Effects of Paclobutrazol on Seedling Growth of the Typical Psammophyte Hedysarum mongolicum: A Postprint

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Abstract

Paclobutrazol (PP333) is a gibberellin inhibitor that can enhance plant stress resistance by regulating plant growth and physiological processes. To investigate the effects of exogenous PP333 application on the growth of Hedysarum leave seedlings under salt stress and to screen for the optimal concentration of PP333 to improve salt tolerance in Hedysarum leave, this study used Hedysarum leave seedlings as materials and employed a pot culture method. After treatment with 250 mmol · L-1 NaCl stress, PP333 at concentrations of 0, 150, 300, 450, and 600 mg · L-1 was applied via root irrigation, and changes in seedling growth, photosynthetic characteristics, and stress-resistance physiological indices were analyzed under each treatment, with evaluation conducted using the membership function method. The results showed that after salt stress, the basal diameter growth increment and plant height growth increment of Hedysarum leave seedlings were inhibited; net photosynthetic rate (Pn), transpiration rate (Tr), stomatal conductance (Gs), photosynthetic pigment content, and superoxide dismutase (SOD) activity decreased; intercellular CO2 concentration (Ci), malondialdehyde (MDA) content, peroxidase (POD) activity, soluble sugar (Ss) content, and proline (Pro) content increased. Root application of PP333 could effectively regulate the growth of Hedysarum leave seedlings, alleviate the adverse effects of salt stress on photosynthetic efficiency and antioxidant enzyme activity, and reduce the degree of membrane lipid peroxidation. Comprehensive analysis indicated that treatment with 600 mg · L-1 PP333 could enhance photosynthetic efficiency, antioxidant enzyme defense, and osmotic regulation capacity of Hedysarum leave seedlings under salt stress, effectively regulating growth to cope with salt stress.

Full Text

Effects of Paclobutrazol on the Growth of Typical Psammophyte *Corethrodendron fruticosum* Seedlings

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Abstract

Paclobutrazol (PP333) is a gibberellin biosynthesis inhibitor that enhances plant stress resistance by regulating growth and physiological processes. This study investigated the effects of exogenous PP333 application on *Corethrodendron fruticosum* seedlings under salt stress to identify the optimal concentration for improving salt tolerance. Using pot experiments, seedlings were subjected to 250 $mmol \cdot L^{-1}$ NaCl stress and treated with PP333 at concentrations of 0, 150, 300, 450, and 600 $mg \cdot L^{-1}$ via root irrigation. Growth metrics, photosynthetic characteristics, and stress-resistance physiological indices were measured, and comprehensive evaluation was performed using the membership function method. The results demonstrated that salt stress significantly inhibited basal diameter and height growth of *C. fruticosum* seedlings, reduced net photosynthetic rate (Pn), transpiration rate (Tr), stomatal conductance (Gs), photosynthetic pigment content, and superoxide dismutase (SOD) activity, while increasing intercellular CO_2 concentration (Ci), malondialdehyde (MDA) content, peroxidase (POD) activity, soluble sugar (SS) content, and proline (Pro) content. PP333 application effectively regulated seedling growth, mitigated the adverse effects of salt stress on photosynthetic efficiency and antioxidant enzyme activity, and reduced membrane peroxidation. Comprehensive analysis revealed that 600 $mg \cdot L^{-1}$ PP333 treatment optimally enhanced photosynthetic efficiency, antioxidant defense, and osmotic adjustment capacity under salt stress, effectively regulating growth to cope with saline conditions.

Keywords: *Corethrodendron fruticosum* seedlings; salt stress; paclobutrazol (PP333); growth characteristics; physiological characteristics

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1. Introduction

Soil salinization represents a major challenge to ecological environments and agricultural production in China, particularly in arid and semi-arid regions where salinized areas continue expanding, posing significant obstacles to vegetation restoration and ecological management. Excessive soil salt accumulation causes ion toxicity, intensifies oxidative and osmotic stress, reduces photosynthetic efficiency, elevates reactive oxygen species (ROS) levels, and disrupts membrane structures and enzyme system functions. When salt stress exceeds plant tolerance thresholds, growth stagnation or even death may occur. Consequently, identifying effective methods to enhance plant salt tolerance is crucial for promoting vegetation recovery and ensuring stable crop yields.

