicatum	13.1±3.3d	1.5±0.4d	0.6±0.1c	0.3±0.1c
Glomus mosseae	27.2±5.7c	2.1±0.1bc	1.3±0.2b	0.6±0.1bc
Glomus versiforme	53.9±2.6a	2.9±0.2a	1.9±0.2a	0.9±0.3a
Paraglomus occultum	16.7±2.6d	1.8±0.2cd	0.8±0.2c	0.5±0.3bc
Non-AMF	0.0±0.0e	0.0±0.0e	0.0±0.0d	0.0±0.0d

Table II: Plant growth of trifoliate orange (*Poncirus trifoliata*) seedlings inoculated with or without arbuscular mycorrhizal fungi (AMF) exposed to 100 mM NaCl

Mycorrhizal inoculation	Plant height (cm)	Stem diameter (cm)	Leaf number per plant	Dry weight (g)			Mycorrhizal dependency (%)
				Shoot	Root	Total	
Diversispora spurca	13.52±1.27b	0.209±0.006b	12.1±2.1a	0.334±0.029b	0.077±0.009b	0.411±0.033b	25.3
Glomus etunicatum	10.48±0.08c	0.163±0.008e	10.9±0.6a	0.227±0.005d	0.043±0.008d	0.270±0.013d	-17.7
Glomus mosseae	13.48±0.66b	0.201±0.002bc	13.6±2.1a	0.343±0.015b	0.078±0.002ab	0.421±0.014b	28.4
Glomus versiforme	15.64±0.20a	0.227±0.007a	13.9±1.2a	0.440±0.033a	0.088±0.005a	0.528±0.033a	61.0
Paraglomus occultum	12.82±0.96b	0.196±0.011c	9.7±1.0a	0.316±0.033b	0.068±0.004b	0.384±0.033b	17.0
Non-AMF	11.18±0.31c	0.183±0.004d	11.4±2.5a	0.272±0.002c	0.056±0.004c	0.328±0.004c	

Table III: Root architecture of trifoliate orange (*Poncirus trifoliata*) seedlings inoculated with or without arbuscular mycorrhizal fungi (AMF) exposed to 100 mM NaCl

Mycorrhizal inoculation	Number of tip	Average diameter (mm)	Length (cm)	Surface area (cm^2)	Projected area (cm^2)	Volume (cm^3)
Diversispora spurca	551.7±17.7a	0.382±0.007c	178.79±8.67a	21.38±0.78ab	6.81±0.25ab	0.204±0.006ab
Glomus etunicatum	218.0±13.2c	0.475±0.047a	91.20±8.25d	12.59±2.74d	4.01±0.87d	0.145±0.048c
Glomus mosseae	273.0±43.1bc	0.443±0.008ab	139.20±6.59b	19.66±1.03bc	6.26±0.33bc	0.224±0.018a
Glomus versiforme	558.2±73.5a	0.391±0.013c	188.13±9.14a	23.02±1.22a	7.33±0.39a	0.225±0.018a
Paraglomus occultum	331.3±29.2b	0.403±0.031bc	142.73±12.68b	18.12±2.11c	5.77±0.67c	0.185±0.033abc
Non-AMF	285.1±27.6bc	0.422±0.026bc	112.15±8.73c	14.79±1.66d	4.71±0.53d	0.158±0.026bc

Table IV: Sugar contents and allocation of sugar to root of trifoliate orange (*Poncirus trifoliata*) seedlings inoculated with or without arbuscular mycorrhizal fungi (AMF) exposed to 100 mM NaCl

