Acta Physiologiae Plantarum (2023) 45:96
https://doi.org/10.1007/s11738-023-03574-z

ORIGINAL ARTICLE

Methyl jasmonate mitigates osmotic stress by regulating carbon and nitrogen metabolism of *Glycyrrhiza uralensis* seedlings subjected to salt stress

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Received: 18 September 2021 / Revised: 2 June 2022 / Accepted: 26 May 2023 / Published online: 10 June 2023

Abstract

Salt stress seriously affects C and N metabolism, and secondary metabolites, further have adverse effects on the growth and yield of *Glycyrrhiza uralensis*. Methyl jasmonate (MeJA) plays a significant role in influencing C and N metabolism and improving the accumulation of secondary metabolites. However, the underlying mechanism of MeJA in alleviating salt stress in *G. uralensis* remains unknown. A pot experiment was employed to explore the responses of C and N, and secondary metabolisms to MeJA in *G. uralensis* seedling under salt stress. Salt significantly inhibited growth, affected activities of key enzymes involved in C and N metabolisms and decreased contents of carbohydrates and N-containing compounds, and secondary metabolites in *G. uralensis*, while the adverse effect was counteracted by MeJA. MeJA remarkably increased the diameter of main root and main stem, and the length of main root in the salt-stressed seedling. In addition, MeJA remarkably increased soluble sugar content and the sucrose synthase (SS) and sucrose phosphate synthase (SPS) activities. Nitrate (NO_3^-) and nitrite (NO_2^-) contents, glutamine synthetase (GS), glutamate synthase (GOGAT) and nitrate reductase (NR) activities were also higher in seedlings that were treated with MeJA. Moreover, MeJA significantly increased licochalcone A, glycyrrhizic acid, total flavonoids and total polysaccharides contents. MeJA improves the capacity of osmotic adjustment by regulating C and N metabolism, further promote the synthesis of secondary metabolites in *G. uralensis* seedling; it also employed different metabolites against membrane lipid peroxidation, further to improve the plant growth.

Keywords Methyl jasmonate · Salinization stress · Carbon and nitrogen metabolism · Secondary metabolism · *G. uralensis*

Abbreviations

GS	Glutamine synthetase
GOGAT	Glutamate synthetase
NR	Nitrate reductase
GOT	Glutamic-oxaloacetic transaminase
GPT	Glutamic-pyruvic transaminase
N	Nitrogen
NH_4^+	Ammonium
SS	Sucrose synthase
SPS	Sucrose phosphate synthase
MeJA	Methyl jasmonate
C	Carbon
NO_3^-	Nitrate
NO_2^-	Nitrite
GDH	Glutamine dehydrogenase

Communicated by S. Renault.

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Introduction

Salinization is one of the main threats to crop production in arid regions, and it causes severe reduced biomass and productivity (Taïbi et al. 2016). Salinization also alters various biochemical and physiological processes, thereby resulting in a metabolic imbalance in plants (Li et al. 2016). Generally, salinization negatively affected plants in three ways as follows: (1) the soil has a high concentration of salt leads to high osmotic potential in plants; (2) imbalance of ions in cells such as Na^+ and Cl^- leads to ion toxicity in plants; (3) excessive production of reactive oxygen species (ROS) leads to oxidative stress in plants (Salimi et al. 2016; Ahmadi et al. 2018).

Osmotic regulation is one of the biochemical changes in plants under salt stress. It promotes the protection of plant cell structure, prevents ionic toxicity, and improves water absorption through the synthesis and accumulation of a large number of compatible solutes in plants (Khan et al. 2015; Zhang et al. 2018). Many compatible solutes such as carbohydrates, amino acids and proteins which are products of carbon (C) and nitrogen (N) metabolism (Liu et al. 2014b, a). C and N metabolisms are very sensitive to environmental stress that generally decreases chlorophyll contents, depresses photosynthesis, alters expression of genes and activities of enzyme, which thus inhibit growth (Flores et al. 2004; Debouba et al. 2006; Cuellar-Ortiz et al. 2008). When plants are subjected to salt stress, the cell membrane is firstly affected and the membrane permeability is increased (Liu et al. 2015). Other significant effects of salt stress are changes in soluble sugar content and in invertase (INV) activities, sucrose synthase (SS), sucrose phosphate synthase (SPS) (Fernandes et al. 2004). Moreover, the yield of secondary metabolites is closely related to the growth conditions, and plants usually produce more secondary metabolites under moderate environmental stresses (Kleinwächter and Selmar 2013). Thus, C and N metabolism and secondary metabolites are of vital importance for stress tolerance.

Methyl jasmonate (MeJA), as an inducer or signal transduction agent, is involved in many physiological and biochemical processes of plants (Fan et al. 2016; Zaid and Mohammad 2018). MeJA also elicits beneficial effects on active components in plant. Takahashi and Hara (2014) sprayed MeJA on leaf number of plants and found that MeJA promotes the accumulation of starch by up-regulating the expression genes of starch biosynthetic in *Arabidopsis thaliana*. Furthermore, MeJA induces the accumulations of monoterpene and sesquiterpene by stimulating oxygenated linalool and (E)-β-farnesene or forming traumatic resin (TDs) ducts in xylem and foliage of *Norway spruce* (Martin et al. 2002, 2003). Zaid and Mohammad (2018) studied the interactive effect of MeJA and N in reducing the toxicity of Cd in an important medicinal and aromatic plant.

Glycyrrhiza uralensis Fisch. (*G. uralensis*) is one of the most widely used herbal medicine and food additives (Egamberdieva et al. 2017). Generally, wild *G. uralensis* resource grows in arid and salinization areas and therefore has the ability to adapt to drought and salt conditions. Nevertheless, studies and practices proved that the salt tolerance ability of cultivated *G. uralensis* is lower than wild plants (Zhang et al. 2018). Actually, soil salinization and water resource shortage are universal in regions of *G. uralensis* cultivation. Thus, improving the salt and drought tolerance of cultivated *G. uralensis* has become an important goal for sustainable development. However, there is limited information on MeJA's response to C and N metabolism and secondary metabolites to abiotic stresses including salt stress, and thus in light of the important role of MeJA in plant stress response, this research was conducted to study the effects of MeJA on the growth parameters, key metabolites and key enzyme activities related to C and N metabolism, and the contents of bioactive components in *G. uralensis* under salt stress.

Materials and methods

Plant materials and growth conditions

The seeds of *G. uralensis*, we utilized were provided by Ningxia Academy of Agriculture and Forestry Sciences, China, Yinchuan, Ningxia Province, China, and it is identified as *G. uralensis* by Ming Li Professor.

