Physiological Stress-Resistance Responses of Seedlings of Two Typical Desert Plants Mediated by Arbuscular Mycorrhizal Networks Under Salt Stress

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Abstract

The symbiosis between arbuscular mycorrhizal fungi (AMF) and desert plants has an important influence on their stress resistance. In this study, Glycyrrhiza inflata and Lycium ruthenicum from the lower reaches of the Tarim River were used as research objects, and conspecific (Glycyrrhiza inflata–Glycyrrhiza inflata, GG) and heterospecific (Glycyrrhiza inflata–Lycium ruthenicum, GL) combination systems were established, with 0 mmol·L-1, 150 mmol·L-1, 250 mmol·L-1, and 350 mmol·L-1 NaCl salt treatments applied. A two-compartment device was used, in which donor plants (inoculated with AMF) were subjected to salt stress, while recipient plants (not inoculated with AMF) were not stressed. Plant biomass, chlorophyll content, photosynthetic fluorescence parameters, antioxidant enzyme activities, osmotic regulatory substances, and the contents of the phytohormones abscisic acid (ABA), salicylic acid (SA), and jasmonic acid (JA) were measured. The results showed that: (1) salt stress significantly reduced the mycorrhizal colonization rate of donor plants ($P<0.05$), and the non-photochemical quenching coefficient (NPQ) showed a trend of first increasing and then decreasing; (3) under salt stress, the activities of superoxide dismutase (SOD) and peroxidase (POD), as well as the contents of soluble sugars (SS) and proline (Pro), in recipient plants increased significantly ($P<0.05$). The increases in SOD and POD activities in recipients of the GL group were significantly higher than those in the GG group ($P<0.05$), and their malondialdehyde (MDA) accumulation was also significantly higher than that in the GG group ($P<0.05$); (4) ABA and SA contents in recipients of the GG group increased significantly, while JA decreased significantly; in recipients of the GL group, ABA and JA contents increased significantly, while SA decreased significantly (P

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Abstract: The symbiosis between arbuscular mycorrhizal fungi (AMF) and desert plants has an important influence on plant stress resistance. Taking *Glycyrrhiza inflata* and *Lycium ruthenicum* from the lower reaches of the Tarim River as research objects, conspecific (*G. inflata*–*G. inflata*, GG) and heterospecific (*G. inflata*–*L. ruthenicum*, GL) combination systems were established and subjected to NaCl salt treatments of 0 mmol · L^{-1}, 150 mmol · L^{-1}, 250 mmol · L^{-1}, and 350 mmol · L^{-1}. Using a two-compartment device, donor plants (inoculated with AMF) were placed under salt-stress conditions, while recipient plants (not inoculated with AMF) were not stressed. The experiment measured plant biomass, chlorophyll content, photosynthetic fluorescence parameters, antioxidant enzyme activities, osmotic-regulation substances, and the contents of the plant hormones abscisic acid (ABA), salicylic acid (SA), and jasmonic acid (JA). The results showed that: (1) salt stress significantly reduced the mycorrhizal colonization rate of donor plants ($P < 0.05$); (2) with increasing salt concentration, the chlorophyll content (SPAD value) and maximum photochemical efficiency (Fv/Fm) of both donor and recipient plants decreased significantly ($P < 0.05$), while the non-photochemical quenching coefficient (NPQ) first increased and then decreased; (3) under salt stress, the activities of superoxide dismutase (SOD) and peroxidase (POD), as well as the contents of soluble sugars (SS) and proline (Pro), increased significantly in recipient plants ($P < 0.05$). The increases in SOD and POD activities in GL-group recipients were significantly greater than those in the GG group ($P < 0.05$), and their malondialdehyde (MDA) accumulation was also significantly higher than that in the GG group ($P < 0.05$); (4) in GG-group recipients, ABA and SA contents increased significantly while JA decreased significantly; in GL-group recipients, ABA and JA contents increased significantly while SA decreased significantly ($P < 0.05$). Recipient plants not directly subjected to salt stress exhibited hormonal changes synchronized with those of donor plants, photosynthetic inhibition (declines in SPAD and Fv/Fm), activation of photoprotection (increase in NPQ), and systemic defense responses (enhanced SOD and POD activities and accumulation of Pro and SS). These changes indicate that donor plants transmitted "early-warning" signals to recipient plants through common mycorrhizal networks (CMNs). The GG system mainly protected the photosynthetic apparatus by increasing ABA and SA contents, whereas the GL system activated the antioxidant system through increases in ABA and JA, accompanied by greater MDA accumulation. This regulatory mode reveals the core role of CMNs in plant-to-plant communication and coordinated adaptation to salt stress, providing a theoretical basis for understanding symbiotic mechanisms in desert plants and for ecological restoration.

