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Changes of antioxidative enzymes and cell membrane osmosis in tomato colonized by arbuscular mycorrhizae under NaCl stress

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Abstract

Salinity toxicity is a worldwide agricultural and eco-environmental problem. Many literatures show that arbuscular mycorrhizal fungi (AMF) can enhance salt tolerance of many plants and some physiological changes occurred in AM symbiosis under salt stress. However, the role of ROS-scavenging enzymes in AM tomato is still unknown in continuous salt stress. This study investigated the effect of *Glomus mosseae* on tomato growth, cell membrane osmosis and examined the antioxidants (superoxide-dismutase, SOD; catalase, CAT; ascorbate peroxidase, APX; peroxidase, POD) responses in roots of mycorrhizal tomato and control under different NaCl stress for 40 days in potted culture. NaCl solution (0, 0.5 and 1%) was added to organic soil in the irrigation water after 45 days inoculated by AMF (*Glomus mosseae*). (1) AMF inoculation improved tomato growth under salt or saltless condition and reduced cell membrane osmosis, MDA (malonaldehyde) content in salinity. So the salt tolerance of tomato was enhanced by AMF; (2) SOD, APX and POD activity in roots of AM symbiosis were significantly higher than corresponding non-AM plants in salinity or saltless condition. However, CAT activity was transiently induced by AMF and then suppressed to a level similar with non-AM seedlings; (3) higher salinity (1% level) and long stress time suppressed the effect of AMF on SOD, APX, POD and CAT activity; (4) this research suggested that the enhanced salt tolerance in AM symbiosis was mainly related with the elevated SOD, POD and APX activity by AMF which degraded more reactive oxygen species and so alleviated the cell membrane damages under salt stress. Whereas, the elevated SOD, POD and APX activity due to AMF depended on salinity environment.
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Keywords: Arbuscular mycorrhizal fungi; Tomato; Salt stress; Antioxidative enzymes; Cell membrane osmosis

1. Introduction

Extensive areas of the arid and semiarid regions have soils containing concentrations of soluble salts sufficient to adversely affect plant growth. One of the cost-effective strategies for coping with salinity involves growing crops that have an inherent ability to tolerate saline conditions [1]. In recent years, studies indicated that arbuscular mycorrhizal fungi (AMF) can increase plant growth and uptake of nutrients, decrease yield losses of tomato under saline conditions and improve salt tolerance of tomato [2–6]. Root colonization by AMF involves a series of morpho-physiological and biochemical events that are regulated by the interaction of plant and fungus, as well as by environmental factors. The physiological and biochemical mechanisms improving salt tolerance of AM tomato are still unclear, although the improved nutrition acquisition may be one of the reasons [4,7]. Reactive oxygen species (ROS) such as superoxide radical (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radical (OH) [8] and singlet oxygen (O_1^-) [9] generated in plants during the salt stress. These cytotoxic activated oxygen species can seriously disrupt normal metabolism through oxidative damage to lipids [10,12], protein and nucleic acids [10–11]. This lead to change in selective permeability of bio-membranes [13] and thereby membrane leakage and change in activity of enzymes bound to membrane occurred [14].

The induction of ROS-scavenging enzymes, such as SOD, POD, APX and CAT is the most common mechanism for detoxifying ROS synthesized during stress responses [15]. In

Abbreviations: AMF, arbuscular mycorrhizal fungi; SOD, superoxide-dismutase; CAT, catalase; APX, ascorbate peroxidase; POD, peroxidase; ECs, electrical conductivity of substrate

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bean (*Phaseolus vulgaris*) colonized by *Glomus clarum*, SOD and CAT were induced in roots at late stage of the symbiosis development under low P and the activities of SOD and CAT were evaluated [16]. Higher levels of SOD activities were also observed in lettuce (*Lactuca sativa*) roots colonized by *Glomus mosseae* or *Glomus deserticola* under drought stress [17]. Induction of CAT had been observed in nodulated soybean (*Glycine max* Merr.) roots colonized by *G. mosseae* under watered but not drought stress conditions [18]. However, the roles of these enzymes in AM tomato are poorly being understood especially under continuous salt stress condition. In this study, we detected the growth parameters, cell membrane osmosis and the activities of SOD, POD, APX and CAT in roots of AM and non-AM tomato under 0.5, 1% NaCl and normal condition. We evaluated the effects of these enzymes in ROS scavenging on the enhanced salt tolerance by AMF. We also tried to explain the salt tolerance improvement of AM tomato from the other side."