The seeds of *G. uralensis* were steeped with 85% H_2SO_4 for 45 min to break the seed coat, then surface sterilized with 0.1% H_2O_2 for 10 min, cleaned 3 times using distilled water and imbibed in distilled water for 8 h at 25 °C. Eighty seeds of uniform size that were pre-treated were planted in plastic boxes (6 × 12 × 12 cm) filled with 1400 g autoclaved sand medium that were pre-irrigated. The treatments include control group (CK), with 370 mL of distilled water; salt stress group (S), with 370 mL of distilled water containing 75 mM NaCl; salt stress combined with methyl jasmonate group (S + MeJA), with 370 mL of distilled water containing 75 mM NaCl and 30 µM MeJA. Seedling growth conditions were maintained at 12 h/12 h, 28 °C/20 °C (day/night).

A weighing method (every afternoon weighing and watering) was used to control saturation moisture content 65–75% for all treatments. Three replications per treatment were used, and all pots were randomly arranged and periodically rotated to minimize the effects of environmental heterogeneity. Whole *G. uralensis* seedlings from all treatments were

collected in the morning at 45 day after treatment for determination of all parameters.

Determination of carbohydrates

Soluble sugar and sucrose were determined according to the method of Loutfy et al. (2012). Specifically, 0.2 g of fresh seedlings were extracted with 10 mL of distilled water at 100 °C for 30 min, then the homogenate was centrifuged at 3000 g for 10 min, and 0.5 mL of supernatant added 5 mL of ketone concentrated sulfuric acid reagent at 100 °C for 1 min.

Finally, the absorbance was measured at 630 nm. In addition, a standard curve was plotted with 0–100 mg of glucose, and standard curves as $Y=0.00847X-0.0059$. For sucrose, 0.2 g fresh seedlings were extracted with 4 mL distilled water, then homogenate was centrifuged at 3000 g for 10 min and supernatant (1 mL) contained 2 M of NaOH (1 mL), then kept in boiling water bath for 10 min, stop the reaction by adding 1 mL of 0.1% (w/v) resorcinol, and 10 M of HCl, stop the reaction by keeping in boiling water bath for 8 min. Finally, the absorbance was measured at 500 nm. In addition, the standard curve was plotted with 0–100 mg of glucose, and standard curves as $Y=0.00847X-0.0059$ for soluble sugar and $Y=0.019X+0.0009$ for sucrose.

Determination of N forms

To determine NO_3^-, NH_4^+ and NO_2^-, 0.2 g fresh seedlings were homogenized with deionized water, centrifuged at 4 °C and 8300 g for 10 min. The NO_3^- and NH_4^+ in the supernatant were quantified photometrically at 410 and 630 nm, respectively, and KNO_3 and $(NH_4)_2SO_4$ were used as standard, respectively (Zhang et al. 2017). The NO_2^- in the supernatant was quantified photometrically at 520 nm.

C and N metabolism-related enzyme extraction and assays

Invertase (INV) activity was determined as described by Yang et al. (2004). 0.2 g fresh seedlings were homogenated with chilled distilled water for 3 h at 4 °C and the mixture was centrifuged at 8000 g for 10 min at 4 °C. INV activity was assayed using the DNS method, which measures reducing sugar content at 540 nm.

To measure sucrose synthase (SS) and sucrose phosphate synthase (SPS) activities, 0.2 g fresh seedlings were homogenized with 50 mM HEPES–NaOH (pH 7.5) and the mixture was centrifuged at 12000 g for 10 min at 4 °C. The assay mixture of SS containing the supernatant, 50 mM HEPES–NaOH (pH 7.5), 50 mM $MgCl_2$, 100 mM uridine diphosphoglucose (UDPG) and 100 mM fructose. After incubation at 30 °C for 30 min, 2 M NaOH was added to the assay mixture to terminate the reaction, then, the mixture was boiled for 10 min and cooled. After that, 30% (w/v) HCl and 0.1% (w/v) m-dihydroxybenzene were added, the mixture was shaken thoroughly, kept in a water bath for 10 min at 80 °C, and once the mixture was cooled, its absorbance was measured at 480 nm. SPS activity was determined in the same way as SS activity; the only difference is that fructose was substituted by fructose-6-phosphate (Xie et al. 2021).

To measure nitrate reductase (NR) activity, 0.2 g fresh seedlings were homogenized with 3 mL of 25 mM potassium phosphate buffer (pH 7.5) containing 10 mM L-cysteine and 1 mM EDTA-Na_2 and centrifuged at 8300 g for 10 min at 4 °C. The NR activity in the supernatant was quantified photometrically at 540 nm based on the reduction of nitrate to nitrite during 30 min at 25 °C (Du et al. 2008).

To measure the activities of glutamine synthetase (GS) and glutamate synthetase (GOGAT), 0.2 g fresh seedlings were homogenized with 3 mL of 50 mM Tris–HCl buffer (pH 8.0, containing 2 mM Mg^{2+}, 2 mM DTT, and 0.4 M sucrose) and the mixture was centrifuged at 8300 g for 10 min at 4 °C, and the supernatant as enzyme extract. GS activity was assayed by monitoring the formation of glutamyl hydroxamate at 540 nm after reacting with acidified ferric chloride (Liu et al. 2014a, b). GOGAT activity was measured by estimating the oxidation of NADH at 340 nm was assayed according to Wang et al. (2018).

Determination of glycyrrhizic acid, liquiritin and licochalcone A contents

The determination was carried out by HPLC on the C18 column (4.6 mm × 15 cm, 5 μm). The mobile phase consisted of acetonitrile-1% acetic acid with 0.6 mL·min^{-1} of the flow rate, and the temperature of column was 25 °C. To determine the quantitative assay using the external standard method.

Determination of total flavonoids, total saponins and total polysaccharide contents

For determination of total flavonoids, the powder sample (0.05 g) was extracted with 80% ethanol for 40 min at 40 °C in an ultrasonic bath and the supernatant was used as the extract. 400 μL extract contained 1 mL 70% methanol and 2 mL 10% sodium hydroxide for 10 min, then added 1 mL 70% methanol again, finally the supernatant was measured photometrically at 410 nm.

For determination of total saponins, the powder sample (0.05 g) was extracted with 80% (containing 0.3% ammonia water) ethanol for 80 min at 40 °C in an ultrasonic bath and the supernatant used as the sample extract. 200 μL extract contained 0.25 mL 5% vanillin glacial acetic acid solution and 0.8 mL perchloric acid, react at 55 °C for 20 min in a water bath, then added 2 mL glacial acetic acid under

temperature, the absorbance of the supernatant at 590 nm was measured.