Keywords: common mycorrhizal network (CMN); desert plants; physiological response; plant hormones

Salt stress is one of the major environmental factors limiting plant growth and yield; it is especially prominent in arid and semi-arid regions and poses a serious threat to the stability of regional ecosystems [1]. The lower reaches of the Tarim River constitute a typical degraded desert ecosystem in arid areas, where high

soil salinity severely restricts the growth of riparian plant species of different life forms [2–5]. To cope with stress, plants establish symbiotic relationships with arbuscular mycorrhizal fungi (AMF), thereby enhancing tolerance to salt stress; this symbiotic mechanism plays a key role in alleviating salt-stress damage [6–9]. Further studies have found that most AMF do not exhibit host specificity. Their extraradical hyphae extend outward through the soil while simultaneously infecting the root systems of different plants; the same plant species can also be colonized by multiple AMF fungi, and extraradical hyphae can fuse with one another, ultimately forming common mycorrhizal networks (CMNs) that improve nutrient efficiency and increase the stability of plant–hyphal systems [10]. Underground CMNs can serve as "information-exchange pipelines" among plant hosts [11–13].

In recent years, studies have shown that CMNs can transmit signal substances produced by plants attacked by herbivores or pathogens (donor plants) to neighboring healthy plants (recipient plants), thereby inducing defense responses in adjacent plants [13–15]. However, most current studies focus on biotic stress; with respect to abiotic stress—especially salt stress—whether and how CMNs mediate "plant–plant" signal transmission remains poorly understood. Plant hormones, such as abscisic acid (ABA), salicylic acid (SA), and jasmonic acid (JA), are important signaling molecules that regulate plant stress resistance [16], and studies have shown that they may participate in CMN-mediated communication processes [17]. Therefore, exploring whether these key hormonal signals are transmitted among plants through CMNs under salt stress is important for understanding plant populations

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···the key to collaborative adaptation to adverse environments.

Glycyrrhiza inflata and *Lycium ruthenicum* are typical mycorrhizal plants in the desert ecosystem of the lower reaches of the Tarim River and have important ecological and economic value [18–24]. Against the background of increasingly severe salt stress, exploring the differences between these two plant species in signal transmission and defense responses through the CMN helps reveal the mechanisms of collaborative adaptation among desert plants. In this study, *G. inflata* was used as the donor plant, while *L. ruthenicum* and *G. inflata* were used respectively as recipient plants. Through a pot experiment, conspecific and heterospecific plant combination systems were established, and three gradient levels of salt concentration were designed, with the aim of investigating the following scientific questions: (1) Under salt stress, can the stress signals of donor plants induce systemic physiological responses in recipient plants that are not

directly stressed through the CMN? (2) Are hormones such as ABA, SA, and JA involved in CMN-mediated salt-stress signal transmission? (3) Are there differences between conspecific and heterospecific plant combinations in the mode of signal transmission through the CMN and in physiological defense strategies? This study aims to reveal the communication and regulatory mechanisms of the CMN in desert plants responding to salt stress, and to provide theoretical support for a deeper understanding of the functions of plant symbiotic networks and ecological restoration in arid regions.

1 Materials and Methods

1.1 Experimental materials

Seeds of *G. inflata* and *L. ruthenicum* and river sand were all collected from riparian areas in the lower reaches of the Tarim River. Full *G. inflata* seeds were selected, and the seed coat was lightly scarified with a file to promote germination; after scarification, the seeds were set aside for use. *L. ruthenicum* seeds were first subjected to pregermination treatment in a 40 °C water bath for 48 h. After pregermination, they were disinfected together with the *G. inflata* seeds using 75% ethanol for 15 min, and then thoroughly rinsed clean with distilled water for later use.

