Physiological Responses of Lycium ruthenicum Seedlings to Exogenous Salicylic Acid Under Dual Stress of NaCl and Drought: Postprint

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Abstract

Drought and salinity have become major factors limiting plant growth and development, and plant growth and development are affected to a certain extent under dual stress of drought and NaCl. To investigate the adaptability of Lycium ruthenicum to salt-drought stress, this study employed a pot experiment to examine the effects of combined NaCl and drought stress on seedling growth, and observed the physiological responses of Lycium ruthenicum seedlings to exogenous salicylic acid under salt-drought stress, aiming to improve the survival rate of Lycium ruthenicum seedlings under NaCl and drought stress. The results showed that under exogenous salicylic acid treatment (0.1, 0.5 $mmol \cdot L^{-1}$), the contents of soluble sugars, soluble protein, and proline (Pro) in Lycium ruthenicum leaves increased, while malondialdehyde (MDA) content decreased significantly ($P < 0.05$), and the activities of catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD) increased, with the 0.5 $mmol \cdot L^{-1}$ salicylic acid treatment being more effective than the 0.1 $mmol \cdot L^{-1}$ treatment. Based on these results, it can be concluded that Lycium ruthenicum possesses certain adaptability to mild salt-drought stress, and appropriate concentrations of salicylic acid can enhance the contents of osmotic adjustment substances and antioxidant enzyme activities in Lycium ruthenicum leaves under salt-drought stress, providing a theoretical basis for further understanding the growth and development of Lycium ruthenicum seedlings under dual salt-drought stress.

Full Text

Preamble

Physiological Responses of Lycium ruthenicum Seedlings to Exogenous Salicylic Acid Under Combined Salt and Drought Stress

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Abstract

Drought and salinity are major environmental factors limiting plant growth and development, and their combined effects significantly impact plant performance. To investigate the adaptability of *Lycium ruthenicum* to combined salt and drought stress, we conducted a pot experiment to examine the effects of NaCl and drought stress on seedling growth and the physiological responses to exogenous salicylic acid (SA) under these conditions, with the aim of improving seedling survival rates. The results demonstrated that exogenous SA treatments (0.1 and $0.5\ \mathrm{mmol \cdot L^{-1}}$) increased the contents of soluble sugars, soluble proteins, and proline in *L. ruthenicum* leaves while significantly decreasing malondialdehyde (MDA) content ($P < 0.05$). Additionally, SA application enhanced the activities of catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD), with the $0.5\ \mathrm{mmol \cdot L^{-1}}$ treatment showing superior effects compared to $0.1\ \mathrm{mmol \cdot L^{-1}}$. These findings indicate that *L. ruthenicum* possesses a certain capacity to adapt to mild salt-drought stress, and that appropriate SA concentrations can enhance osmotic adjustment substance content and antioxidant enzyme activity under combined stress conditions. This study provides a theoretical foundation for understanding the growth and development of *L. ruthenicum* seedlings under combined salt and drought stress.

Keywords: *Lycium ruthenicum*, salt-drought stress, salicylic acid, physiology, stress resistance

Introduction

Lycium ruthenicum is a perennial shrub belonging to the family Solanaceae and genus *Lycium*, widely distributed in northwestern China. Due to its strong environmental adaptability, it predominantly grows in environments characterized by combined drought and salt stress. In recent years, *L. ruthenicum* has been extensively planted as a soil and water conservation species. The wild berries contain the highest known concentration of proanthocyanidins among natural fruits and are rich in anthocyanins, flavonoids, and polysaccharides, exhibiting hypolipidemic and antioxidant effects. As one of the most effective natural antioxidants, it has been dubbed "soft gold" and shows significant market potential, with relevant extraction processes already reported. However, the habitats of *L. ruthenicum* face increasing stress factors, particularly severe salt and drought conditions. While numerous studies have investigated physiological and biochemical responses to either drought or salinity stress individually, this study examines the combined effects of NaCl and drought stress on *L. ruthenicum* seedlings to improve survival rates under dual stress conditions.

