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Effects of methyl jasmonate on growth, antioxidants, and carbon and nitrogen metabolism of *Glycyrrhiza uralensis* under salt stress

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Abstract

We investigated the effects of 0.025 or 0.05 mM methyl jasmonate (MeJA) on the growth characteristics, antioxidant enzyme activities, non-enzymatic antioxidant content, and carbon and nitrogen metabolizing enzyme activities in *Glycyrrhiza uralensis* exposed to 100 mM NaCl. Results showed that salt stress decreased the stem length and lateral root number and the treatment with 0.025 or 0.05 mM MeJA increased the root length of salt-stressed *G. uralensis* seedlings but decreased root diameter, stem length, and stem diameter. MeJA application modulated oxidative stress in salt-stressed *G. uralensis* seedlings. It decreased the catalase activity but enhanced peroxidase activity and ascorbate content. However, treatment with 0.05 mM MeJA significantly increased the malondialdehyde content of salt-stressed seedlings. Salt stress inhibited carbon and nitrogen metabolism. The application of MeJA enhanced the activities of sucrose synthase, and sucrose phosphate synthase, and nitrate reductase in salt-stressed seedlings.

Additional key words: ascorbate, catalase, H_2O_2, malondialdehyde, nitrate reductase, peroxidase, sucrose synthase, superoxide dismutase.

Introduction

Glycyrrhiza uralensis Fisch. is a member of an ancient legume family native to Asia. The genus *Glycyrrhiza* comprises 18 wild and cultivated species. The Chinese licorice (*G. uralensis*) is widely used as a herbal medicine (Pan *et al*. 2006) and its main active compounds exhibit anticancer, antiviral, anti-inflammatory, and immuno-regulative properties (Schrofelbauer *et al*. 2009).

Salinity is one of the most severe problems of agriculture worldwide, especially in arid and semi-arid regions. High salt concentrations can impair growth and physiological activities of plants by inducing osmotic stress, ionic stress, or a combination of these stresses (Zhang *et al*. 2008, Slama *et al*. 2015). Wild *G. uralensis* possesses the excellent resistance to cold, heat, drought, and salinity. Nevertheless, high salt concentration remains an important factor that affects the growth and quality of cultivated *G. uralensis*. Pan *et al*. (2006) stated that the growth and metabolism of *G. uralensis* are negatively affected by 1.5 % (m/v) NaCl and some of physiological and biochemical indexes are abnormal under 2 % NaCl stress. Yang *et al*. (2006) found that the maximum NaCl concentration that *G. uralensis* can tolerate ranges from 100 to 200 mM.

The production of reactive oxygen species (ROS) is one of the main responses of plants to salt stress (Eraslan *et al*. 2007). Excessive amounts of ROS, such as hydrogen peroxide and superoxide radicals, can first enhance membrane lipid peroxidation and damage of chloroplasts,

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Abbreviations: ABA - abscisic acid; AsA - ascorbic acid; CAT - catalase; GS - glutamine synthetase; MDA - malondialdehyde; MeJA - methyl jasmonate; NR - nitrate reductase; $O_2^{\cdot-}$ - superoxide anion; POD - peroxidase; PR - pathogenesis-related; ROS - reactive oxygen species; SOD - superoxide dismutase; SPS - sucrose phosphate synthase; SS - sucrose synthase.
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then inhibit photochemical reactions and reduce photosynthesis (Gunes 2007). Abdelhamid *et al*. (2015) observed that salinity induces oxidative stress in *Phaseolus vulgaris* plants by promoting ROS production. Wutipraditkul *et al*. (2015) demonstrated that salt stress causes oxidative stress in rice seedlings by increasing H_2O_2 content. Pan *et al*. (2006) found that salt stress stimulates oxidative stress in *G. uralensis* seedlings by elevating lipid peroxidation. Salt stress also changes carbon and nitrogen metabolism in plants. Salt stress inhibits carbon metabolism by affecting photosynthesis, consequently decreasing the energy available for biomass production. The regulation of nitrogen metabolism is crucial for salt tolerance, and the highly complex interaction between salinity and nitrogen nutrition affects almost all plant processes. Wang *et al*. (2012) showed that salt stress negligibly influences the accumulation of ammonium nitrogen in young rice leaves and drastically stimulates ammonium nitrogen accumulation in old rice leaves.