The arbuscular mycorrhizal fungus (AMF) used was *Funneliformis mosseae*, purchased from the Institute of Plant Nutrition and Resources, Beijing Academy of Agriculture and Forestry Sciences; the spore density was approximately 25 spores · g$\widehat{}$-1. During inoculation, 20 g of inoculum was evenly added between the soil layer of the donor chamber and the connection zone in the inoculated treatment groups; in the non-inoculated groups, an equal amount of inoculum sterilized at high temperature was added as the control.

The experimental substrate was prepared by mixing river sand and vermiculite at a volume ratio of 1:1. The river sand was first passed through a 2 mm sieve to remove impurities, then mixed evenly with vermiculite, and sterilized by moist heat at 110 °C and 0.14 MPa for 1 h before use. During the seedling stage, each pot apparatus was irrigated twice per week with distilled water, with 100 mL of water each time, to maintain normal plant growth.

1.2 Experimental design

The experimental apparatus (Fig. 1) consisted of two PVC tee pipes forming a two-chamber system. Stainless-steel mesh pieces with a pore diameter of 20 μm were fixed at both ends of the connecting pipe opening (20 μm pores allowed extraradical hyphae to pass while preventing plant roots from passing through). The left side of the apparatus was the donor chamber, and the right side was the recipient chamber. After assembly, the apparatus was disinfected with 75% ethanol.

Fig. 1 Schematic diagram of the experimental apparatus

Schematic labels: 20 μm mesh; 3 mm air gap; common mycelial network; donor; recipient.

Two donor–recipient combinations were designed: GG (*G. inflata*–*G. inflata*) and GL (*G. inflata*–*L. ruthenicum*). Five treatments were established, with three replicates for each treatment ($n = 3$). Only the donor *G. inflata* was subjected to salt-stress treatment and AMF inoculation. The treatments were as follows: CK was the blank control, with no AMF inoculation and no salt stress; S0 involved AMF inoculation of the donor with no salt stress; S1 involved AMF inoculation of the donor and 150 mmol · L^-1 NaCl stress; S2 involved AMF inoculation of the donor and 250 mmol · L^-1 NaCl stress; and S3 involved AMF inoculation of the donor and 350 mmol · L^-1 NaCl stress. This study considered only the influence of plant-hormone transmission under hyphal connection; therefore, no treatment was designed to examine the effect of salt stress on the tested plants in the absence of AMF. The experimental seeds were first germinated in seedling trays. After emergence, seedlings with consistent growth were selected and transplanted into the donor and recipient chambers of the experimental apparatus, with three plants per chamber and 30 plants in total. The greenhouse conditions for plant growth were: constant temperature of 28 °C, 16 h light and 8 h dark, LED lamps simulating outdoor illumination, light intensity of 500 μmol · m$^{-2 \cdot s}$-1, and indoor air humidity controlled between 30% and 50%. From transplantation, the plants were cultivated for a total of 100 d. Salt stress was applied after 60 d of transplant growth and lasted for 40 d until the end of the experiment. For salt stress, 150 mL of NaCl solution at the prescribed concentration was applied to the donor every 3 d, for a total of 600 mL; for the non-stress treatment, 150 mL of distilled water was added. A tray was placed under the apparatus, and any leached solution was poured back into the apparatus. At the end of the stress experiment, indices were measured and the plants were harvested.

1.3 Measurement indices and experimental methods

1.3.1 Determination of colonization rate

Trypan blue staining method [25]: Fresh fine roots of plants in the treatments were selected, rinsed clean with water, and cut into root segments approximately 1 cm in length. The segments were placed in FAA solution for fixation and storage. After treatments including alkaline clearing, acidification, and staining, slides were prepared and observed under a 40× microscope. The mycorrhizal colonization rate was calculated according to the cross-intersection method, using the following formula:

$$\text{AMF infection rate} = \frac{\text{Number of infected root segments}}{\text{Total number of root segments}} \times 100\%$$

1.3.2 Measurement of biomass

After the plants were washed clean, the leaves, aboveground parts, and belowground parts were separately placed into envelopes, killed at 105 °C for 15 min, and then dried in a constant-temperature drying oven at 80 °C to constant weight for later use. Biomass was then measured with an analytical balance.