2. Materials and methods

2.1. Plant materials and mycorrhizal fungus inoculums

Seeds of tomato (*Lycopersicon esculentum* cv Zhongzha no. 9) were obtained from Institute of Vegetables and Flowers, CAAS, Beijing, PR China. Mycorrhizal fungus inoculums, consisting of spores, soil, hyphae and infected clove (*Trifolium repens*) root fragment from a stock culture of *Glomus mosseae*, was provided by Hungarian institute of soil research. The inoculated dosage was 10 g of inoculums per pot containing approximately 720 spores.

2.2. Experimental fields

Seeds were sterilized by immersion in 70% alcohol for 5 min, rinsed four times with distilled water, and kept for germination on wet filter paper in Petri dishes at 28 °C. After 3 days, the seeds were planted into polystyrene trays. At the same time, half of the pots (AM plants) were inoculated with 10 g *Glomus mosseae* per pot. Non-AM plants received the same weight of autoclaved inoculums. The inoculums was placed adjacent to each seeding root. Thirty-day-old seedlings, uniform in size, were transplant into 13 cm × 13 cm plastic pots containing 0.88 kg organized soil mixture (organic manure, soil and straw = 1:2:1). The soil mix was collected from greenhouse of Institute of Vegetables and Flowers and sterilized (160 °C, 4 h). Soil properties were pH 7.26, 11.1% organic matter, 150 mg kg^{-1} available phosphorus, 451 mg kg^{-1} available nitrogen, 518 mg kg^{-1} available potassium. The experimental pots were placed in greenhouse with natural light at average temperature 28/20 °C (day/night) from June to October 2005. The photon flux density ranged from 600 to 1200 μmol m^{-2} s^{-2}, relative humidity was between 65 and 95%.

2.3. Experimental design

The experimental design consisted of six treatments crossing two mycorrhizal inoculations levels (non-AMF and *Glomus mosseae*) with three soil salt levels (NaCl solution: 0, 0.5, 1%). Pots were arranged in a completely randomized block design. Six replicates of each treatment were applied totalling 36 pots (two seedlings per pot). From the 45th day after AMF inoculation, plants (salt treatments) were irrigated every 2 or 3 days with 0.5, 1% NaCl water solution. Salt-free treatments were irrigated with tap water (EC = 0.8 dS m^{-1}). Soil EC values reached 0.9, 4.2 and 7.1 dS m^{-1}, respectively in the 0, 0.5 and 1% treatments and then salt solution irrigation was stopped. After NaCl solution irrigated, measurement of SOD, POD, APX and CAT activity were performed every 5–10 days and kept the electrical conductivity in the growth substrate (ECs) value until the 100 days after planting. ECs were regularly monitored with a Model LF539 Conductivity Meter (WTW, Weilheim, Germany). When leaching occurred, the leachate was collected and added back to soil to maintain salinity treatments near target levels.

2.4. Collection and measurement of parameters

Roots were cut in different direction of each pot (containing two seedlings) with borer (2 cm), repeated in all the pots of each treatment.

SOD (EC1.15.1.1) was determined by the method described by Giannopolitis and Ries [19]. POD (EC1.11.1.7) and CAT (EC1.11.1.6) were determined by the method described by Li [20] and Liu [21]. APX (EC 1.11.1.11) was determined using the method described by Amako et al. [22]. MDA detecting was done by referring to Li [20]. The thiobarbituric acid (TBA) was adopted to measure lipid peroxidation in roots. Cell membrane osmosis was showed by leakage value of macromolecules and measured according to Li [20]. AMF colonization was measured 40 days after salt stress [23].

The chemicals used in experiment came from the Sigma company of Amerian.

All data presented were the mean values of six replicates and were analyzed by Duncan's multiple new range test using SAS software. The small letters and capital letters mean significance of difference under $p < 0.05$ and $p < 0.01$ level, respectively.