Methyl jasmonate (MeJA) is an important phyto-hormone that participates in diverse processes, such as seed germination, root growth, gravitropism, trichome formation, embryonic development, seedling develop-ment, tuber formation, leaf movement, fruit ripening, and leaf senescence (Wasternack and Hause 2002, Wasternack *et al*. 2014, Gumerova *et al*. 2015). Exogenous MeJA may be involved in the plant response to salinity and water stress (Kang *et al*. 2005). MeJA triggers the reprogramming of gene expression, which allows plant cells to adapt to insect-driven wounding, pathogen attack, and environmental stresses, including drought, low temperature, and salinity (Wolucka and Goossens 2005). The application of MeJA to non-stressed and stressed *Artemisia annua* and strawberry plants enhances antioxidant enzyme activities, including those of catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD), thus improving the ROS scavenging mechanism of the treated plants (Tariq *et al*. 2011, Faghih *et al*. 2017). MeJA decreases ion concentration and ROS content and increases antioxidant enzyme activities to alleviate salt stress in *Robinia pseudoacacia* (Jiang *et al*. 2016). In salinity-stressed rice, the application of MeJA modifies the content of abscisic acid (ABA) and diminishes the inhibitory effect of salt stress on photosynthetic rate (Kang *et al*. 2005, Walia *et al*. 2006). Ji *et al*. (2009) found that MeJA treatment counteracts the negative effects of salt stress on the growth, chlorophyll content, leaf photosynthetic rate, leaf transpiration rate, and proline content of soybean plants grown in a hydroponic medium. MeJA induces the expression of pathogenesis-related proteins (PR), such as PR-1 and PR-10, and salt-stress responsive protein in the roots of rice plants to combat stress (Moons *et al*. 1997). Furthermore, MeJA can affect the whole-plant resource allocation of nitrogen- and carbon-containing substrates under stress (Gómez *et al*. 2010). These studies clearly demonstrated that exogenous MeJA can effectively alleviate the detrimental effects of salt stress on plants. This effect and its underlying mechanism vary across plant species. However, the application of MeJA on *G. uralensis* seedlings under salt stress has not been reported. The present work was conducted to study the effects of MeJA on the growth, antioxidant system, and carbon and nitrogen metabolism of salt-stressed *G. uralensis* seedlings.

Materials and methods

Seed germination: *Glycyrrhiza uralensis* Fisch. seeds were obtained from wild plants in the Ningxia Hui Autonomous Region, China, in August 2015. The seeds were steeped with 85 % (m/v) H_2SO_4 for 2.5 h, then surface sterilized with 0.1 % (v/v) H_2O_2 for 10 min, rinsed three-times in distilled water, and imbibed in distilled water at 4 °C for 12 h. Then, 50 seeds were sown in Petri dishes (95 × 15 mm) with two layers of *Whatman No. 2* filter paper (*Runyan Technology*, Yin chuan, P.R. China). Treatments included application of 0.025 or 0.05 mM MeJA in combination with 100 mM NaCl and control (CK) with distilled water alone. MeJA was dissolved in a small amount of *Tween 20* and purchased as a 95 % (m/v) aqueous solution. Germination experiments were carried out in an incubator maintained at day/night temperatures of 28/20 °C in the dark. We considered germination to have occurred when the radicle had emerged by at least 1.0 mm. The number of germinated seeds was recorded every day. After growing for 10 d, length of stems and roots, diameter of main stems and main roots were recorded. Each treatment was replicated four times, the whole experiment was repeated twice.

Antioxidants and lipid peroxidation: Fresh shoot and root samples (0.5 g) were homogenized at 4°C in 8 cm^3 of extraction buffer [50 mM phosphate buffer (pH 7.0) containing 1 mM ascorbic acid (AsA), 1 mM dithiothreitol (DTT), 1 mM glutathione (GSH), and 1 mM $MgCl_2$] with mortar and pestle. The homogenate was then centrifuged at 4 000 *g* for 20 min and was used for determination of catalase (CAT) and peroxidase (POD) activities and malondialdehyde (MDA) and ascorbate (AsA) content.