1.3.3 Measurement of chlorophyll content and chlorophyll fluorescence parameters

Chlorophyll content was measured with a SPAD chlorophyll meter (TYS-4N; Tuopu Instrument Equipment Co., Ltd., Xiamen, China), selecting the 3rd–5th functional leaves from the top for clamp measurement. Chlorophyll fluorescence parameters were measured using a portable modulated chlorophyll fluorometer (MINI-PAM-II). Before measuring chlorophyll fluorescence, seedlings were dark-adapted for 30 min; subsequently, the 3rd–5th functional leaves from top to bottom were selected to determine the non-photochemical quenching coefficient (NPQ) and maximum photochemical efficiency (Fv/Fm).

1.3.4 Measurement of antioxidant enzyme systems and osmotic-regulating substances

Superoxide dismutase (SOD) activity was determined by the hydroxylamine method; peroxidase (POD) activity was determined by the guaiacol method; malondialdehyde (MDA) content was determined by the thiobarbituric acid method; proline (Pro) content was determined by the sulfosalicylic acid method; and soluble sugar (SS) content was determined by the anthrone colorimetric method. The reagent kits were provided by Suzhou Grace Biotechnology Co., Ltd.

1.3.5 Determination of plant hormones

Determination of plant hormones: abscisic acid (ABA), salicylic acid (SA), and jasmonic acid (JA) were determined using the double-antibody sandwich method. First, a standard curve was established; then the ground sample was added to the enzyme-labeled plate, followed by incubation at 37 °C. The plate was then washed, color development was carried out in the dark, and finally stop solution was added to terminate the reaction. The reagent kits were provided by Keqiao Biotechnology (Jiangsu) Co., Ltd.

1.4 Data analysis

Excel 2018 was used for data organization and processing. SPSS 26.0 statistical software was used for analysis; one-way analysis of variance was performed, and Duncan's method was used for multiple comparisons among different treatments ($P < 0.05$). Results are expressed as mean ± standard error. Figures were prepared using Origin 2018.

2 Results and Analysis

2.1 Effects of CMN under salt stress on AMF infection rates in different plants

As shown in Fig. 2, under arbuscular mycorrhizal fungi (AMF) inoculation, the root infection rates of donor and recipient plants in different combinations (GG, GL) showed a consistent decreasing trend with increasing salt-stress gradient. No AMF infection was detected in the uninoculated control group (CK) throughout the experiment, whereas effective infection was observed in both donor and recipient plants in the GG and GL treatment groups, indicating that a CMN was successfully established between donor and recipient plants. Under normal growth conditions (S0), the infection rates of both donor and recipient plants in the GG group were higher than those in the GL group. However, under salt stress (S3), infection rates in all treatment groups decreased significantly ($P < 0.05$). Further intergroup comparison of the magnitude of decline in infection rate, i.e., the percentage decrease from S0 to S3, showed that the decline in recipient infection rate in the GG group (37.26%) was significantly smaller than that in the GL group (42.10%) ($P < 0.05$). Similarly, the decline in donor infection rate in the GG group (28.30%) was also significantly lower than that in the GL group (31.97%) ($P < 0.05$). These results indicate that salt stress significantly affected mycorrhizal infection rates, and that the decline in recipients in the GL group was significantly greater than that in the GG group, demonstrating significant differences in root infection rates between recipient plants of the two combinations.

Note: Different lowercase letters indicate significant differences among treatments at the 0.05 level ($P < 0.05$); S0 indicates inoculation without salt stress, S1 indicates inoculation with mild salt stress, S2 indicates inoculation with salt stress, and S3 indicates inoculation with severe salt stress; D indicates donor, and R indicates recipient. The same applies below.

Figure 2. Effects of different salt stresses on infection rates

Fig. 2 Effects of different salt stresses on infection rates

2.2 Effects of CMN on Biomass of Different Plants Under Salt Stress

Salt stress significantly inhibited biomass accumulation in both donor and recipient plants (Table 1). Although the leaf dry weight and aboveground and belowground biomass of plants inoculated with AMF were significantly higher than those of the uninoculated control (CK) group ($P < 0.05$), biomass in all treatment groups showed a graded declining trend as NaCl concentration increased. For donor plants, there was no significant difference in the reduction of leaf biomass between the two combinations (GG and GL). However, in terms of total biomass and belowground biomass, the decreases in GL donors (54.55% and 61.90%, respectively) were significantly smaller than those in GG donors

(62.30% and 71.11%, respectively) ($P < 0.05$). In contrast, the decrease in aboveground biomass of GL donors (41.67%) did not differ significantly from that of GG donors (37.50%). For recipient plants, the reduction in total biomass of recipients in the GL combination (53.85%) was significantly lower than that in the GG combination (55.36%) ($P < 0.05$), while reductions in biomass of other plant parts showed no significant differences between groups. These results indicate that donor plants in the conspecific combination responded more sensitively and that recipient biomass was more strongly suppressed, whereas recipients in the heterospecific combination exhibited better salt-adaptation capacity.