3. Results

3.1. Effect of AMF on ECs

Fig. 1 showed the changes of ECs after NaCl treatment. Larger change of ECs was observed at 5 and 10 days but there

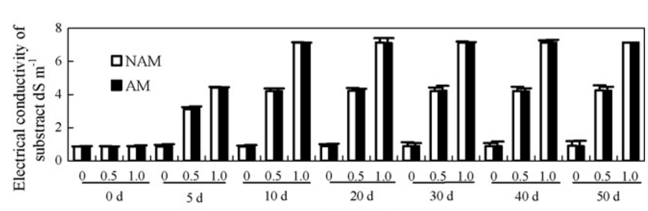

Fig. 1. Effect of AMF on ECs under NaCl stress. Asterisk denotes that AM and non-AM treatments differed significantly under the same salt level, $*p < 0.05$, $**p < 0.01$. In contrast, no asterisk denotes no significant difference. Values are mean ± S.E. ($n = 6$).

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Table 1
Effect of salinity on root colonization

NaCl status (%)	AMF status	Root colonization (%)	
		0 days after salt stress	40 days after salt stress
0	AMF	58.6 aA	60.8 aA
	Non-AMF	0.0 bB	0.0 dD
0.5	AMF	58.4 aA	44.9 bB
	Non-AMF	0.0 bB	0.0 dD
1	AMF	60.2 aA	32.3 cC
	Non-AMF	0.0 bB	0.0 dD

Note: date were analyzed by Duncan's multiple new range test and the different capital and small letters indicate significant differences at $p < 0.01$ and $p < 0.05$ level, respectively.

was no significant difference between AM and non-AM plants. ECs arrived at 4.2 and 7.1 dS m^{-1} in 0.5 and 1% treatment, respectively at 10 days and then we stopped irrigating salt solution. From 20 to 50 days, little change of ECs occurred at the same salt level.

3.2. Effect of salinity on root colonization

According to Table 1, salt concentration significantly changed the root colonization. With the salt concentration increasing, the root colonization reduced. It was also observed that the root colonization reduced after a long salt stress time.

3.3. Effects of AMF on tomato growth under NaCl stress

NaCl stress significantly reduced plant growth (Table 2). However, AM seedlings under salt and saltless conditions were significantly taller and stem diameter, shoot and root dry weight increment were significantly larger than corresponding non-AM seedlings.

Table 2
Effect of AMF on the seedlings growth in tomato under salt stress

NaCl status (%)	AMF status	Increase (cm)		Dry weight (g)	
		Height	Stem diameter	Shoot	Root
0	AMF	4.80 aA	0.115 aA	6.26 aA	1.37 aA
	Non-AMF	3.84 bB	0.096 bB	5.98 bB	1.10 bB
0.5	AMF	2.38 cC	0.086 bB	5.64 cC	0.86 cC
	Non-AMF	2.10 dCD	0.050 cC	5.32 eE	0.67 dD
1	AMF	2.20 cdC	0.052 cC	5.38 deDE	0.42 eE
	Non-AMF	1.80 eD	0.018 dD	5.08 fF	0.28 fF

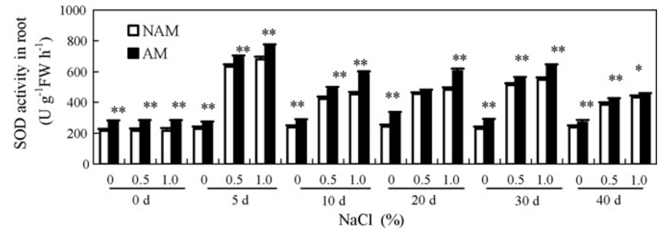

Fig. 2. Effect of AMF on SOD activity in root of tomato under NaCl stress. Rest legend is same as in Fig. 1.

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3.4. Effects of AMF on SOD activity of tomato under NaCl stress

As shown in Fig. 2, AM inoculation significantly induced SOD activity in saltless treatments and declined after 20 days. SOD activity in roots was largely induced in salinity, and then followed a decline. At the same salt level, SOD activity in AM tomato was significantly higher than that in non-AM ones (Duncan's $p < 0.05$) during the salt stress period. At 5 days, SOD activity was higher (14.4, 9.6 and 12.8%) in AM symbiosis than corresponding non-AM plants at 0, 0.5 and 1% level, respectively. Similarly, at 40 days, SOD activity in AM roots was (12.8, 7.8 and 6.7%) higher than non-AM controls, respectively. So, compared with the early stage of salt stress time, the relative effect of AMF on SOD activity reduced after salt stress, especially in 1% level.