For determination of total polysaccharide, the powder sample (0.05 g) was extracted with 80% ethanol for 80 min at 40 °C in an ultrasonic bath and the supernatant was used as the sample extract. 40 µL extract contained 0.5 mL 5% phenol solution, then added 2.5 mL concentrated sulfuric acid, finally the supernatant was measured photometrically at 490 nm.

Statistical analysis

Each treatment of the experiment was designed completely randomly. SPSS 17.0 software (SPSS, Inc., Chicago, IL, USA) was used for principal component analysis (PCA) and Pearson's correlation analysis. Significant differences were tested using the least significant difference (LSD) test at $P < 0.05$. Mean values and standard errors (SEs) were presented.

Results

Effects of MeJA on growth in salt-stressed *G. uralensis* seedlings

Exposure of *G. uralensis* plants to salt stress leads to a significant decline in growth parameters including main root length, main root diameter and secondary root number (Fig. 1), and reduced by 28.11%, 23.04% and 48.01%, respectively compared with control. Salt stress also decreased plant height, leaf number and biomass yield by 46.67%, 31.75% and 56.19%, respectively, relative to control. Supply of MeJA showed an enhancement by 23.61%, 16.04% and 24.58% at axial root length, secondary root numbers and biomass yield as compared with salt stress, respectively (Table 1).

A significant negative correlation was observed between soluble sugar and main root length, main shoot diameter, secondary root numbers and leaf number, respectively. A significant negative correlation was observed between sucrose and main root diameter, also a significant negative correlation was observed between NO_3^- and plant height, leaf number, respectively. In addition, a significant positive correlation was observed between NR and plant height, a

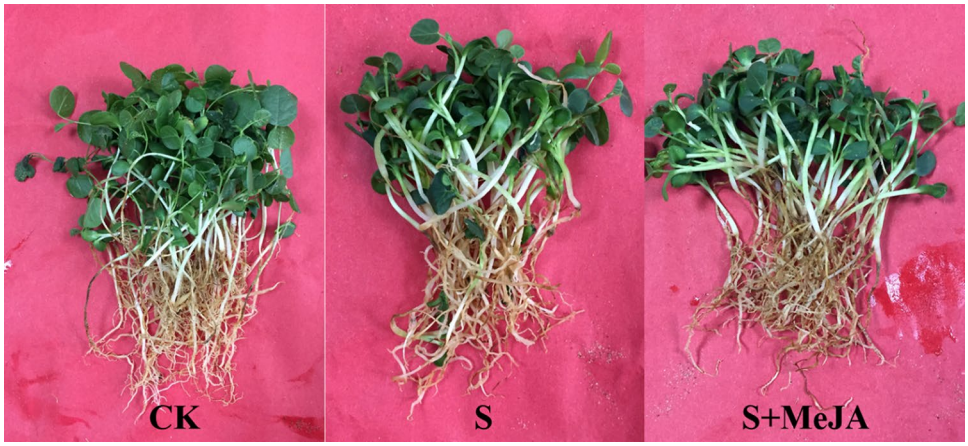

Fig. 1 Effect of MeJA on growth property of *G. uralensis* grown under salt stress. CK, control group; S (75 mM NaCl), salt stress group, S + MeJA (75 mM NaCl + 30 µM MeJA), salt stress combined with methyl jasmonate group

Table 1 Effects of MeJA on growth and biomass in salt-stressed *G. uralensis* seedlings

Treatment	Main root length (cm)	Plant height (cm)	Main root diameter (mm)	Shoot diameter (mm)	Secondary root number	Leaf number	Biomass yield (g/pot)
CK	4.92 ± 0.51a	2.89 ± 0.07a	0.75 ± 0.06a	0.86 ± 0.02ab	7.06 ± 0.64a	4.50 ± 0.12a	0.26 ± 0.07a
S	3.54 ± 0.21b	1.53 ± 0.01b	0.57 ± 0.01c	0.97 ± 0.01ab	3.67 ± 0.33b	3.07 ± 0.07b	0.09 ± 0.03b
S + MeJA	4.37 ± 0.03a	1.58 ± 0.03b	0.62 ± 0.01b	1.01 ± 0.02a	4.26 ± 0.22b	2.30 ± 0.10b	0.14 ± 0.02ab

Data presented are the means ± SE ($n = 6$). Different letters next to the number indicate significant difference ($P \leq 0.05$)

CK, control group; *S (75 mM NaCl),* salt stress group; *S + MeJA (75 mM NaCl + 30 µM MeJA),* salt stress combined with methyl jasmonate group

significant negative correlation was observed between NR and shoot diameter (Table 2).

A significant positive correlation was observed between leaf number and glycyrrhizic acid and glycyrrhizin, while a significant positive correlation was observed between biomass and glycyrrhizic acid, glycyrrhizin and licochalcone A. A significant positive correlation was observed between total flavonoids and leaf number and biomass yield (Table 3).

Effects of MeJA on carbohydrates contents in salt-stressed *G. uralensis* seedlings

Salt stress enhances soluble sugar and sucrose contents by 69.74% and 36.05% in salt-stressed *G. uralensis* plants relative to control. MeJA further induces an enhancement of soluble sugar and sucrose contents by 7.80% and 8.69%, respectively, as compared with plants treated with salt only (Fig. 2).

A significant positive correlation was observed between soluble sugar, SS and SPS (Table 2).

Effects of MeJA on the activities of INV, SS and SPS in salt-stressed *G. uralensis* seedlings

The activities of SS, SPS and INV in *G. uralensis* plants were not affected by salt stress compared to control. MeJA triggered the enhancement of SS and SPS activities compared to salt stress, and increased by 43.08% and 66.74%, respectively, compared to salt stress (Fig. 2).

Effects of MeJA on NR, GS and GOGAT activities in salt-stressed *G. uralensis* seedlings

The results regarding the impacts of MeJA on NR, GS and GOGAT activities in salt-stressed *G. uralensis* plants are depicted in Fig. 4. Reduction in NR and GOGAT activities were observed in *G. uralensis* plants under salt condition compared to control. MeJA increases NR, GS and GOGAT activities by 31.06%, 8.42% and 47.38% in *G. uralensis* plants, respectively, as compared with salt alone (Fig. 3).

Effects of MeJA on NO_2^-, NO_3^- and NH_4^+ concentrations in salt-stressed *G. uralensis* seedlings

Salt stress triggered the increase of NO_2^- and NH_4^+ contents by 21.76% and 47.43%, respectively, compared to control. Supplementation of MeJA to *G. uralensis* plants displayed a remarkable increase in NO_3^- and NO_2^- contents, which rose by 21.67% and 28.99%, respectively, as compared to salt alone. In addition, MeJA effectively reduced NH_4^+ content compared to salt alone (Fig. 3).