2.3 Effects of CMN on Chlorophyll Fluorescence Parameters of Different Plants Under Salt Stress

As shown in Figure 3, with increasing salt-stress intensity, the chlorophyll fluorescence parameters and SPAD values of donor and recipient plants exhibited coordinated changes. In the two plant combinations, the non-photochemical quenching coefficient (NPQ) of both donors and recipients first increased and then decreased, whereas the maximum photochemical efficiency (Fv/Fm) and relative chlorophyll content (SPAD) declined continuously. Specifically, NPQ reached its peak at the S2 level, but under S3, the NPQ values of all treatment groups showed no significant differences from those at S0. Statistical analysis of the decline in each parameter under S3 showed that, for Fv/Fm, the decreases in GG donors (11.11%) and recipients (19.28%) were both significantly smaller than those in GL (19.48% and 21.05%, respectively) ($P < 0.05$). For SPAD, the decreases in GG donors (11.29%) and recipients (4.38%) were likewise significantly lower than those in GL (27.12% and 42.26%, respectively) ($P < 0.05$). Thus, the conspecific combination was less affected under high-salt conditions.

2.4 Effects of CMN on Antioxidant Enzymes of Different Plants Under Salt Stress

As shown in Figure 4, with increasing salt-stress concentration, SOD and POD activities in donor and recipient plants of all treatments increased significantly, and MDA content also gradually increased; all were significantly higher than CK. AMF inoculation significantly enhanced SOD and POD activities ($P < 0.05$). Under AMF inoculation, for SOD activity, the increases in GG donors and recipients (151% and 157.84%, respectively) were both significantly greater than those in GL (109.79% and 89.76%, respectively) ($P < 0.05$). For POD activity, the increase in GG donors (66.63%) was significantly smaller than that in GL donors (74.25%), and the increase in GG recipients (42.85%) was significantly smaller than that in GL recipients (60.53%) ($P < 0.05$). For MDA content, the increases in GG donors and recipients (102.49% and 134.73%, respectively) were both significantly lower than those in GL (179.57% and 205.92%, respectively) ($P < 0.05$). These results indicate that the antioxidant enzyme system of recipient plants was successfully activated in response to salt stress. Overall, the

conspecific combination induced a stronger increase in SOD activity under salt stress, while its degree of membrane lipid peroxidation (increase in MDA) was significantly lower than that of the heterospecific combination. This suggests that conspecific plant combinations can initiate a more effective coordinated antioxidant defense mechanism.

2.5 Effects of CMN on Osmoregulatory Substances of Different Plants Under Salt Stress

As shown in Figure 5, with increasing salt-stress concentration, the donors in each treatment—

Table 1 Effects of CMN on biomass of different plants under salt stress

Tab. 1 Effects of CMN on biomass in different plants under salt stress /mg

Treatment	Plant combination	Donor leaf dry weight	Donor aboveground dry weight	Donor belowground dry weight	Donor total biomass	Recipient leaf dry weight	Recipient aboveground dry weight	Recipient belowground dry weight	Recipient total biomass
CK	GG	65.83$±0.39c	64.55±4.83d	193.13±14.43c	257.68±11.61d	66.84±1.38c	65.18±5.56b	198.80±10.46	

Note: Different lowercase letters in the same column indicate significant differences among different stress treatments within the same combination at the 0.05 level ($P < 0.05$); S0 indicates inoculation without stress, S1 indicates inoculation under mild salt stress, S2 indicates inoculation under salt stress, and S3 indicates inoculation under severe salt stress; GG denotes (*Glycyrrhiza inflata*-*Glycyrrhiza inflata*), and GL denotes (*Glycyrrhiza inflata*-*Lycium ruthenicum*).