3.5. Effects of AMF on APX activity of tomato under NaCl stress

AM plants had higher APX activity than corresponding non-AM ones under saltless condition (Fig. 3). Under salt stress, it was observed that APX activity increased and the value on this parameter in AM plants was always higher than that in non-AM plants, although there was a decline after 20 days. At 20 days, APX activity in AM roots was distinctly higher (67.2, 45.1 and 23.4%) than that in non-AM plants under 0, 0.5 and 1%, respectively. At 40 days, APX activity in AM roots was 68.6, 26 and 12.35% higher than that in non-AM ones at 0, 0.5 and 1%, respectively.

3.6. Effects of AMF on CAT activity of tomato under NaCl stress

Under saltless condition, CAT activity in roots colonized by AMF was significantly induced compared with non-AM ones at

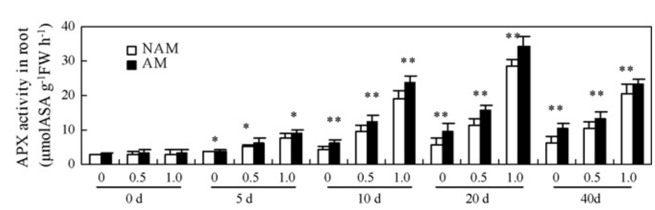

Fig. 3. Effect of AMF on APX activity in root of tomato under NaCl stress. Rest legend is same as in Fig. 1.

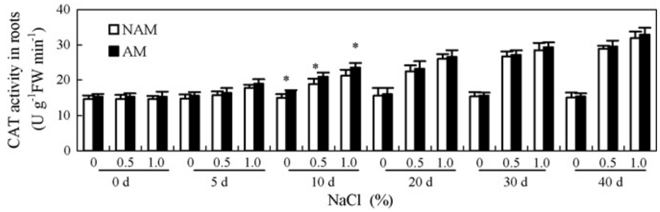

Fig. 4. Effects of AMF on CAT activity in root of tomato under NaCl stress. Rest legend is same as in Fig. 1.

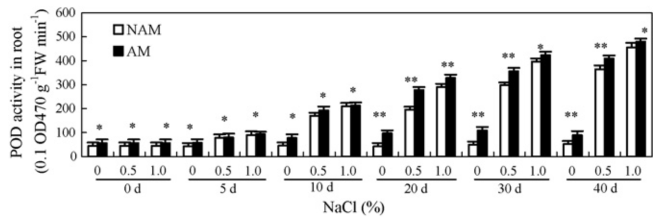

Fig. 5. Effects of AMF on POD activity in root of tomato under NaCl stress. Rest legend is same as in Fig. 1.

10 days and then reduced to the level similar with that in non-AM ones (Fig. 4 Duncan's $p < 0.05$). When subjected to salt stress, CAT activity increased, but AM plants showed significant differences in CAT activity from corresponding non-AM seedlings just at 10 days. So, the effect of AMF on CAT activity was not so obvious in salinity. In contrast, CAT activity induced by salinity was much larger than that induced by AMF.

3.7. Effects of AMF on POD activity of tomato under NaCl stress

From Fig. 5, POD activity in roots significantly induced by AMF under saltless condition and then declined after 30 days. Under salt stress condition, although POD activity in AM seedlings was always significantly higher than corresponding non-AM ones during the experiment time, the effect of AMF on POD activity was reduced. For example, at 40 days, POD activity in AM seedlings was 72.1, 12.2 and 11.8% higher than corresponding non-AM plants at 0, 0.5 and 1% level, respectively.