Salt and drought-induced osmotic stress substantially affects plant growth and development. Previous experiments demonstrated that both drought and salt stress inhibit *L. ruthenicum* seed germination, reducing germination rate, germination potential, germination index, and relative root length to varying degrees. Exogenous salicylic acid application can alleviate these inhibitory effects by accelerating germination rate and improving seed vigor.

Salicylic acid (SA), or o-hydroxybenzoic acid, is a simple phenolic compound that functions as a signaling molecule regulating physiological and metabolic processes in plants. It plays important roles in plant responses to various abiotic stresses including salinity, drought, low temperature, and disease. Research has demonstrated that exogenous SA effectively enhances plant salt tolerance, drought resistance, and stomatal regulation. This study investigates the physiological responses of *L. ruthenicum* to combined salt-drought stress under exogenous SA application—a topic with limited existing research. The objective is to determine whether exogenous SA can mitigate physiological damage under combined stress and to elucidate the physiological mechanisms involved, thereby providing theoretical and technical support for artificial cultivation and vegetation restoration of this valuable species in saline and arid lands.

Materials and Methods

1.1 Plant Material

Seeds of *Lycium ruthenicum* were collected in 2018 from the Kaidu River basin in Bohu County, Xinjiang. Bohu County is located in an arid oasis region with a dry climate and scarce precipitation. The Kaidu River basin lies within a central Eurasian inland desert, characterized by a warm temperate desert climate. The regional vegetation consists primarily of xerophytic shrubs, succulent halophytic woodlands, and *Achnatherum splendens* communities. Plant materials were cultivated in the Xinjiang Key Laboratory of Special Species Conservation and Regulatory Biology.

1.2 Experimental Design

Seeds were pre-soaked in a 40°C water bath for 48 hours to break dormancy, then sterilized with sodium hypochlorite solution. Uniform, plump seeds were selected and sown in plastic pots containing 1 kg of oven-dried soil with a bulk density of 1.23 $\mathrm{g \cdot cm^{-3}}$ and field capacity of 20.16%. All pots were placed in a natural environment for germination and growth. Drought stress was initiated by withholding water until soil moisture naturally declined to target levels.

Drought stress was applied at three levels: control (CK) with relative water content (RWC) of 85–90%, mild drought (D1) with RWC of 60–65%, and severe drought (D2) with RWC of 20–25% (Hsiao et al., 1973). NaCl concentrations were set as: control at 0 $\mathrm{mmol \cdot L^{-1}}$ (CK, distilled water), mild salt stress (T1, 100 $\mathrm{mmol \cdot L^{-1}}$), and severe salt stress (T2, 400 $\mathrm{mmol \cdot L^{-1}}$). Five combined stress treatments were established: CK (no NaCl, no drought), T1D1 (mild stress), T1D2 (mild salt + severe drought), T2D1 (severe salt + mild drought), and T2D2 (severe stress). Salicylic acid solutions were prepared at concentrations of 0, 0.1, and 0.5 $\text{mmol} \cdot \text{L}^{-1}$, resulting in 15 total treatments with three replicates each.

SA was applied via root irrigation. NaCl solution was first applied to the roots, followed by drought stress treatment according to the experimental design. Water was withheld until target moisture levels were reached, marking the initiation of drought stress. Exogenous SA treatments were applied on days 1, 3, and 5 after drought initiation. Each evening at 20:00, 20 mL of SA solution was applied to each pot. Pot weights were recorded daily using an electronic balance, and water was supplemented to maintain target soil moisture content. The stress period lasted 28 days.

Given that *L. ruthenicum* naturally inhabits saline-alkali soils frequently subjected to drought, this study investigated the effects of combined stress on physiological and biochemical parameters. The objective was to understand how *L. ruthenicum* regulates its antioxidant system under varying abiotic stress levels and whether exogenous SA application could alleviate damage caused by different intensities of NaCl and drought stress.