Fig. 3 Effects of CMN on photosynthesis in different plants under salt stress

The contents of soluble sugar (SS) and proline (Pro) in both donor and receiver plants increased significantly. Under AMF inoculation, the increases in SS content in the donor and receiver plants of the GG group—206.20% and 282.53%, respectively—were both significantly greater than those in the GL group—45.86% and 44.54%, respectively ($P < 0.05$). For Pro content, the increases in the donor and receiver plants of the GG group—262.97% and 240.74%, respectively—were likewise significantly greater than those in the GL group—18.98% and 31.95%, respectively ($P < 0.05$). Thus, in the conspecific combination, the ability of donor and receiver plants to accumulate osmotic regulatory substances (SS and Pro) was significantly stronger than that in the heterospecific combination.

2.6 Effects of CMN on Hormones in Different Plants Under Salt Stress

As shown in Fig. 6, salt stress induced synchronized changes in hormone contents in receiver plants through CMN. As salt concentration increased, the ABA contents of both donor and receiver plants in the two combinations increased consistently and significantly ($P < 0.05$). Under the inoculation treatment, the ABA content ranged from 19.45-

Fig. 4 Effects of CMN on antioxidant enzymes in different plants under salt stress

Panels (a) and (b): superoxide dismutase (SOD) activity / $(\mathrm{U} \cdot \mathrm{g}^{-1}$ FW).
Panels (c) and (d): peroxidase (POD) activity / $(\mathrm{U} \cdot \mathrm{g}^{-1}$ FW).
Panels (e) and (f): malondialdehyde (MDA) content / $(\mathrm{mmol} \cdot \mathrm{g}^{-1}$ FW).
The x-axis in all panels is "Different treatment groups" $(\mathrm{CK}, \mathrm{S0}, \mathrm{S1}, \mathrm{S2}, \mathrm{S3}; \mathrm{D}, \mathrm{R})$.
Legends indicate *Glycyrrhiza inflata* and *Glycyrrhiza inflata* in panels (a), (c), and (e), and *Glycyrrhiza inflata* and *Lycium ruthenicum* in panels (b), (d), and (f).

31.6 $\mathrm{ng} \cdot \mathrm{g}^{-1}$. The increases in ABA content in the recipient plants of the GG and GL combinations were 36.97% and 35.33%, respectively. Changes in JA and SA showed differences among combinations. In the GG combination, the SA content of recipient plants increased significantly while JA decreased; conversely, in the GL combination, the JA content of recipient plants increased significantly, with an increase of 64.70%, whereas SA decreased, with a decrease of 19.52% ($P < 0.05$). Thus, under increasing salt concentrations, the changes in ABA, SA, and JA contents in donor and recipient plants were consistent, while the changes in SA and JA contents differed between conspecific and heterospecific plant combinations.

3 Discussion

3.1 CMN Mediated the Transmission of Salt-Stress Signals

This study found that recipient plants not directly subjected to salt stress exhibited, through CMN, physiological and hormonal changes synchronized with those of donor plants.

Fig. 5. Effects of CMN on osmoregulatory substances in different plants under salt stress

Panel labels and axes: (a, b) proline content, Pro ($\mu\mathrm{g} \cdot \mathrm{g}^{-1}$ FW); (c, d) soluble sugar content, SS ($\mathrm{mg} \cdot \mathrm{g}^{-1}$ FW). The treatment groups are CK, S0, S1, S2, and S3, with D and R shown within each group. Legends: *Glycyrrhiza inflata* and *Glycyrrhiza inflata* in (a, c); *Glycyrrhiza inflata* and *Lycium ruthenicum* in (b, d). The x-axis is "different treatment groups."

response. Specifically, the photosynthetic parameters ($F_\mathrm{v}/F_\mathrm{m}$ and SPAD) of the receiver plants were inhibited, while their photoprotective capacity (NPQ), antioxidant system (SOD, POD), and osmotic adjustment capacity (Pro, SS)

were activated (Figs. 3–5). Similar conclusions have been obtained in previous studies

25–26

. This series of systematic and directionally consistent changes strongly indicates that, after sensing salt stress, the donor plants transmitted some form of "early-warning" signal to the receiver plants through the CMN, thereby initiating defensive preparation in advance. This provides new support for CMN-mediated signal transmission between plants and reveals a CMN-mediated systemic stress-resistance response under salt stress, an abiotic stress condition.

3.2 Biomass changes and plant salt-resistance strategies

This study further revealed the decisive role of plant combination type—conspecific or heterospecific—in CMN signal transmission. Although ABA increased significantly in the receivers of all combinations, indicating its universality in CMNs as a core stress-signaling molecule

27–28

, the changes in SA and JA showed distinct combination specificity (Fig. 6).