Mycorrhizal inoculation	Sucrose (mg/g)		Glucose (mg/g)		Allocation of sugar to root (%)	
	Leaf	Root	Leaf	Root	Sucrose	Glucose
Diversispora spurca	28.43±1.96a	11.50±1.04b	24.02±0.94c	15.51±1.69ab	28.85±3.22bc	39.20±3.57bc
Glomus etunicatum	25.79±0.53ab	6.06±1.00d	14.26±1.48e	13.79±1.61bc	18.94±2.25d	49.14±5.40a
Glomus mosseae	25.79±2.61ab	13.24±0.87a	21.27±1.42d	15.47±1.66ab	34.01±2.92a	42.06±1.61bc
Glomus versiforme	28.45±0.16a	13.75±0.59a	33.60±1.65a	16.85±1.04a	32.58±1.00ab	33.42±2.44d
Paraglomus occultum	23.00±0.88b	13.01±0.12ab	27.37±1.20b	15.83±0.40ab	36.15±0.83a	36.66±0.91cd
Non-AMF	28.84±2.52a	9.76±1.14c	15.57±0.72e	12.39±0.81c	25.33±3.01c	44.29±2.33ab

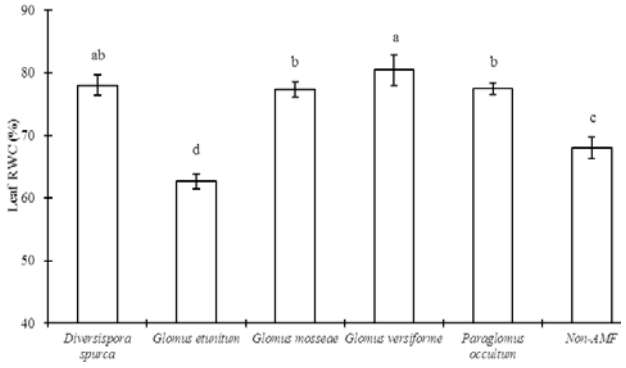
Note: Mean±SD (n=3) with same letter is not significantly different (P<0.05) as determined by LSD

variation within the fungal species (Tian *et al*., 2004). Therefore, mycorrhizal development would absolutely depend on the compatibility of both AMF and host plants.

Plant growth performance: Compared to non-AMF seedlings, inoculation with *D. spurca*, *G. mosseae*, *G. versiforme* and *P. occultum* significantly improved plant height, stem diameter, shoot, root and total dry weights of the seedlings except leaf number per plant under 100 mM NaCl condition (Table II). Based on mycorrhizal dependency, the beneficial effects of mycorrhizas on growth were as follows: *G. versiforme* > *G. mosseae* > *D. spurca* > *P. occultum* > non-AMF > *G. etunicatum*. Generally, mycorrhizal inoculation increased plant growth performance (Carretero *et al*., 2009), which is in accordance with the finding of the present work based on inoculation with *D. spurca*, *G. versiforme*, *G. mosseae* and *P. occultum*. However, *G. etunicatum* did not affect or even significantly reduced the growth performance of the saline seedlings (Table II). It is in agreement with the findings of Dunham *et al*. (2003) in *Typha latifolia*. The growth depressions due to mycorrhization might be the cause of the host-fungus competition for photosynthetically-derived carbon (Buwalda & Goh, 1982).

Root architecture: Root architecture, the spatial configuration of a root system in soil, plays an important role in below-ground resource acquisition, because it determines the ability of a plant to exploit heterogeneous soil resources (Ho *et al*., 2004). In the present study, root architecture of salt-stressed trifoliate orange seedlings differed strongly among mycorrhizal fungal species

Fig. 1: Leaf relative water content (RWC) of trifoliate orange (*Poncirus trifoliata*) seedlings inoculated with or without arbuscular mycorrhizal fungi (AMF) exposed to 100 mM NaCl. Mean±SD (*n*=3) followed by the same letter above the bars is not significantly different at *P*<0.05