1.3 Physiological Measurements

On day 28 of combined stress treatment, fully expanded functional leaves from the shoot apex of *L. ruthenicum* seedlings were harvested for determination of soluble sugar, soluble protein, free proline (Pro), and malondialdehyde (MDA) contents, as well as antioxidant enzyme (CAT, POD, SOD) activities. Soluble sugar content was measured using the anthrone colorimetric method (Wang, 2000). Soluble protein content was determined via the Coomassie brilliant blue method (Bradford, 1976). Free proline content was analyzed using the acidic ninhydrin colorimetric method (Gao, 2006). MDA content and antioxidant enzyme activities were measured using commercial assay kits (Nanjing Jiancheng Bioengineering Institute).

All experimental data were processed using Microsoft Office Excel and analyzed statistically with SPSS 22.0. One-way ANOVA and Duncan's multiple comparison tests ($P < 0.05$) were performed among different stress treatments, along with correlation analysis. Graphical presentations were created using Origin software.

Results

2.1 Effects of Exogenous SA on Soluble Sugar Content

As shown in [Figure 1: see original paper], soluble sugar content in *L. ruthenicum* leaves increased with intensifying salt-drought stress across all treatments, following the pattern: distilled water (CK) < 0.1 $\text{mmol} \cdot \text{L}^{-1}$ SA <

$0.5\ \mathrm{mmol \cdot L^{-1}}$ SA. Exogenous SA application induced accumulation of soluble sugars under combined stress, with the most significant increase observed under severe combined stress (T2D2) at $0.5\ \mathrm{mmol \cdot L^{-1}}$ SA ($P < 0.05$). These results indicate that soluble sugar content is sensitive to NaCl and drought stress and can serve as an indicator of plant stress resistance. Moreover, SA-promoted soluble sugar accumulation represents one strategy for coping with combined salt-drought stress, playing an important role in alleviating synergistic toxicity. Two-way ANOVA revealed that salt-drought stress, SA treatment, and their interaction all significantly affected soluble sugar content ($P < 0.05$), with salt-drought stress and SA × stress interaction showing highly significant effects ($P < 0.001$) ().

2.2 Effects of Exogenous SA on Soluble Protein Content

After 28 days of combined stress, soluble protein content in *L. ruthenicum* leaves showed an initial increase followed by a decrease compared to CK, with increases of 47.6%, 51.4%, 61.7%, and 44.1% across treatment groups. The lowest content occurred under severe stress, suggesting that new soluble proteins are synthesized under mild combined stress to enhance stress resistance. Exogenous SA application increased soluble protein content under NaCl and drought stress, with 0.1 and $0.5\ \mathrm{mmol \cdot L^{-1}}$ SA treatments showing significant increases ($P < 0.05$) of 34.6%/41.3%, 62.0%/72.8%, 74.7%/89.4%, and 49.5%/50.1% compared to CK. Under severe stress (T2D2), soluble protein content decreased substantially, though SA application still demonstrated positive effects on salt and drought tolerance. The $0.5\ \mathrm{mmol \cdot L^{-1}}$ SA treatment was most effective in promoting soluble protein accumulation. Two-way ANOVA indicated that combined stress and SA × stress interaction had highly significant effects on soluble protein content, while SA treatment alone showed no significant effect ().

2.3 Effects of Exogenous SA on Free Proline Content

Proline content in *L. ruthenicum* leaves increased significantly with stress intensity, showing increases of 20.9%, 44.1%, 48.8%, and 77.1% compared to CK ($P < 0.05$). Exogenous SA application effectively promoted proline accumulation under NaCl and drought stress, with 0.1 and $0.5\ \mathrm{mmol \cdot L^{-1}}$ SA treatments increasing proline content by 27.2%/29.0%, 50.8%/65.7%, 68.4%/74.8%, and 88.7%/96.6% compared to CK. These results demonstrate that proline accumulation becomes more pronounced with increasing combined stress intensity within a certain range, and that appropriate SA concentrations can enhance proline accumulation, with $0.5\ \mathrm{mmol \cdot L^{-1}}$ SA showing the greatest effect. Two-way ANOVA revealed that combined stress had a highly significant effect on proline content, while SA × stress interaction was significant ($P < 0.05$) and SA treatment alone had no significant effect.