In the conspecific combination (GG), the receiver plants showed a coordinated increase in ABA and SA, together with a decrease in JA. This signaling pattern is generally associated with enhanced tolerance to abiotic stress

1, 29

. The corresponding physiological performance of this combination was that damage to the photosynthetic system was relatively slight (small decreases in F_v/F_m and SPAD), the accumulation of osmotic adjustment substances (SS, Pro) was more pronounced, and the degree of membrane lipid peroxidation (MDA) was lower. This indicates that the GG combination may mainly coordinate ABA through the SA pathway, focusing on protecting photosynthetic structures and maintaining osmotic balance

30–32

, and represents a "conservative" defensive strategy.

By contrast, in the heterospecific combination (GL), the receiver plants showed a coordinated increase in ABA and JA, together with a decrease in SA. JA is usually more closely associated with rapid defensive responses to biotic stress, and its activation may be accompanied by burst-like production of reactive oxygen species (ROS)

33–35

. This is consistent with the present study: although the receivers in the GL combination initiated a stronger increase in antioxidant enzyme activities (SOD,

POD), their MDA accumulation was significantly higher than that in the GG combination. This indicates that, in the GL combination, the JA signal transmitted through the CMN may have induced a more powerful but more "costly" defense mode—while activating a strong antioxidant system, it may also have triggered more severe oxidative damage—

Figure 6. Effects of CMN on different plant hormones under salt stress

Visible panel labels and axes:

- **(a)** Legend: *Glycyrrhiza inflata*; *Glycyrrhiza inflata*. Y-axis: ABA content (ABA)/(ng · g^{-1} FW). X-axis: Different treatment groups.
- **(b)** Legend: *Glycyrrhiza inflata*; *Lycium ruthenicum*. Y-axis: ABA content (ABA)/(ng · g^{-1} FW). X-axis: Different treatment groups.
- **(c)** Legend: *Glycyrrhiza inflata*; *Glycyrrhiza inflata*. Y-axis: jasmonic acid content (JA)/(ng · g^{-1} FW). X-axis: Different treatment groups.
- **(d)** Legend: *Glycyrrhiza inflata*; *Lycium ruthenicum*. Y-axis: jasmonic acid content (JA)/(ng · g^{-1} FW). X-axis: Different treatment groups.
- **(e)** Legend: *Glycyrrhiza inflata*; *Glycyrrhiza inflata*. Y-axis: salicylic acid content (SA)/(ng · g^{-1} FW). X-axis: Different treatment groups.
- **(f)** Legend: *Glycyrrhiza inflata*; *Lycium ruthenicum*. Y-axis: salicylic acid content (SA)/(ng · g^{-1} FW). X-axis: Different treatment groups.

damage. This phenomenon may be because the activation rate, spatial distribution, and capacity ceiling of the antioxidant system may all be unable to match the salt-stress-induced "explosive and sustained generation of ROS leading to ROS imbalance" [^36]. This represents a "radical" defense strategy.

3.3 Ecological Significance and Cost Trade-offs of Different Defense Strategies

Plant interpretation of defense signals is highly dependent on the signal type, its own genetic background, and the type of environmental stress[^37]. The differences in defense strategies between the GG and GL combinations indicate that CMN-mediated plant communication is not a homogeneous process, but is profoundly influenced by plant relatedness. Plants of the same species may exchange more "precise" and "efficient" signals through CMNs, thereby coordinating group defense responses at lower cost; this is consistent with the manifestation of "kin selection" theory in the plant kingdom[^38]. By contrast, hetero-

Among different plant species, although CMN likewise enabled signal transmission, the content of the signals or the way in which receptors interpreted them may have led to a mismatch in defense responses, thereby incurring a higher cost of oxidative damage. This difference further confirms that different strategies of material transfer in different plant systems may allow certain plants to gain a stronger survival and competitive advantage within mycorrhizal symbioses,

thereby intensifying intra- or interspecific competition among plants [39–40].