Effects of MeJA on the contents of glycyrrhizic acid, liquiritin and licochalcone A in salt-stressed *G. uralensis* seedlings

Salt stress induced the decreased of glycyrrhizic acid content by 12.72%, respectively, compared to control in *G. uralensis* plants, but glycyrrhizin and licochalcone A contents unchanged compared with the control. MeJA significantly increased glycyrrhizic acid and licochalcone A contents by 12.04% and 10.01%, respectively, compared to salt stress (Fig. 4).

A significant positive correlation was observed between glycyrrhizic acid and licochalcone A and glycyrrhizin (Table 3).

Effects of MeJA on contents in total flavonoids, total saponins, total polysaccharide in salt-stressed *G. uralensis* seedlings

Salt stress triggered the decrease of total flavonoids and polysaccharides contents by 27.83% and 37.01%, respectively, compared to control in *G. uralensis* plants, while salt stress also increased total saponin content. MeJA increased total flavonoids and total polysaccharides contents by 15.75% and 41.82%, respectively, compared to salt stress (Fig. 4).

PCA of growth and physio-biochemical characteristics in *G. uralensis*

PCA divided the total variance into five PCs with the largest contribution (88.799%) (Table 4). The higher eigenvectors of PC I are soluble sugar, SS, SPS and GS. The higher eigenvectors of PC II are INV and NR. The higher eigenvectors of PC III is NO_3^-. The higher eigenvectors of PC IV are sucrose and NO_2^-. The higher eigenvectors of PC V is GOGAT (Fig. 5).

Discussion

Salt stress usually causes a severe reduction in plant biomass. In this study, the length and diameter of main root and the number of secondary root of *G. uralensis* seedling significantly reduced by salt stress, which is consistent with previous reports on various plants such as wheat (Bot et al. 2013), tomato (Latef et al. 2011), pepper (Latef et al. 2014) and others (Duan et al. 2013; Mostofa et al. 2015; Ahmad et al. 2016). MeJA can alleviate the inhibition effect of salt stress on plant growth (Ahmadi et al. 2018). The present results showed that MeJA significantly increased main root length, secondary root numbers and biomass while did not

Table 2 Linear correlations (Pearson's coefficient) between growth and physiochemical characteristics in *G. uralensis*

Pearson's correlations	Main root length	Plant height	Main root diameter	Shoot diameter	Leaf number	Secondary roots	Biomass yield	Soluble sugar	Sucrose	SS	SPS	INV	NO_3^-	NO_2^-	NH_4^+	NR	GS
Soluble sugar	−0.677*	−0.815**	−0.561	0.611	−0.934**	−0.884**	−0.368										
Sucrose	0.304	0.213	−0.671*	−0.439	−0.33	−0.044	−0.407	0.431									
SS	0.045	−0.142	−0.305	−0.057	−0.417	−0.31	−0.331	0.571*	0.395								
SPS	−0.079	−0.262	−0.19	0.088	−0.419	−0.369	−0.326	0.634*	0.318	0.961**							
INV	−0.304	−0.452	−0.464	0.297	−0.509	−0.478	−0.131	0.419	0.174	0.003	−0.007						
NO_3^-	−0.342	−0.686*	−0.527	0.444	−0.739*	−0.629	−0.496	0.519	0.385	0.309	0.400	0.211					
NO_2^-	−0.009	−0.248	−0.200	0.178	−0.132	−0.134	−0.037	−0.210	0.016	−0.234	−0.335	0.068	0.244				
NH_4^+	−0.152	−0.150	−0.223	0.182	−0.372	−0.283	0.194	0.501	0.431	0.128	0.069	0.239	−0.008	−0.132			
NR	0.594	0.671*	−0.321	−0.791*	0.233	0.423	−0.381	−0.350	0.475*	0.139	−0.014	−0.364	−0.177	0.054	0.014		
GS	−0.021	−0.156	−0.084	0.160	−0.355	−0.304	−0.344	0.422	0.223	0.704**	0.696**	−0.007	0.274	−0.083	0.073	0.162	
GOGAT	0.626	0.208	0.271	−0.068	0.187	0.353	0.284	−0.117	0.115	−0.003	0.023	0.220	0.173	−0.039	0.253	0.029	0.171

SS sucrose synthase, *SPS* sucrose phosphate synthase, *INV* invertase, NO_3^- nitrate, NO_2^- nitrite, NH_4^+ ammonium, *NR* nitrate reductase, *GS* glutamine synthetase, *GOGAT* glutamate synthase

*Correlations are significant at the 0.05 level (two-tailed)

**Correlations are significant at the 0.01 level (two-tailed)

Table 3 The correlations analysis between glycyrrhizic acid, liquiritigenin, licochalcone A and growth in *G. uralensis*

	Glycyrrhizic acid	Liquiritin	Licochalcone A
Main root length	0.128	0.089	0.092
Plant height	−0.466	−0.318	−0.485
Main root diameter	−0.481	−0.553	−0.378
Shoot diameter	−0.679	−0.592	−0.669*
Secondary roots	0.271	0.309	−0.078
Leaf number	0.709*	0.690*	0.298
Biomass yield	0.994**	0.976**	0.914**
Glycyrrhizic acid		0.995**	0.994**
Liquiritin			0.805**

*Correlations is significant at the 0.05 level (two-tailed)

**Correlations is significant at the 0.01 level (two-tailed)

have a significant effect on shoot diameter of *G. uralensis* seedling subjected to salt stress, indicating that MeJA application alleviates the inhibited effect of salt to the growth of root and biomass, which is consistent with previous results in cowpea (Sadeghipour 2017) and strawberry (Faghih et al. 2017).