The CAT activity was assayed, according to Sohn *et al*. (2005) with minor modifications. The CAT reaction solution comprised 50 mM phosphate buffer (pH 7.8), 100 mM H_2O_2, and 0.1 cm^3 of enzyme extract. Changes in the absorbance of the reaction solution at 240 nm were recorded for 5 min.

The POD activity was assayed according to Pan *et al*. (2006) with minor modifications. The enzyme extract (0.2

cm^3) was mixed with 2.7 cm^3 of 50 mM phosphate buffer (pH 7.8), 0.1 cm^3 of 50 mM of guaiacol, and 1 cm^3 of 2 % (v/v) H_2O_2 and the change in absorbance was measured at 470 nm for 5 min.

The AsA content was determined according to Li *et al*. (2015) using 0.2 g of fresh tissue. Standards for AsA was prepared in the range of 0 - 15 mg dm^{-3} in 1 cm^3 of 5 % (m/v) trichloroacetic acid (TCA), 1 cm^3 of ethanol, 0.5 cm^3 of 0.4 % (m/v) H_3PO_4, 1 cm^3 of 0.5 % bathophenanthroline (BP), and 0.5 cm^3 of 0.03 % (m/v) $FeCl_3$ at 30 °C for 90 min and measured at 534 nm. For each sample AsA was estimated as above.

Membrane lipid peroxidation was determined by measuring the MDA content using the method of Zhou *et al*. (2004) with minor modifications. The enzyme extract (1 cm^3) was mixed with 2.5 cm^3 of 0.5 % (m/v) thiobarbituric acid (TBA) and then was heated at 100 ºC for 20 min. The absorbance was determined at 450, 532, and 600 nm respectively.

Determination of superoxide anion production and H_2O_2 content: For the extraction of superoxide radical (O_2^{-}), ascorbate and glutathione (reduced and oxidized), 1 g of the tissue from control and stressed plants were ground in 5 cm^3 of chilled 0.8 M $HClO_4$ and centrifuged at 10 000 *g* for 25 min. The clear supernatant was decanted carefully and O_2^{-} was measured by monitoring the nitrite formation from hydroxylamine following the method of (Chawla *et al.* 2013). Amount of NO_2^{-} formed which corresponded to O_2^{-} production was calculated from standard curve.

H_2O_2 was extracted by homogenizing 4 g tissue in 5 cm^3 of ice cold 0.01 M phosphate buffer (pH 7.0) and centrifuging the homogenate at 8 000 *g* for 10 min. The supernatant was added to 1.95 cm^3 of 0.01 M phosphate buffer (pH 7.0). To the mixture, 2 cm^3 of 5 % (m/v) potassium dichromate and glacial acetic acid (1:3, v/v) was added. The absorbance was read at 570 nm against the reagent blank without sample extract (Chawla *et al.* 2013).

Carbon and nitrogen metabolism: Fresh shoots and roots (0.5 g) were homogenized at 4 °C in 3 cm^3 of extraction buffer [100 mM Tris-HCl buffer (pH 7.2) containing 10 mM $MgCl_2$, 1 mM EDTA-Na_2, 10 mM β-hydrophobic base ethanol, 2 % (v/v) ethylene glycol, and 1 % (m/v) polyvinyl pyrrolidone] with mortar and pestle. The homogenate was then centrifuged at 12 000 *g* for 10 min and the supernatant was used for determination of sucrose synthase (SS) and sucrose phosphate synthase (SPS) activities by the method described by Zhang *et al*. (2017). For SS activity, reaction mixtures contained 100 mM Tris-HCl buffer (pH 7.2), 10 mM $MgCl_2$, 5 mM uridine diphosphate glucose (UDPG), 5 mM fructose, and the 0.3 cm^3 of sample. For SPS activity, 5 mM fructose was substituted for 5 mM fructose-6-phosphate.