2.4 Effects of Exogenous SA on MDA Content

Malondialdehyde (MDA), a product of membrane lipid peroxidation, indicates the degree of cell membrane damage. As shown in [Figure 4: see original paper], MDA content in *L. ruthenicum* leaves increased rapidly with intensifying NaCl and drought stress, with greater accumulation under more severe stress. This indicates that varying degrees of combined stress caused different levels of membrane lipid peroxidation in *L. ruthenicum* leaves, with excessive free radicals triggering membrane damage that was most severe under combined stress. Exogenous SA application reduced MDA content compared to CK, demonstrating that appropriate SA concentrations can decrease MDA accumulation under combined stress. The 0.5 $\mathrm{mmol \cdot L^{-1}}$ SA treatment showed the most significant reduction in MDA content compared to both CK and 0.1 $\mathrm{mmol \cdot L^{-1}}$ treatments, effectively enhancing salt and drought tolerance. Two-way ANOVA confirmed that both combined stress and SA treatment significantly affected MDA content.

2.5 Effects of Exogenous SA on CAT Activity

Catalase (CAT) is a protective enzyme in plant membrane systems that scavenges hydrogen peroxide accumulated during environmental stress, mitigating damage. As shown in [Figure 5: see original paper], CAT activity increased to varying degrees under NaCl and drought stress, suggesting that *L. ruthenicum* may enhance CAT activity to resist abiotic stress. Exogenous SA at 0.1 and 0.5 $\mathrm{mmol \cdot L^{-1}}$ increased CAT activity compared to CK by 0.5%/6%, 7.7%/3.0%, 6.2%/12.3%, 5.2%/10.4%, and 13.5%/57.8%. The 0.5 $\mathrm{mmol \cdot L^{-1}}$ SA treatment was markedly more effective than 0.1 $\mathrm{mmol \cdot L^{-1}}$. Under severe stress (T2D2), CAT activity decreased substantially due to severe membrane damage, but 0.5 $\mathrm{mmol \cdot L^{-1}}$ SA effectively enhanced CAT activity and alleviated NaCl and drought-induced damage. Two-way ANOVA showed that combined stress and SA × stress interaction had highly significant effects on CAT activity.

2.6 Effects of Exogenous SA on POD Activity

Peroxidase (POD) activity in *L. ruthenicum* leaves showed a slight increase after 28 days of combined stress. Exogenous SA at 0.1 and 0.5 $\mathrm{mmol \cdot L^{-1}}$ enhanced POD activity compared to CK by 3.0%/6.1%, 16.2%/16.9%, 27.1%/34.5%, 34.9%/38.2%, and 41.6%/53.8%. The 0.5 $\mathrm{mmol \cdot L^{-1}}$ SA treatment was most effective in enhancing POD activity. Under mild combined stress, POD activity changed minimally, indicating that *L. ruthenicum* can tolerate mild stress. Under severe stress, SA application substantially increased POD activity, enhancing stress resistance. Two-way ANOVA revealed that combined stress and SA × stress interaction significantly affected POD activity, while SA treatment alone had no significant effect.

2.7 Effects of Exogenous SA on SOD Activity

Under increasing NaCl and drought stress without SA application, SOD activity in *L. ruthenicum* leaves initially increased then decreased. Following SA application, SOD activity increased across all treatments, with 0.1 and 0.5 mmol $\cdot$ L^{-1} SA treatments increasing activity by 2.8%/6.1%, 14.0%/17.0%, 19.6%/19.5%, 22.6%/24.5%, and 22.5%/25.8% compared to CK. Appropriate SA concentrations enhanced SOD activity under combined stress, reducing damage and improving stress resistance. Two-way ANOVA showed that combined stress had a highly significant effect on SOD activity, while SA treatment alone and SA × stress interaction had no significant effects.