Paclobutrazol (PP333), a widely used plant growth regulator, delays plant growth, promotes tillering, thickens stems and roots, and enhances photosynthetic capacity and stress resistance. Under salt stress, PP333 increases photosynthetic pigment content, reduces malondialdehyde (MDA) accumulation, delays pigment degradation and membrane lipid peroxidation, promotes osmotic adjustment substance accumulation, improves cellular water retention, and alleviates ion toxicity. However, the mechanisms and optimal application concentrations of PP333 vary among plant species and developmental stages. For instance, 1500 $mg \cdot L^{-1}$ PP333 proved most effective for enhancing antioxidant capacity and osmotic adjustment in mango (*Mangifera indica*) seedlings, whereas 400 $mg \cdot L^{-1}$ was optimal for tall fescue (*Festuca arundinacea*). Therefore, investigating PP333 effects on specific plants under salt stress is essential for optimizing application strategies and improving salt tolerance.

Corethrodendron fruticosum (formerly *Hedysarum leave*), a leguminous semishrub typical of sandy environments, is widely distributed across arid and semiarid regions of northern China, including the Mu Us Sandy Land, Kubuqi Desert, Hunshandake Sandy Land, and Horqin Sandy Land. Renowned for its wind erosion resistance, heat and drought tolerance, and adaptability to infertile soils, this species serves as a pioneer plant for soil conservation and desertification control, extensively used in aerial seeding and shelterbelt construction. However, extreme water scarcity and intensifying soil salinization in these regions severely constrain *C. fruticosum* growth. While the species can actively adapt to adverse conditions through its antioxidant system and osmotic adjustment mechanisms, these processes are limited by physiological characteristics and stress intensity, proceeding relatively slowly. Thus, exploring effective artificial regulation measures to enhance its salt tolerance is vital for both species development and sustainable utilization of sandy land plant resources.

Currently, research on PP333 application for alleviating salt stress in *C. fruticosum* remains limited, with unclear mechanisms regarding its effects on growth, photosynthetic characteristics, and stress physiology. This study investigated *C. fruticosum* seedlings under salt stress, applying different PP333 concentrations via root irrigation to measure growth indices, photosynthetic parameters, and stress-resistance indicators. The objective was to elucidate PP333 regulatory effects on salt tolerance and identify the optimal concentration, providing a scientific basis for cultivating and protecting psammophytes in arid regions.

2. Materials and Methods

2.1 Experimental Materials Healthy, uniformly sized *C. fruticosum* seedlings were collected from Minqin County, Wuwei City, Gansu Province. The test reagents included PP333 powder (analytical grade, \$ \$99.5% purity, Sichuan Runer Technology Co., Ltd.) and NaCl (analytical grade, Sinopharm Chemical Reagent Co., Ltd.). The cultivation substrate consisted of field soil from the greenhouse area at Inner Mongolia Agricultural University, sieved through a 2 mm mesh.

2.2 Experimental Design The experiment was conducted in an intelligent greenhouse at Inner Mongolia Agricultural University. In early May, uniformly sized seedlings were transplanted into pots (15 cm diameter $\times$ 18 cm height) containing 2.5 kg of soil substrate, with trays placed underneath. During the recovery period, seedlings received routine management and regular weeding. To ensure uniform environmental conditions (light, temperature, humidity), pots were repositioned every 7 days along diagonal lines.

After recovery, 250 $\text{mmol} \cdot \text{L}^{-1}$ NaCl was selected for stress treatment based on preliminary experiments and literature review, representing severe salt stress for *C. fruticosum* seedlings. The experiment comprised six treatment groups with five replicates each:

- **CK:** Control group, no treatment
- **NP:** Salt stress control, single salt treatment without PP333
- **NP150, NP300, NP450, NP600:** Salt stress plus PP333 at 150, 300, 450, and 600 $\text{mg} \cdot \text{L}^{-1}$, respectively

To avoid salt leaching, NaCl solution was applied in three portions (300 mL each time). On the evening of day 3 after salt application, specific PP333 concentrations were applied via root irrigation (200 mL each). Following stress and chemical treatments, seedlings received quantitative watering to maintain soil moisture while preventing salt and PP333 loss. Any water collected in trays was poured back into pots. Growth and physiological indices were measured 30 days after PP333 application (early July).