3.8. Effects of AMF on leakage value of macromolecules of tomato under NaCl stress

According to Fig. 6, AMF inoculation reduced the leakage value of macromolecules compared to non-AM plants. With the

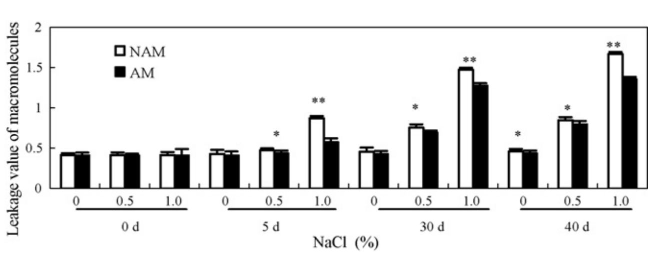

Fig. 6. Effects of AMF on leakage value of macromolecules of tomato under NaCl stress. Rest legend is same as in Fig. 1.

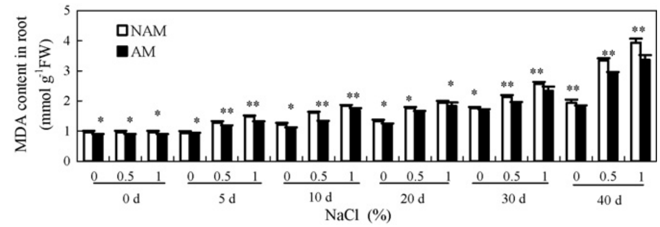

Fig. 7. Effects of AMF on MDA content in root under NaCl stress. Rest legend is same as in Fig. 1.

salt concentration increasing, leakage value of macromolecules in roots significantly increased and the value in AM plants was significantly lower than the corresponding non-AM ones at 1% salt level, whereas no distinct difference was recorded at 0.5% and saltless level at 0 day. At 40 days, AM symbiosis greatly decreased (18.8%) leakage value of macromolecules compared to corresponding non-AM seedlings at 1% level.

3.9. Effects of AMF on MDA content of tomato under NaCl stress

MDA content increased during the experiment and AM colonization reduced MDA accumulation significantly as compared to non-AM plants in all treatments ($p < 0.05$) (Fig. 7). Under salt stress, the difference in MDA content between AM and non-AM plant was more obvious.

4. Discussion

AM are probably the most ancient type of symbiosis between plants and microorganisms. AM symbiosis can frequently increase host resistance to salinity stress although salinity attenuates AMF growth in different degree according to salt level [24]. The mechanism that AMF improve salt resistance remains unclear. Many studies have indicated that the enhanced salt tolerance mainly contributes to mycorrhizal-mediated enhancement of host mineral nutrient uptake, especially of immobile soil nutrients (P, Cu, Zn) [4,6,25]. In recent studies, other potential mechanisms were put forward, such as greater osmotic adjustment in AM plants, reduced oxidative damage [26] and over-expression of aquaporins induced by the AM symbiosis [27]. Little was known on AM-induced changes of antioxidative enzymes (CAT, APX, POD, SOD) in tomato plants under salt stress.

In this work, we adjusted the ECs to 4.2 and 7.1 dS m^{-1} by irrigating 0.5 and 1% NaCl solution, respectively. The results (Fig. 1) indicated that the effect of AMF on ECs was not obvious and ECs in AM and non-AM treatment was nearly consistent at the same salt level. Under this experiment condition, we observed the positive effects of AMF on tomato growth, which was the same with the studies by Al-Karaki et al. [4]. In addition, lower leakage value of macromolecules and MDA content in AM plants were also detected under salt or saltless condition. Leakage value of macromolecules reflects the cell membrane osmosis and the concentration of MDA reflects an end product of lipid peroxidation. The lower leakage value of macromolecules and

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MDA content display lower cell membrane damage or higher salt tolerance. Our results confirmed that AM inoculation enhanced the tomato salt tolerance. MDA content in AM seedlings was also significantly lower than that in non-AM plants. This may be due to the enhanced anti-oxidative enzymes by AMF invasion. When subjected to salinity, although the induction by AMF was suppressed by salinity, it also helped to alleviate the salinity damage to plants. Porcel et al. [28] reported that AM soybean had lower oxidative damage to lipids under drought stress which was similar with our results. So, AM tomato is supposed to have some special mechanisms to alleviate the cell membrane damage. One of the earliest responses of plants to pathogens, wounding, salinity and drought is the accumulation of reactive oxygen species (ROS). The steady-state levels of ROS in plants cells may be determined by the balance between the activities of SOD, POD and CAT [15].