For the nitrate reductase (NR) activity assay, approximately 0.5 g samples of fresh tissue were ground in a prechilled mortar and pestle on ice in 4 cm^3 of extraction buffer. The extraction 25 mM buffer (pH 8.7) contained 10 mM cysteine and 1 mM EDTA. The mixture was centrifuged at 4 000 *g* and 4 °C for 15 min and then 0.5 cm^3 of supernatant was added to the reaction mixture. The reaction mixture comprised of 1.2 cm^3 of 100 mM KNO_3-phosphate buffer (pH 7.5) and incubated at 25 °C for 30 min. The reaction was terminated by adding 1 cm^3 of 1 % (m/v) sulfanilamide in 3 M HCl. For nitrite determination, 1 cm^3 of 0.02 % (m/v) N-naphthyl-(1)-dihydrochloride was added, and the colour was allowed to develop at 25 °C for 15 min. The mixture was centrifuged at 4 000 *g* and 4 °C for 5 min, and then the absorbance of the supernatant at 540 nm was measured (Yang *et al*. 2014).

To measure glutamine synthetase (GS) activity freshly harvested shoots and roots were ground on ice in an extraction Tris-HCl (pH 8.0) buffer containing 2 mM $MgSO_4$, 2 mM DTT, 400 mM sucrose. Total GS activities were determined in Tris-HCl (pH 7.4) consisting of 80 mM $MgSO_4$, 20 mM sodium glutamate, 20 mM cysteine, 2 mM ethylene glycol tetraacetic acid (EGTA), and 80 mM hydrochloric acid hydroxylamine. The reaction was terminated at 37 °C after 30 min by adding acidic $FeCl_3$ solution (370 mM $FeCl_3$, 600 mM HCl, and 200 mM trichloroacetic acid). The mixture was left for 10 min to allow the colour to develop, and then centrifuged at 15 000 *g* at room temperature for 10 min. The supernatant was then transferred from each well into a new tube and the absorbance at 540 nm was measured (Yang *et al*. 2014).

Statistical analysis: The experiment was arranged in a completely randomized design with four replicates and the whole experiment was repeated twice. All experimental data were analyzed by *ANOVA* using *SPSS v. 17.0* software (*SPSS Inc*, Chicago, IL, USA). Significant differences were tested using the least significant difference (LSD) test at $P < 0.05$.

Results

Salt stress decreased stem length and lateral root number of *G. uralensis* seedlings compared with control. The addition of 0.025 mM or 0.05 mM MeJA markedly increased root length compared with control or NaCl alone. However, 0.025 mM or 0.05 mM MeJA reduced stem length, root diameter, and stem diameter compared with control or NaCl alone (Fig 1).

Salt stress significantly decreased POD and CAT activities of *G. uralensis* seedlings compared with control. The addition of 0.025 mM or 0.05 mM MeJA significantly

increased POD activity compared with NaCl. However, MeJA reduced CAT activity (Fig. 2*A*,*B*).

Salt stress slightly decreased AsA content *G. uralensis* seedlings and increased MDA content compared with control. But the changes were not significant. The addition of 0.025 mM or 0.05 mM MeJA significantly increased AsA content compared with control or NaCl alone (Fig. 2*C*). Only 0.05 mM MeJA significantly increased

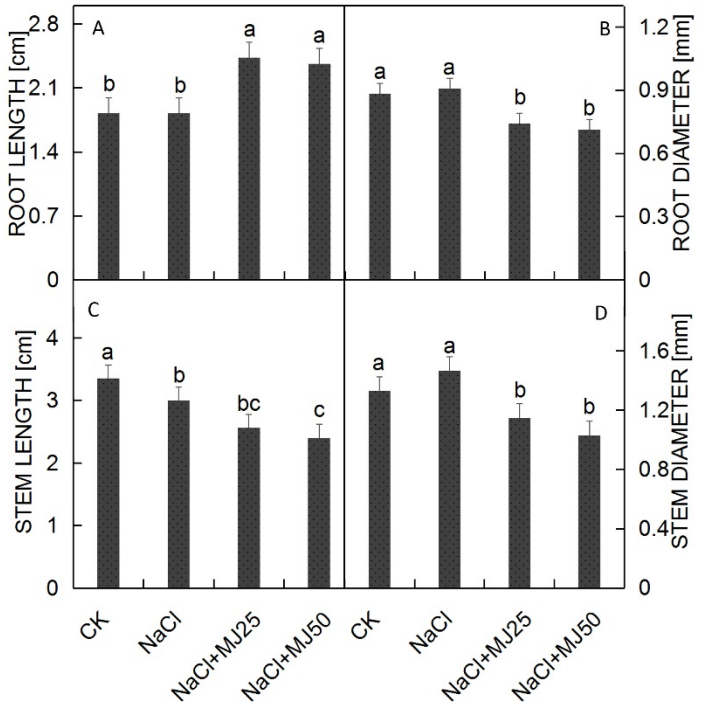

Fig. 1. Effect of MeJA on root length (*A*), root diameter (*B*), stem length (*C*), and stem diameter (*D*) of *Glycyrrhiza uralensis* seedlings grown under 100 mM NaCl. Means ± SE, $n = 6$, the different letters indicate the significant difference at $P \leq 0.05$.