2.3 Measurement Methods 2.3.1 Growth Indices

Basal diameter and plant height were measured before and after treatment. Basal diameter was measured with digital calipers (precision 0.01 mm), and plant height with a tape measure (precision 0.01 cm). Growth increments were calculated as:

Basal diameter increment = post-treatment diameter - initial diameter
Plant height increment = post-treatment height - initial height

2.3.2 Photosynthetic Parameters

On clear, windless days, a portable photosynthesis system (GFS-3000) was used to measure the third fully expanded leaf from the top. Net photosynthetic rate (Pn), transpiration rate (Tr), stomatal conductance (Gs), and intercellular CO_2 concentration (Ci) were recorded between 9:00-11:00 AM. Photosynthetic pigment content was determined using the ethanol-acetone extraction method. Each treatment was measured five times.

2.3.3 Stress-Resistance Physiological Indices

Fresh leaf samples were wrapped in aluminum foil, flash-frozen in liquid nitrogen, and stored at -85°C. Superoxide dismutase (SOD) activity, peroxidase (POD) activity, malondialdehyde (MDA) content, proline (Pro) content, and soluble sugar (SS) content were measured using assay kits from Beijing Solarbio Science & Technology Co., Ltd. Each treatment was measured five times.

2.4 Salt Tolerance Evaluation The membership function method was used to comprehensively evaluate salt tolerance under different PP333 treatments. Higher average membership function values indicate stronger salt tolerance. The formulas were:

For positive correlation with salt tolerance:
U(X) = (X - X_{min}) / (X_{max} - X_{min})

For negative correlation with salt tolerance:
U(X) = 1 - (X - X_{min}) / (X_{max} - X_{min})

Where X is the measured value, and X_{min} and X_{max} are the minimum and maximum values for each indicator.

2.5 Data Analysis Data were recorded and organized using Excel 2019. One-way ANOVA and multiple comparisons (Duncan' s method) were performed using SPSS 27.0, with significance set at $P < 0.05$. Figures were created using Origin 2022. Data are presented as means ± standard deviation.

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3. Results

3.1 Effects of PP333 on Growth Characteristics Under Salt Stress Compared with the control, salt stress significantly reduced basal diameter increment by 41.26% and height increment by 68.60% in *C. fruticosum* seedlings. Under PP333 treatment, basal diameter increment initially increased then decreased, peaking at NP450 (0.59 mm), which was significantly higher than NP (0.38 mm). Height increment showed a continuous decreasing trend, reaching its lowest value at NP600 (1.69 cm), which was significantly reduced by 30.17% compared to NP.

3.2 Effects of PP333 on Photosynthetic Pigment Content Under Salt Stress Salt stress significantly decreased chlorophyll a, chlorophyll b, total chlorophyll [Chl(a+b)], and carotenoid content by 50.21%, 36.47%, 45.23%, and 48.08%, respectively, while reducing the chlorophyll a/b ratio [Chl(a/b)] by 21.68% compared to the control. Under PP333 treatment, all pigment contents and the Chl(a/b) ratio showed gradual increasing trends, peaking at NP600. Specifically, NP600 significantly increased chlorophyll a, chlorophyll b, total chlorophyll, carotenoids, and Chl(a/b) by 19.66%, 10.96%, 23.03%, 25.97%, and 13.60%, respectively, compared to NP.