In our experiment, SOD activity was largely induced by AMF or salinity regardless salt or saltless condition (Fig. 2). Despite the symbiotic nature of arbuscular mycorrhizal associations, they represent a massive invasion of plant roots by glomalean fungi. SOD which play a role in detoxification processes by catalyzing the conversion of free $O_2{}^-$ to O_2 and H_2O_2, very often is associated with stress situations including plant/pathogen interactions [29]. There were reports of a general stimulation of constitutive SODs in different AM symbiosis [30–31]. It was also reported that specific SOD isoforms were induced. Pioneer studies on this subject had shown that the AM fungus *G. mosseae* possesses CuZn-SOD activity and that mycorrhizal clover roots exhibit two additional SOD isoforms as compared to non-mycorrhizal roots: a mycCuZn-SOD and a Mn-SOD [32]. Mycorrhizal lettuce plants subjected to drought had increased SOD activity compared to non-mycorrhizal controls [17] and molecular analyses also confirmed this response at the transcriptional level [33]. However, in nodulated soybean roots colonized by *G. mosseae* such induction was not observed [18]. So, the effect of AMF on different plants was not always the same. In addition, under salt stress, we also observed that SOD activity presented a decline, which may be the results of plant adaptation to salt stress. As to the reduced effects of AMF on SOD activity after long salt stress, it might be the result of AM colonization inhibit by stress (Table 1), which had been reported in previous literatures [34–35]. In terms of plant growth maintenance and reduced cell membrane damage in AM plant, our results suggested that the SOD response was associated with AM colonization and the induced SOD activity by AMF may contribute to the enhanced tolerance of AM plant in salinity.

Other important antioxidant enzymes such as APX, POD and CAT were also studied in this paper. Little attention has been paid to the role of these enzymes in AM plants. In tobacco colonized by *G. mosseae*, the transient induction of APX and CAT observed during appressoria formation likely indicates a defense response during the early stages of symbiosis development [36]. Whereas, it was also reported that soybean colonized by *G. intraradices* had lower APX activity under well watered or drought stress condition [28]. Induction of CAT had also been observed in nodulated soybean roots colonized by *G. mosseae* under well watered but not drought stress conditions [18]. However, the data from our experiments showed that higher APX activity was induced gradually by AMF. POD activity in roots was significantly elevated by AM colonization during the experiment, although it presented a decline after 30 days. Whereas, CAT activity was transiently induced at 10 days and then suppressed to the level similar with that in non-AM plants. Accordingly, the above results showed that AM symbiosis really influenced these enzymes in different degree, which may be the results of common response to invasion of fungi. Compared to previous studies, our results were not consistent completely with them. The different results involved in fungal and plant species. When the plants were subjected to salt stress, APX, POD and CAT activity were all largely induced which was consistent with the previous studies in salinity. But the AM plant showed higher value in APX and POD activity than corresponding non-AM plants, it may be a complex interaction of AMF, plant and salinity and need molecular analyses. These enzymes in AM tomato especially under continuous salt stress were little known, but studies on antioxidants in tomato under salt stress had been reported. Shalata and Tal [37] reported that in *Lycopersicon pennellii*, the wild salt tolerant species, CAT activity and glutathione reductase were lower, whereas, SOD, APX were higher than those in the cultivated tomato. Mittova et al. [38] found that compared with cultivated tomato (*Lycopersicon esculentum*), the better protection of *pennellii* root plastids from salt induced oxidative stress was correlated with increased activities of SOD, APX and POD. All our observations suggested that higher APX and POD activity in AM tomato may be associated with the enhanced plant growth and salt tolerance under salt or saltless condition. However, the CAT activity induced by AMF may not be important for the enhanced salt tolerance in AM tomato, although it may play important role in salinity.

Since cell membrane damage was lower in AM symbiosis compared to non-AM plants and SOD, APX and POD activity was contributed to protect plant from salinity injury, the induced SOD, APX and POD activity in AM symbiosis may be an important mechanism to improve salt resistance of AM plants. However, the effect of these enzymes induced by AMF on salt tolerance of AM plants depended on the salt condition, which was important aspect for the AMF application in salinity.

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