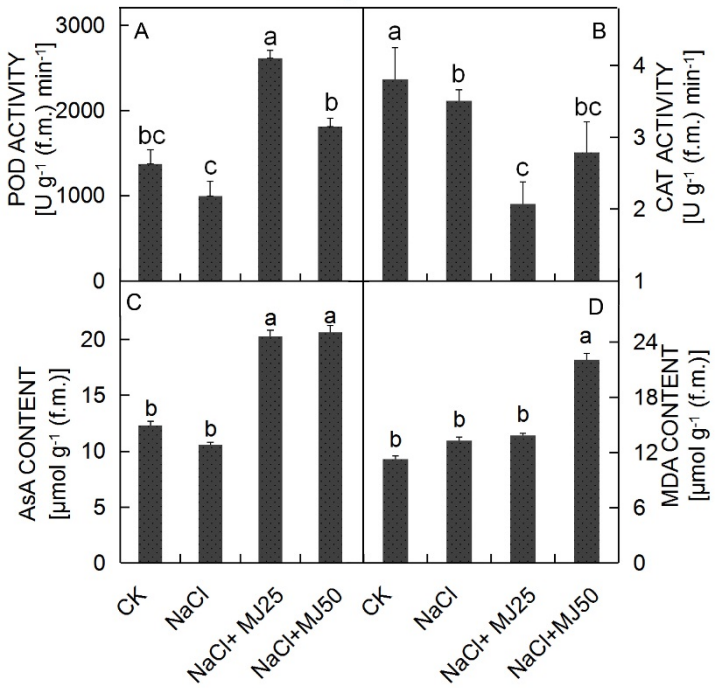

Fig. 2. Effect of MeJA on POD activity (*A*), CAT activity (*B*), AsA content (*C*), and MDA content (*D*) of *G. uralensis* seedlings grown under 100 mM NaCl. Means ± SE, $n = 6$, the different letters indicate the significant difference at $P \leq 0.05$.

MDA content compared with control or NaCl alone (Fig. 2*D*).

Salt stress increased the content of H_2O_2 and the rate of superoxide production compared with control. The addition of 0.025 mM or 0.05 mM MeJA significantly decreased H_2O_2 content compared with NaCl alone. However, 0.05 mM MeJA increased the production rate of $O_2^{\cdot-}$ (Fig. 3*A*, *B*).

Salt stress slightly reduced GS and NR activities of *G. uralensis* seedlings compared with control (Fig. 4*A*). However, salt stress had no significant effect on the activities of SS and SPS compared with control (Fig. 4*B*,*C*,*D*). The addition of 0.025 mM MeJA but not 0.05 mM MeJa enhanced SPS, SS, and NR activities in both salt-stressed and control seedlings. However, both MeJA concentrations inhibited GS activity (Fig. 4*A*).

Discussion

Salinity stress can change most plant physiological and biochemical processes and disturbs normal plant growth and development (Golldack *et al*. 2014). Faghih *et al*. (2017) found that exposure to NaCl, especially at high concentrations, reduces the growth of strawberry seedlings. Jiyoung *et al*. (2009) demonstrated that salt