3.3 Effects of PP333 on Photosynthetic Gas Exchange Parameters Under Salt Stress Salt stress significantly reduced Pn, Tr, and Gs by 66.59%, 82.51%, and 84.16%, respectively, while increasing Ci by 72.59% compared to the control. Under PP333 treatment, Pn, Tr, and Gs showed initial increases followed by decreases, peaking at NP600. NP600 significantly increased Pn, Tr, and Gs by 230.10%, 65.72%, and 161.11%, respectively, compared to NP. Ci exhibited a decreasing-then-increasing pattern, reaching its minimum at NP600 (178.03 $\text{mol} \cdot \text{mol}^{-1}$), which was significantly lower than NP by 19.96%.

3.4 Effects of PP333 on Antioxidant System Under Salt Stress 3.4.1 Malondialdehyde Content

Under salt stress, membrane lipid peroxidation occurs in plant organs, with MDA accumulation reflecting membrane damage. Salt stress significantly increased MDA content by 235.09% compared to the control. PP333 treatment reduced MDA content continuously, with NP600 showing the most significant reduction (34.14% lower than NP).

3.4.2 Antioxidant Enzyme Activities

Superoxide dismutase (SOD), a key antioxidant enzyme and the first line of defense against free radical damage, showed decreased activity under salt stress. PP333 treatment enhanced SOD activity, which initially increased, then decreased, then increased again, peaking at NP600 (77.74 $\text{U} \cdot \text{g}^{-1}$), significantly higher than NP by 50.34%.

Peroxidase (POD), primarily expressed during stress or senescence, exhibited dual roles in the antioxidant system. Salt stress significantly increased POD activity by 52.78% compared to the control. Under PP333 treatment, POD activity first decreased, then increased, then decreased again, reaching its minimum at NP600 (808.41 $\text{U} \cdot \text{g}^{-1}$), significantly lower than NP by 45.12%.

3.5 Effects of PP333 on Osmotic Adjustment Substances Under Salt Stress Soluble sugars and proline are crucial osmotic adjustment substances that help plants adapt to saline environments. Salt stress significantly increased SS and Pro contents by 48.98% and 16.33%, respectively. PP333 treatment further enhanced these contents, with both showing initial increases followed by decreases, peaking at NP450. NP450 significantly increased SS and Pro contents by 20.13% and 4.84%, respectively, compared to NP.

3.6 Comprehensive Salt Tolerance Evaluation The membership function analysis integrated all indicators to evaluate salt tolerance comprehensively (Table 2). The ranking of average membership function values was: NP600 (0.69) > NP450 (0.57) > NP300 (0.47) > NP150 (0.42) > NP (0.28) > CK (0.78). This indicates that while salt stress damaged seedling development, PP333 root irrigation effectively mitigated these effects, with 600 mg $\cdot$ L^{-1} showing the optimal effect.

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4. Discussion

Salt stress is a primary abiotic factor limiting plant growth and productivity. Studies have shown that salt stress significantly inhibits basal diameter growth in poplar (*Populus* spp.) and reduces plant height in maize (*Zea mays*), while PP333 application alleviates these inhibitory effects on basal diameter but continues to reduce plant height. Our findings align with these results: salt stress significantly reduced both basal diameter and height increments in *C. fruticosum* seedlings, while PP333 increased basal diameter but further decreased height. This occurs because PP333 breaks apical dominance while increasing cell volume and layer numbers in the stem base, enhancing wind erosion and salt damage resistance, optimizing light distribution, and improving energy utilization efficiency. These changes strengthen lodging resistance and improve light interception, enabling more rational nutrient allocation under salt stress.

Plants depend on photosynthesis for energy and biomass accumulation, with photosynthetic capacity directly reflecting assimilatory power. Salt stress inhibits photosynthesis, indirectly affecting growth. Research on physic nut (*Jatropha curcas*) demonstrated that salt stress significantly reduced photosynthetic pigments, Pn, Tr, and Gs while increasing Ci, whereas PP333 alleviated pigment degradation, improved photosynthetic efficiency, and maintained ion balance. Similarly, our study found that salt stress degraded photosynthetic pigments and reduced Pn, Tr, and Gs while increasing Ci, with PP333 effectively reversing these effects, particularly at 600 mg $\cdot$ L^{-1}. Salt stress constrains photosynthesis primarily through non-stomatal limitations (reduced mesophyll photosynthetic activity). PP333 enhances gas exchange, light capture, chloroplast protection, pigment synthesis, and carbon assimilation rates, accelerating enzymatic reactions, reducing cellular osmotic potential, and alleviating non-stomatal limitations to stabilize photosynthetic machinery function.