Osmotic stress affects plant growth and biomass under salt stress condition. To respond to the harmful impact of osmotic stress induced by salt stress, plants produce and accumulate higher levels of compatible solutes in the cytosol and other organelles (Latef and Miransari 2014). Compatible solutes such as proline, soluble sugar and soluble protein are mainly accumulated in response to salt stress in *G. uralensis* (Lu et al. 2013; Zhang et al. 2021). Among them, soluble sugar maintains cell homeostasis and improves plant tolerance to osmotic stress (Ahmad et al. 2016; Bai et al. 2013). In which sucrose plays an important role in plant structure and metabolism and it is also involved in responses to various stresses (Qiu et al. 2014). In this study, a significant accumulation trend in soluble sugar and sucrose was recorded in *G. uralensis* seedling exposed to salt stress (Fig. 2), which is similar to previous results in *Zea mays* L. (Feng et al. 2002), *Lupinus albus* L. (Fernandes et al. 2004) and *Nitraria tangutorum* (Liu et al. 2016). A previous study reported that MeJA enhanced the protective property of the osmolytes in peach (Yu et al. 2016). Moreover, the present results showed that the increase in contents of soluble sugars accompanied by the decrease in growth parameters under salt treatment, which explain the negative Pearson's coefficient of soluble sugars for the growth parameters (Table 2). Our results also showed that application of MeJA to salt-stressed *G. uralensis* seedlings induced an increase in sucrose level, which perhaps provide better protection to *G. uralensis* seedlings subjected to osmotic stress. Therefore, MeJA may be an effective method for protecting plants against osmotic stress through regulating carbohydrate accumulation.

Accumulation of carbohydrates is closely relevant to the activities of INV, SS and SPS that are involved in sucrose synthesis and metabolism. Salt stress affected the levels of INV, SS and SPS activities in various plants such as *Cicer arietinum* (Kaur et al. 2003), *Lotus japonicus* (Miguel et al. 2008), and *Triticum aestivum* L. (Fresneau et al. 2007). In the present study, INV activity increased in *G. uralensis* under salt stress with the increased sucrose content, while the activities of SS and SPS had slight change in *G. uralensis*, indicating that INV plays a vital role in buffer regulation of the carbohydrates contents for salt-induced osmotic stress. This is supported by the previous results in *Dwarf bamboo* (Liu et al. 2014a, b) and *Cicer arietinum* (Kaur et al. 2003). Moreover, MeJA markedly enhanced INV, SS and SPS activities, which is in harmony with the results in *Hericium erinaceus* (Wang et al. 2011). These results suggested that MeJA could further alleviate salt stress by inducing INV, SS and SPS activities, and then these enzymes could affect carbohydrate levels of *G. uralensis* under salt stress (Table 2).

The regulation of N metabolism is an important property to responding to stress, which affects almost all physiological processes in plants. Salt stress interferes with NO_3^- uptake and decreases NO_3^- contents in *Triticum aestivum* L. (Elbaki et al. 2017), *Citrullus lanatus* (Yang et al. 2013), *Helianthus annuus* L. (Silva et al. 2014) and *Cucumis sativus* L. (Shao et al. 2015). In this study, salt stress has no effect on NO_3^- content in *G. uralensis* seedlings, this may be due to the NO_3^-supply and transfer rate from the vacuole into the cytoplasm, which is supported by the previous found in *Fargesia denudata* (Liu et al. 2014a, b). Increased NO_3^- assimilation is beneficial for improving the resistance of plants under stresses via regulating stomatal opening and the synthesis of osmotic substances (Yi et al. 2014; Wilkinson et al. 2007). Interestingly, MeJA application significantly increased NO_3^- content in *G. uralensis* under salt stress. It suggests that MeJA enhanced NO_3^- absorption in *G. uralensis* roots which might improve osmotic regulation, thus strengthen the adaptation to salt stress. NR convert NO_3^- to NO_2^-, then NiR catalyze the conversion of NO_2^- into NH_4^+, further supply more substrate for proline synthesis (Khan et al. 2015). Previous studies showed that salt stress decreased the NR activity in *Populus simonii* (Meng et al. 2016), soybean (Farhangi-Abriz and Torabian 2017) and wheat (Elbaki 2017) under salt stress. Moreover, MeJA can increase N assimilation in *Triticum aestivum* L. by increasing NR and glutamate synthase (GS) activity (Kaya et al. 2021). Present study results found that salt stress significantly decreased NR activity but increased NO_2^- content in *G. uralensis* seedlings. However, MeJA application increased NR activity and NO_2^- content in salt-stressed *G. uralensis*, which in harmony with the results