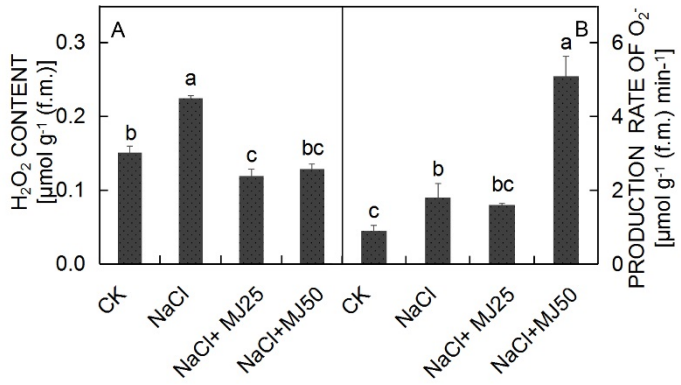

Fig. 3. Effect of MeJA on H_2O_2 content (*A*) and rate of O_2^- production (*B*) of *G. uralensis* seedlings grown under 100 mM NaCl. Means ± SE, $n = 6$, the different letters indicate the significant difference at $P \leq 0.05$.

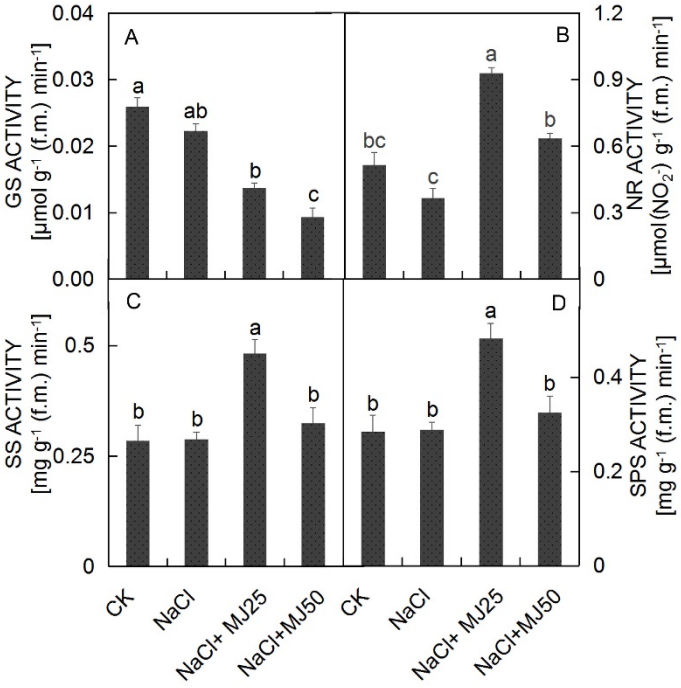

Fig. 4. Effect of MeJA on GS activity (*A*), NR activity (*B*), SS activity (*C*), and SPS activity (D) of *G. uralensis* seedlings grown under 100 mM NaCl. Means ± SE, $n = 6$, the different letters within the different treatments indicate the significant difference at $P \leq 0.05$.

stress significantly reduces soybean growth. Kang *et al*. (2005) revealed that even low NaCl concentrations can remarkably decrease the length of rice roots. Our present results showed that compared with the control, treatment with 100 mM NaCl significantly affected stem length, however, it has no effects on root length, root diameter, and stem diameter. MeJA treatment markedly increased the root length of *G. uralensis* seedlings compared with NaCl alone (Fig. 1*A*). In agreement with previously reported results for *Robinia pseudoacacia* (Jiang *et al*. 2016), *Artemisia annua* (Tariq *et al*. 2011), and strawberry (Faghih *et al*. 2017), we found that MeJA treatment modified the growth characteristics of *G. uralensis* seedlings. However, MeJA treatment significantly decreased stem length, root diameter, and stem diameter (Fig. 1*B*,*C*,*D*). Given that MeJA treatment also decreases the growth of *Pinus sylvestris* (Heijari *et al*. 2005), we hypothesized that the effect of MeJA on salt-stressed plants varies with growth parameter, plant species, and applied concentration of MeJA.