Malondialdehyde, a primary product of membrane lipid peroxidation, is highly cytotoxic and can cross-link with membrane proteins and enzymes, compromising membrane integrity. Exogenous substances like PP333 can intervene in membrane permeability to delay damage. Studies on quinoa (*Chenopodium quinoa*) and Chinese bayberry (*Myrica rubra*) showed that PP333 reduced MDA production and mitigated membrane damage under salt stress. Our results confirm that salt stress significantly elevated MDA content, while PP333 application decreased it, with 600 $mg \cdot L^{-1}$ showing the most pronounced effect. This indicates PP333 enhances antioxidant capacity, reduces free radical generation, and inhibits membrane lipid peroxidation.

Superoxide dismutase, a key antioxidant enzyme, plays a vital role in scavenging superoxide anion radicals and inhibiting membrane lipid peroxidation. Research on Chinese bayberry and tomato revealed that salt stress increased SOD activity, which was further enhanced by PP333. In contrast, our study found SOD activity decreased under salt stress, likely because the 250 $mmol \cdot L^{-1}$ NaCl concentration exceeded the tolerance threshold, causing substantial SOD consumption during early ROS scavenging. However, PP333 application effectively restored SOD activity, particularly at 600 $mg \cdot L^{-1}$, demonstrating its ability to expand free radical scavenging capacity and prevent metabolic disorders.

Peroxidase exhibits dual roles in plant antioxidant systems: it scavenges hydrogen peroxide as an antioxidant enzyme but also promotes ROS production and chlorophyll degradation during stress or senescence, accelerating senescence. Studies on fenugreek (*Trigonella foenum-graecum*) showed salt stress reduced POD activity, while PP333 alleviated this decline. Conversely, research on physic nut reported increased POD activity under salt stress, which PP333 further elevated. Our findings revealed that salt stress significantly increased POD activity, but PP333 reduced it, with 600 $mg \cdot L^{-1}$ showing the most significant decrease. This suggests that under severe salt stress, POD may act as a harmful agent promoting senescence, while PP333 inhibits POD generation, delays chlorophyll degradation, and reduces free radical attack on cell membranes.

Soluble sugars and proline are important osmotic adjustment substances that maintain intracellular-extracellular osmotic balance, regulate membrane transport, and stabilize antioxidant enzyme activity and structure. Studies on *Caragana korshinskii* and strawberry (*Fragaria ananassa*) demonstrated that PP333 significantly increased SS and Pro contents under salt stress. Our results were consistent: salt stress increased SS and Pro accumulation, and PP333 further enhanced these contents, particularly at 450 $mg \cdot L^{-1}$. This indicates PP333 accelerates the synthesis pathways of osmotic adjustment substances, promoting greater accumulation to maintain optimal cellular osmotic potential and enhance water retention capacity.

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5. Conclusions

1. Salt stress inhibits basal diameter and height growth of *C. fruticosum* seedlings, imposes non-stomatal limitations on photosynthesis, degrades photosynthetic pigments, damages cell membranes, reduces antioxidant capacity, and induces premature senescence. However, seedlings can actively resist salt damage by accumulating osmotic adjustment substances.

2. PP333 application positively regulates *C. fruticosum* seedling growth un-

der salt stress, thickening basal diameter while reducing height, thereby enhancing lodging resistance and light interception. PP333 effectively alleviates photosynthetic pigment degradation, reduces intercellular CO_2 concentration, mitigates non-stomatal limitations, and enhances photosynthetic capacity. It increases osmotic adjustment substance content, reduces MDA accumulation, delays senescence and membrane damage, and strengthens antioxidant capacity.

3. The membership function comprehensive evaluation demonstrated that root irrigation with PP333 enhanced salt tolerance in *C. fruticosum* seedlings, with 600 $mg \cdot L^{-1}$ PP333 showing the optimal effect.

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