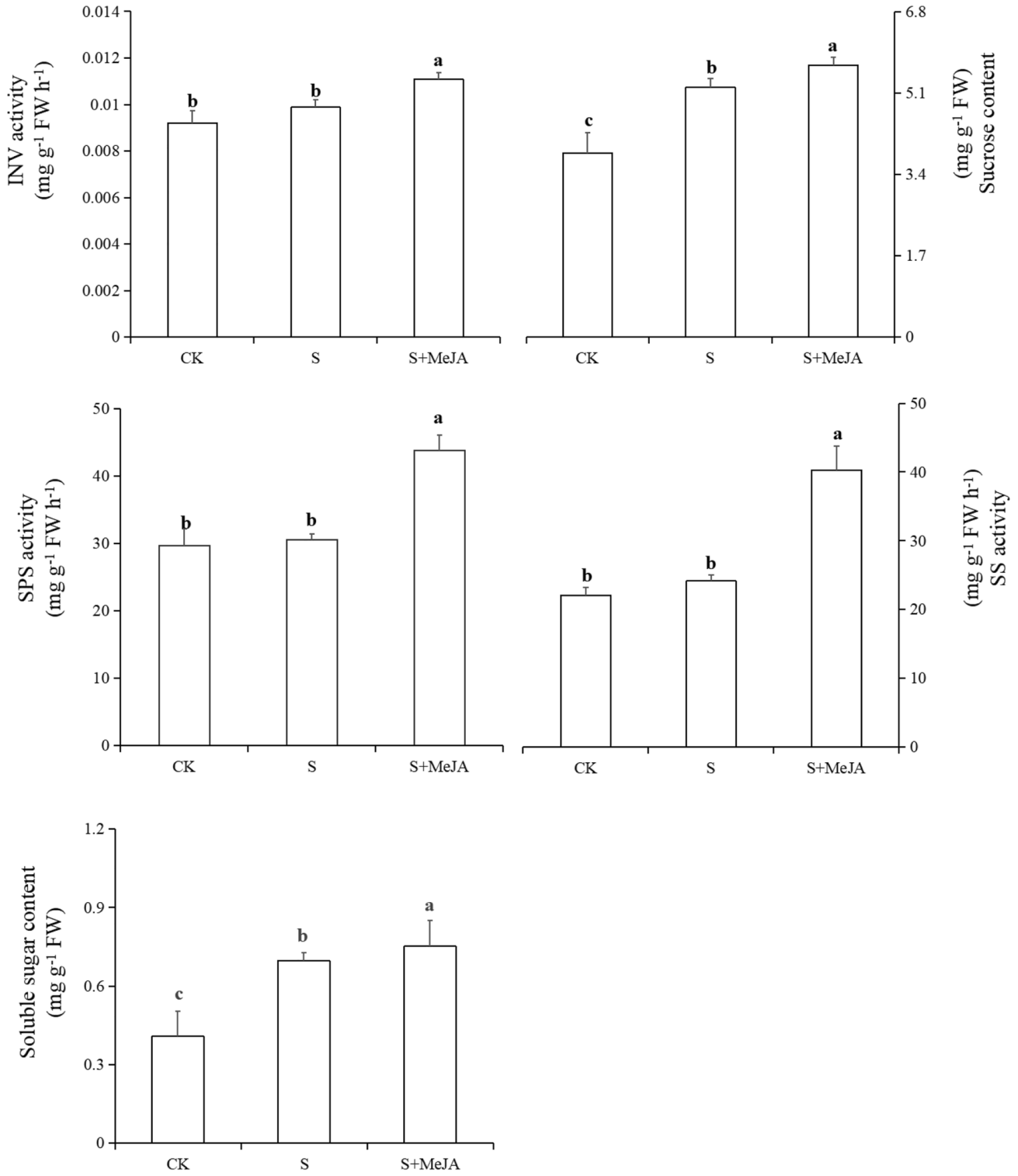

Fig. 2 Effect of MeJA on the soluble sugar, sucrose, SS, SPS and INV in *G. uralensis* grown under salt stress. Values are means ± SE ($n = 6$). CK, control group; S (75 mM NaCl), salt stress group; S + MeJA (75 mM NaCl + 30 μM MeJA), salt stress combined with methyl jasmonate group. The different letters within the different treatments indicate the significant difference at $P \leq 0.05$

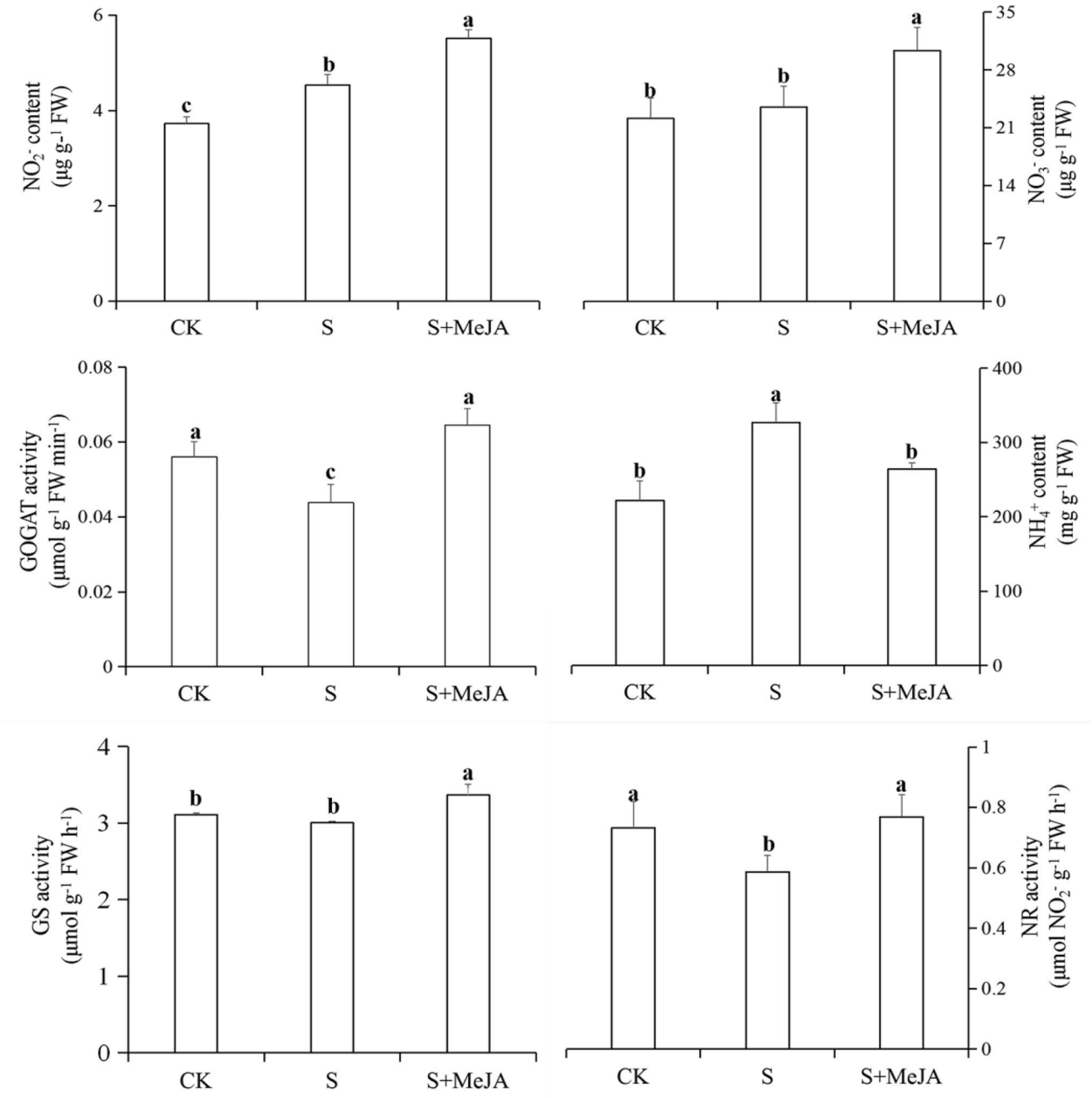

Fig. 3 Effect of MeJA on NO_2^-, NO_3^-, GOGAT, NH_4^+, GS and NR in *G. uralensis* grown under salt stress. Values are means ± SE ($n = 6$). CK, control group; S (75 mM NaCl), salt stress group; S + MeJA (75 mM NaCl + 30 μM MeJA), salt stress combined with methyl jasmonate group. The different letters within the different treatments indicate the significant difference at $P \leq 0.05$

in *Solanum lycopersicum* (Singh et al. 2016). These results suggest that MeJA can promote the conversion of NO_3^- to NO_2^- by increasing the activity of NR, which might facilitating the assimilation of NO_3^- and the synthesis of amino acid subsequently (Kaya et al. 2021).