Discussion and Conclusion

Previous seed germination experiments showed that *L. ruthenicum* seeds germinated well under mild combined stress, but germination capacity decreased with increasing stress intensity, confirming that drought and salinity are important factors limiting seed germination. In this study, combined NaCl and drought stress increased the contents of soluble sugars, soluble proteins, and proline in *L. ruthenicum* leaves. Soluble sugars serve as primary osmotic adjustment substances that stabilize cell membranes and protoplasmic colloids during stress, with greater accumulation indicating stronger stress resistance. The significant increase in soluble sugar content under combined stress ($P < 0.05$) suggests a substantial contribution to osmotic adjustment.

With intensifying stress, soluble protein content initially increased then decreased, with the most significant increase under severe stress. This pattern may be related to degradation rates and is consistent with changes observed in *Ammodendron argenteum* under salt-drought stress. Proline content increased with stress intensity, with progressively greater accumulation under more severe stress, consistent with studies on *Gleditsia sinensis* and *Diospyros lotus*. Under mild stress, increasing soluble sugar and proline contents enhanced osmotic adjustment capacity, maintaining low leaf damage rates and relatively good growth. However, MDA content accumulated substantially with increasing stress intensity. As a primary product of lipid peroxidation, MDA damages biological membrane structure and function, serving as an indicator of membrane injury. The accumulation of reactive oxygen species under combined stress disrupted the protective enzyme system balance, leading to membrane damage. Protective enzymes such as CAT, POD, and SOD function as free radical scavengers.

Previous research on *Gleditsia sinensis* showed that POD and SOD activities initially increased then decreased with prolonged salt-drought stress. In this study, CAT, POD, and SOD activities in *L. ruthenicum* showed different patterns under varying stress intensities. CAT and SOD activities increased under mild and moderate stress (T1D1, T2D1, T1D2) but decreased under severe stress (T2D2). POD activity increased with salt concentration under T1D1 and

T2D1, but showed an initial increase followed by decrease under severe drought conditions (T1D2, T2D2). The antioxidant protection system was disrupted under severe stress, leading to reduced enzyme activity and significant membrane damage that limited plant growth.

Salicylic acid is a simple phenolic acid and endogenous plant hormone that promotes accumulation of osmotic adjustment substances under abiotic stress. This study demonstrated that 0.1 and 0.5 $\mathrm{mmol \cdot L^{-1}}$ exogenous SA enhanced soluble sugar, soluble protein, and proline accumulation under combined stress, with 0.5 $\mathrm{mmol \cdot L^{-1}}$ SA showing more pronounced effects. SA application also reduced MDA content and alleviated membrane damage, with 0.5 $\mathrm{mmol \cdot L^{-1}}$ SA being most effective, though the underlying mechanisms require further investigation.

Lycium ruthenicum exhibits certain stress tolerance under mild salt-drought conditions, but long-term severe stress reduces antioxidant enzyme activity and exacerbates membrane lipid peroxidation, causing irreversible membrane damage. This explains the initial increase followed by decrease in CAT, POD, and SOD activities under severe stress. The results demonstrate that appropriate SA concentrations can enhance osmotic adjustment substance content and antioxidant enzyme activity under combined stress, alleviating membrane lipid peroxidation damage and improving stress adaptation.

Two-way ANOVA of all measured indicators revealed highly significant differences for all physiological parameters under combined stress. Under SA × stress interaction, nearly all indicators showed significant differences, with soluble sugar, soluble protein, and CAT activity reaching highly significant levels. Individual SA treatment only significantly affected soluble sugar and MDA contents, indicating these parameters can serve as characteristic indicators for SA-mediated alleviation of salt-drought stress.

In conclusion, *L. ruthenicum* seedlings can regulate osmotic adjustment substances and antioxidant enzyme activity to cope with combined NaCl and drought stress. Exogenous SA application enhances the accumulation of resistance-related substances such as soluble sugars and proteins, while increasing CAT, POD, and SOD activities, thereby reducing reactive oxygen species levels and MDA content. This alleviates membrane lipid peroxidation damage, demonstrates the physiological response to exogenous SA under combined stress, and promotes seedling growth under dual stress conditions, ultimately improving drought resistance in *L. ruthenicum*.

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