Salt stress can cause the accumulation of ROS, such as H_2O_2 and $O_2^{\cdot-}$, which cause cellular damage by oxidizing lipids, proteins, and nucleic acids (Golldack *et al*. 2014, Noctor *et al*. 2014). MDA is often used as a major indicator of membrane lipid peroxidation, and its content is used to represent the degree of membrane lipid damage (Zhuang *et al*. 2010). H_2O_2 sharply increases during the germination of alfalfa under salt stress (Wang *et al*. 2009). The $O_2^{\cdot-}$ and H_2O_2 content increases in the leaves and petals of *Tagetes erecta* under long-term salt stress (Garg and Bhandari 2016). Salt stress increases the MDA content and membrane permeability of *Ammodendron bifolium*, *Gleditsia sinensis* (Liu *et al*. 2014), and *G. uralensis* plants (Pan *et al*. 2006). These results are similar to those observed in the present study. Here, we observed that $O_2^{\cdot-}$ production rate and H_2O_2 content were increased under 100 mM NaCl (Fig. 3*A*,*B*). Treatments with 0.05 mM MeJA attenuated the increase in $O_2^{\cdot-}$, but it had no effect on H_2O_2 content under both 0.025 or 0.05 mM NaCl (Fig. 3*A*,*B*). These results were similar to those of a previous study showing that MeJA application decreases $O_2^{\cdot-}$ content of the roots and leaves of *A. annua* (Aftab *et al*. 2011) and of diploid and tetraploid *R. pseudoacacia* plants (Jiang *et al*. 2016). The efficient destruction of H_2O_2 and $O_2^{\cdot-}$ in plant cells requires the action of different antioxidants. Salt stress alters enzyme activities involved in ROS scavenging (Hernandez *et al*. 2000, Sreenivasulu *et al*. 2000). In the current study, we found that the highest rate of POD activity occurred under 0.025 mM MeJA treatment and that POD activity slightly decreased under 0.05 mM MeJA treatment (Fig. 2*A*). These results indicated that the changes of POD activity depended on MeJA concentration. These results indicated that the changes of POD activity depended on MeJA concentration. Parida and Das (2005) reported that POD is one of the most important enzymes in H_2O_2 degradation. CAT catalyzes the direct decomposition of H_2O_2 into water and oxygen, does not require reducing power, and exhibits a high reaction rate. Consistent with the results of Pan *et al*. (2006), we found that CAT activity significantly declined in *G. uralensis* seedlings treated with 0.025 or 0.05 mM MeJA (Fig. 2*B*). Non-enzymatic antioxidant, such as AsA, cooperate with antioxidant enzymes to maintain the integrity of photosynthetic membranes under oxidative stress. Koffler *et al*. (2015) found that the AsA content of salt-stressed *Arabidopsis* plants decreased over time. In the present study, we found that the AsA content in salt-stressed *G. uralensis* seedlings was only slightly lower than in control seedlings and 0.025 or 0.05 mM MeJA markedly increased AsA content (Fig. 2*C*).

Salt stress alters a wide array of processes, such as carbon and nitrogen metabolism. Salinity decreases the nitrogen content of the roots and stems of *Sesbania sp*. and the total nitrogen content of alfalfa (Chakrabarti and Mukherji 2003). Salt stress also depresses carbon metabolism, ultimately decreasing energy and sugar production (Cuellar-Ortiz *et al*. 2008). Sucrose synthase plays an important role in phloem loading and unloading and SPS catalyzes the synthesis of sucrose phosphate during the last step of dark CO_2 fixation in plant tissues (Azevedo-Neto *et al*. 2004). Nitrate reductase reduces NO_3^- taken up by plant roots from soil to NO_2^- in the cytosol. NH_4^+ is converted to glutamate by GS. MeJA promotes the transcription of numerous genes that can affect the plant resource allocation (Hanik *et al*. 2010). For example, MeJA increased C:N ratio in tomato leaves (Gómez *et al*. 2010). In the present study, we found that salt stress nonsignificantly decreased the activities of NR and GS in *G. uralensis* seedlings and has no effects on the activities of SPS and SS; these effects are specific responses to salt stress and constitute a strategy for maintaining balanced sucrose content under stress conditions. In salt-stressed *G. uralensis* seedlings, 0.025 mM MeJA treatment significantly up-regulated the activities of NR, SS, and SPS but inhibited activity of GS (Fig. 4). These results indicated that MeJA may alleviate the damage of salt-stressed plant through regulating sucrose synthesis and metabolism for maintaining normal growth under stress conditions. However, more research is need to clarify this effect.

In conclusion, MeJA treatment alleviated oxidative stress through enhancing the activity of ROS scavenging enzyme POD and content of non-enzymatic antioxidant AsA content and by strengthening carbon and nitrogen metabolism enzyme activities (NR, SPS, and SS) at its lower (0.025 mM) concentration.

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