Excessive NH_4^+ from both NO_3^- reduction and photorespiration is toxic to plant cells (Thomas and Hilker 2000). In the present study, salt stress caused a significant increase in NH_4^+ content, which is consistent with the results in tomato (Manai 2012) and cucumber (Shao et al. 2015). Interestingly, MeJA application decreased NH_4^+ content in salt-stressed *G. uralensis* and this may mitigate the cytotoxicity of excess NH_4^+ induced by salinity. The conversion of non-toxic organic N is closely associated

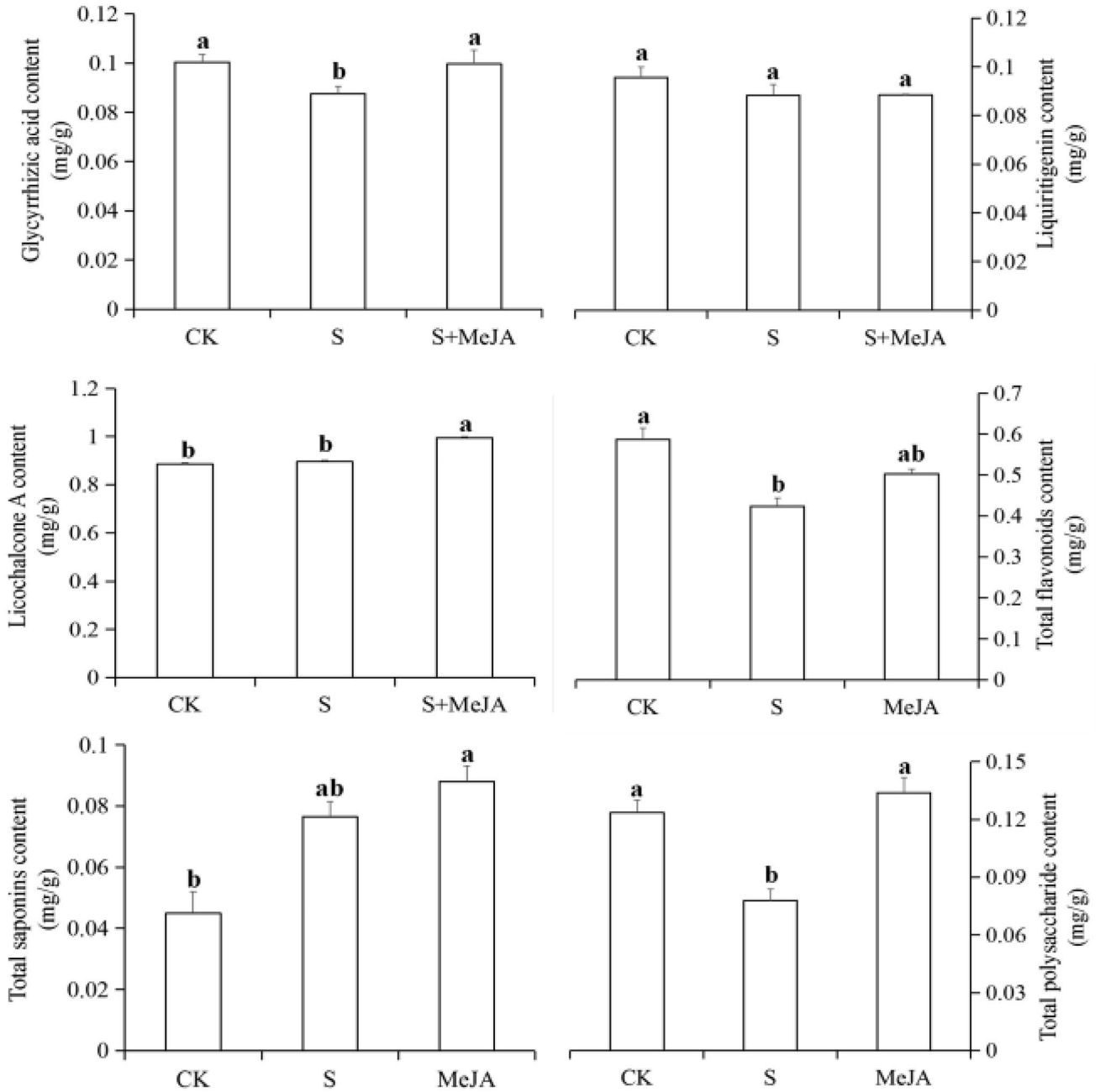

Fig. 4 Effect of MeJA on the contents of glycyrrhizic acid, liquiritin and licochalcone A, and total flavonoids, saponins and polysaccharide in *G. uralensis* grown under salt stress. Values are means ± SE ($n = 6$). CK, control group; S (75 mM NaCl), salt stress group; S + MeJA (75 mM NaCl + 30 μM MeJA), salt stress combined with methyl jasmonate group. The different letters within the different treatments indicate the significant difference at $P \leq 0.05$

with GS/GOGAT cycle, which is the major route for NH_4^+ assimilation (Yang et al. 2010). Our result observed decreased GOGAT activity in *G. uralensis* under salt stress, the results were consistent with those in cucumber (Shao et al. 2015) and soybean (Zilli et al. 2008). These results suggested that the GS/GOGAT cycle is severely blocked in plants subjected to salt stress condition. Whereas, MeJA remarkably improved GOGAT and GS activities in *G. uralensis* under salt stress, suggesting that MeJA could reduce NH_4^+ accumulation by accelerating the interconversion of glutamine (Glu) and glutamic acid (Gln). Taken together, we concluded that MeJA promoted N assimilation and removal of the excess NH_4^+ by increasing the activities of NR, GS and GOGAT under salt stress,

Table 4 Eigenvectors and percentages of accumulated contribution of principal components

Variable	PC I	PC II	PC III	PC IV	PC V
Soluble sugar	0.892	−0.262	0.089	0.114	−0.299
Sucrose	0.557	0.314	−0.31	0.567	0.243
SS	0.861	0.39	−0.02	−0.136	0.039
SPS	0.879	0.307	0.096	−0.293	−0.061
INV	0.429	−0.742	−0.201	0.225	0.123
NO_3^-	0.527	−0.177	0.68	0.265	0.112
NO_2^-	−0.271	−0.017	0.557	0.578	0.259
NH_4^+	0.41	−0.578	−0.591	0.179	0.101
NR	−0.206	0.784	−0.362	0.326	0.24
GS	0.724	0.348	0.102	−0.194	0.191
GOGAT	−0.026	−0.284	0.049	−0.468	0.817
Eigenvalue	3.891	2.147	1.42	1.289	1.02
Contribution rate (%)	35.373	19.52	12.909	11.722	9.274
Cumulative percentage (%)	35.373	54.893	67.802	79.524	88.799

SS sucrose synthase, *SPS* sucrose phosphate synthase, *INV* invertase, NO_3^- nitrate, NO_2^- nitrite, NH_4^+ ammonium, *NR* nitrate reductase, *GS* glutamine synthetase, *GOGAT* glutamate synthase

which helps to maintain the balance of N metabolism in *G. uralensis* exposed to salt stress. In addition, MeJA significantly up-regulated GDH in rice, which plays a role in the re-assimilation of the excess ammonium induced exposed to stress (Wu et al. 2019). The effect of MeJA on GDH activity should be considered subsequently in this study to help clarify in more deeply the mechanisms by which MeJA improves nitrogen metabolism under salt stress.