(Table III). Compared to non-AMF control, only *D. spurca* and *G. versiforme* significantly increased the number of root tip by 93.5% and 95.8%, respectively but did not affect root average diameter (Table III). The result is in accordance with the findings of Orfanoudakis *et al*. (2010), who observed that *Gigaspora rosea* increased root system branching in *Alnus glutinosa*. All the five mycorrhizal fungi, except *G. etunicatum*, markedly increased root length, root surface area and root projected area (Table III). *D. spurca* and *G. versiforme* exhibited the best effects on the three root parameters, and *G. mosseae* and *P. occultum* better. For root volume, only *G. mosseae* and *G. versiforme* significantly increased the parameter by 41.8% and 42.4%, respectively as compared to the control (Table III). These results are consistent with the previous studies on beach plum (*Prunus maritima* Marsh.) and red tangerine (*Citrus tangerine* Hort. ex Tanaka) (Zai *et al*., 2007; Wu *et al*., 2010a). The alteration of root architecture due to mycorrhization may ascribe to the results of improvement of nutrient uptake, allocation of carbohydrates to root, decrease of root peroxidase, and inducing new protein synthesis (Wu *et al*., 2010b). Therefore, mycorrhizal inoculation is to manipulate root architecture towards a distribution of roots in the soil for optimizing water and nutrient uptake, thus enhancing salt tolerance of host plants, which is dependent on mycorrhizal fungal species.

Sugar status: Mycorrhizal symbionts absolutely depend on host plants to supply carbon for sustaining its development, and thus shift an allocation of carbon to pools for turning over roots and fungal hyphae (Rygiewicz & Andersen, 1994; Finlay, 2008). In the present study, only *P. occultum* significantly reduced leaf sucrose contents of salt-stressed trifoliate orange seedlings by 20.2% and the other fungi did not affect leaf sucrose contents (Table IV). For root sucrose content, leaf glucose content, and root glucose content, all the fungi except *G. etunicatum* markedly increased the three values, and the stressed seedlings inoculated with *G. versiforme* exhibited the highest values. Owing to the mutualism association of AMF and plants, mycorrhizas must obtain 4~20% of the plants's total carbon budget (Bago *et al*., 2003). Therefore, we guessed that mycorrhizal symbiosis could induce the allocation of sucrose (a long-distance transported sugar) from leaf to root, thus resulting in the non-significant changes of leaf sucrose by mycorrhizal inoculation but the significant increases of root sucrose. In the present study, it was clear that the effective four fungal species including *D. spurca*, *G. versiforme*, *G. mosseae* and *P. occultum* obviously elevated the allocation of sucrose to root but decreased the allocation of glucose to root (Table IV). Hexose is the main form of carbon and will transform into trehalose and glycogen for hyphal growth and store (Wu *et al*., 2010c). It seems that more sucrose contents of roots might transform into hexose e.g., glucose, thus resulting in the better mycorrhizal development of the stressed seedlings. Moreover, the improved root architecture by mycorrhization would consume more root carbohydrates to sustain its growth. Therefore, mycorrhizal-induced alteration of carbohydrates was related to mycorrhizal and root developments of stressed trifoliate orange seedlings.

Leaf RWC: Compared to the non-AMF control, *D. spurca*, *G. mosseae*, *G. versiforme* and *P. occultum* signficantly increased RWC of the stressed seedlings by 14.7%, 13.7%, 18.2% and 13.9%, respectively (Fig. 1). However, *G. etunicatum* notably decreased RWC by 7.9%. It seems that AMF species exhibited different capacities to alter RWC of the salinity seedlings. Since RWC represents a useful indicator for water balance of a plant (González & González-Vilar, 2001), all the mycorrhizal seedlings except *G. etunicatum*-colonized seedlings maintained better water balance under a salt stress conditions, and thus recorded greater salt tolerance of the host plant.

CONCLUSION

The present study concludes that AMF can be used to alleviate salt stress of trifoliate orange seedlings, but the alleviated effect of symbiotic fungi is dependent on fungal species. In the present work, *G. versiforme* showed the best efficiency in alleviating salt stress of trifoliate orange and *G. etunicatum* exhibited the lowest efficiency.

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