3.4 Response Patterns Under Gradients of Salt-Stress Intensity

The results of this study also show that plant physiological responses changed markedly along the gradient of increasing salt concentration (Fig. 3). Under mild to moderate stress ($S1 \sim S2$), the increase in NPQ and the activation of antioxidant/osmoregulatory systems indicate that plants possessed effective compensatory and adaptive capacity [41–43]. However, under severe stress ($S3$), almost all physiological parameters deteriorated significantly, and NPQ decreased, indicating the collapse of photoprotective mechanisms, while the positive effect of CMN also tended to weaken. This suggests that interspecific interactions and network structure have important effects on system stability; when these interactions or network structures are disrupted, the system may undergo abrupt changes, leading to loss of function [44].

4 Conclusion

(1) CMN can transmit salt-stress signals and induce systemic physiological responses in plants. Unstressed receiver plants received stress signals from donor plants through CMN and showed photosynthetic inhibition synchronous with the donor plants (decreases in SPAD and F_v/F_m), activation of photoprotection (increased NPQ), and enhancement of antioxidant enzyme systems (SOD, POD) and osmoregulatory substances (Pro, SS).

(2) ABA, SA, and JA are key hormones in CMN-mediated signal transmission. ABA increased significantly in all combinations. Changes in SA and JA, however, exhibited combination specificity: in the GG combination, SA increased and JA decreased, whereas in the GL combination, JA increased and SA decreased.

(3) Conspecific and heterospecific plant combinations adopt different defense strategies through CMN. In the GG combination, ABA and SA act synergistically, with an emphasis on protecting the photosynthetic apparatus and osmotic regulation, representing a "conservative" defense; in the GL combination, ABA and JA act synergistically, strongly activating the antioxidant system but accompanied by more severe membrane damage, representing an "aggressive" defense.

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Physiological responses of seedlings of two typical desert plants under salt stress mediated by arbuscular mycorrhizal networks

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Abstract: Arbuscular mycorrhizal fungi (AMF) enhance the stress resistance of desert plants through symbiosis. This study focused on *Glycyrrhiza inflata* and *Lycium ruthenicum*, two typical desert plant species from the lower reaches of the Tarim River, and established conspecific (GG) and heterospecific (GL) plant combinations. The plants were treated with NaCl at concentrations of 0, 150, 250, and 350 mmol·L^{-1}. A two-chamber device was used, with donor plants (inoculated with AMF) subjected to salt stress and receptor plants (not inoculated with AMF) kept under nonstress conditions. The experiment measured plant biomass; chlorophyll content; photosynthetic fluorescence parameters; antioxidant enzyme activity; osmotic regulators; and the levels of plant hormones such as abscisic acid (ABA), salicylic acid (SA), and jasmonic acid (JA). The results were as follows: (1) Salt stress significantly reduced the mycorrhizal infection rate in donor plants ($P < 0.05$). (2) As salt concentration increased, both donor and receptor plants showed a significant reduction in chlorophyll content (SPAD values) and maximum photochemical efficiency (F_v/F_m), and an initial increase followed by a decrease in nonphotochemical quenching (NPQ). (3) Under salt stress, receptor plants showed a significant increase in superoxide dismutase (SOD) and peroxidase (POD) activity as well as soluble sugar (SS) and proline concentrations ($P < 0.05$). The increase in SOD and POD activity in receptor plants was significantly higher in the GL group than in the GG group ($P < 0.05$), and malondialdehyde (MDA) accumulation was also higher ($P < 0.05$). (4) In the GG group, the receptor plants showed significantly increased ABA and SA levels and significantly decreased JA levels, whereas in the

GL group, the receptor plants showed significantly increased ABA and JA levels and significantly decreased SA levels ($P < 0.05$). The receptor plants, which were not under direct salt stress, exhibited synchronized hormonal changes, photosynthetic inhibition (decreases in SPAD and F_v/F_m), photoprotective activation (increase in NPQ), and systemic defense responses (increase in SOD and POD activity and proline and SS accumulation). These changes suggest that donor plants transmit "warning" signals to receptor plants via the common mycorrhizal network (CMN). In the GG combination, ABA and SA levels were primarily enhanced, protecting the photosynthetic apparatus. In the GL combination, ABA and JA levels were enhanced, activating the antioxidant system but with higher MDA accumulation. This regulatory pattern highlights the central role of CMN in interplant communication and collaborative adaptation to salt stress, providing important theoretical insights into symbiotic mechanisms in desert plants and ecological restoration.

Keywords: common mycorrhizal network; desert plants; physiological responses; plant hormones

Note: Figure translations are in progress. See original paper for figures.