Secondary metabolism is the result that the interaction between plants and environments in the long-term evolution, and it is closely correlated with the strengthening of plant tolerance to stresses (Xiao-Hong et al. 2005; Wang et al. 2015). The production of anthraquinone, phenolics and flavonoids was increased in adventitious roots of *Morinda citrifolia* under salt stress (Baque et al. 2010). The contents of secondary metabolites in *Swertia chirata* Buch.-Ham were remarkably increased under salt stress (Abrol et al. 2012). Salt stress also remarkably enhanced the total phenolics and γ- and δ-tocopherols levels in wild almond species (Sorkheh et al. 2012). In this study, the results found that salt stress significantly decreased glycyrrhizic acid content in *G. uralensis* plants, but has no effect on glycyrrhizin and licochalcone A contents. Salt stress also decreased total flavonoids and polysaccharides contents in *G. uralensis* plants, suggesting that salt stress remarkably regulated the synthesis and accumulation of secondary metabolites. However, salt stress significantly increased the total saponin content that perhaps a responsive strategy for *G. uralensis* seedlings adapt to salt stress by producing more secondary metabolites, further promoting plant growth. Previous studies have found that the application of exogenous substances (plant growth regulators) can effectively promote the synthesis of secondary metabolites in plants (Yu et al. 2018). In *Catharanthus roseus* L., MeJA promoted the accumulation of secondary metabolites (Ruiz-May et al. 2011). In *Polygonum multiflorum,* MeJA enriches arachidonic acid and linoleic acid metabolisms, and biosynthesis of stilbenoid by inducing transcriptome changes (Liu et al. 2015). Our results showed that MeJA remarkably enhanced glycyrrhizic acid, licochalcone A contents, total flavonoids and polysaccharides contents compared in salt-stressed *G. uralensis* seedlings. These results indicated that MeJA could induce

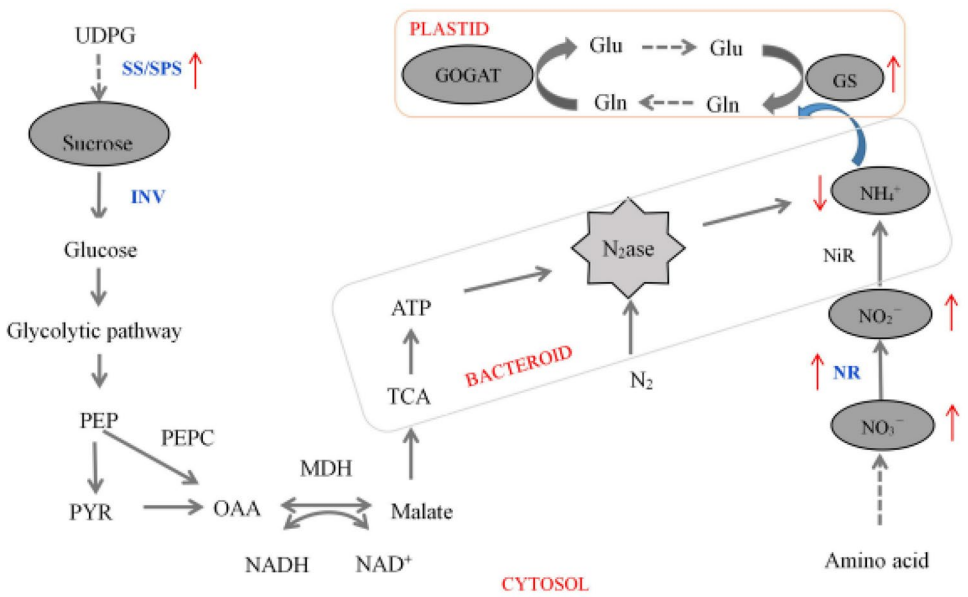

Fig. 5 Effect of MeJA in salt-stressed *G. uralensis* seedlings by carbon and nitrogen metabolism. Sucrose synthase (SS), sucrose phosphate synthase (SPS) and sucrose of carbon metabolism were analyzed, and nitrate (NO_3^-), ammonium (NH_4^+), nitrate reductase (NR), glutamate synthase (GOGAT), nitrite (NO_2^-) and glutamine synthetase (GS) of nitrogen metabolism were also detected. The pointing of red arrows in the figure represent the changes of enzymes and substances in carbon and nitrogen metabolism which were mainly affected by MeJA

the accumulation of secondary metabolites in *G. uralensis* seedlings, the possible reason is that MeJA regulates the key enzymes related to the secondary metabolites and its gene expression in *G. uralensis* which need further research.

Conclusions

MeJA could relieve the harmful effects caused by salt stress on *G. uralensis* seedlings through affecting C and N metabolisms that further trigger the accumulation of secondary metabolites. Specifically, MeJA significantly increased carbohydrate contents by enhancing the activities of related enzymes in C metabolism in *G. uralensis*. Moreover, the increase in soluble sugar and sucrose induced by MeJA plays a protective role in osmotic regulation of salt-stressed *G. uralensis*. Meanwhile, MeJA enhanced the N metabolism that could induce *G. uralensis* seedlings produce more amino acids and total N to overcome osmotic damage. Furthermore, MeJA significantly increased glycyrrhizic acid, licochalcone A, total flavonoids and total polysaccharides contents in salt-stressed *G. uralensis*. Thus, MeJA can effectively regulate different metabolites in *G. uralensis* to relieve osmotic pressure under salt stress to improve growth. Further research should investigate mechanisms of molecular by which MeJA affect secondary metabolism, including signaling pathway to regulate biosynthesis gene expression. The positive MeJA effects on *G. uralensis* for growth and the accumulation of secondary metabolites also need to be tested under field conditions.

Author contribution statement XH Z conceived and designed the experiments; X M, XX Y, GC C and DY L performed the experiments; X M wrote the manuscript; XX Y made the figure; ZG G provided guidance on the whole manuscript, and all authors read and approved the final manuscript and post no conflicting interest.

Acknowledgements Not applicable.

Funding This study was financially supported by the National Natural Science Foundation of China (31860343), the Ningxia Science and Technology Innovation Leader Program (2020GKLRLX12). The authors declare that no funding agency have any role in the design of the study, data collection, analysis, interpretation or manuscript writing.

Availability of data and materials The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no competing interests.

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