

Response of Physiological and Biochemical Indicators of *Davidia involucrata* Seedlings to Heavy Metal Lead and Cadmium Stress: Postprint

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Abstract

Lead and cadmium exhibit strong toxicity in soil, seriously harming plant growth and development. This study focused on *Davidia involucrata*, a Chinese endemic, rare and endangered plant species, to investigate the response patterns of its antioxidant enzyme activity, malondialdehyde (MDA), free proline, and soluble protein to different concentrations of heavy metal lead and cadmium stress under pot experiment conditions. The results showed that: (1) Under different lead concentration treatments, the MDA concentration in *Davidia involucrata* seedlings was significantly higher than that in the control group, while under cadmium stress conditions, except for the $10 \text{ mg} \cdot \text{kg}^{-1}$ concentration, the MDA concentration in the other treatment groups was also significantly higher than that in the control group, indicating that lead and cadmium pollution exacerbated the membrane lipid peroxidation process in *Davidia involucrata*. (2) Free proline exhibited an initial increase followed by a decrease with increasing lead and cadmium concentrations, being significantly lower than the control group under treatments with lead concentration $800 \text{ mg} \cdot \text{kg}^{-1}$ and cadmium concentration $20 \text{ mg} \cdot \text{kg}^{-1}$, respectively. Soluble protein concentration also showed a pattern of initial increase followed by decrease with increasing lead concentration, while its concentration was significantly higher than the control group under all cadmium stress conditions. The increase in soluble protein and free proline could enhance the ability of *Davidia involucrata* to resist low-concentration heavy metal damage, but high-concentration heavy metals had an inhibitory effect on the plant. (3) With increasing lead and cadmium concentrations, the antioxidant enzyme activity in *Davidia involucrata* also exhibited a characteristic of initial increase followed by decrease, indicating that low-concentration heavy metals (lead concentration $600 \text{ mg} \cdot \text{kg}^{-1}$, cadmium concentration $5 \text{ mg} \cdot \text{kg}^{-1}$) could easily activate the antioxidant stress response in *Davidia involucrata*, effectively reducing heavy metal damage,

while high-concentration heavy metals would inhibit antioxidant enzyme activity. (4) Correlation and principal component analyses indicated that antioxidant enzymes and free proline in *Davidia involucrata* seedlings could effectively reflect the response patterns of the plant to the two types of heavy metal stress.

Full Text

Effects of Lead and Cadmium on Physiological and Biochemical Indexes of *Davidia involucrata* Seedlings

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Abstract

Lead and cadmium are highly toxic heavy metals in soil that seriously endanger plant growth and development. This study investigated the responses of antioxidant enzyme activities, malondialdehyde (MDA), free proline, and soluble protein in *Davidia involucrata*—a rare and endangered plant endemic to China—to different concentrations of lead and cadmium stress under pot experiment conditions. The results showed: (1) Under different lead concentrations, MDA concentration in *D. involucrata* seedlings was significantly higher than in the control group. Under cadmium stress, MDA concentration was also significantly higher than the control in all treatment groups except at $10 \text{ mg} \cdot \text{kg}^{-1}$, indicating that lead and cadmium pollution exacerbated membrane lipid peroxidation in *D. involucrata*. (2) Free proline content initially increased then decreased with increasing lead and cadmium concentrations, becoming significantly lower than the control at lead concentrations $800 \text{ mg} \cdot \text{kg}^{-1}$ and cadmium concentrations $20 \text{ mg} \cdot \text{kg}^{-1}$. Soluble protein concentration showed a similar increasing-then-decreasing pattern with lead concentration, while under cadmium stress it was significantly higher than the control across all treatments. The increase in soluble protein and free proline enhanced *D. involucrata*'s ability to resist low-concentration heavy metal damage, but high concentrations exhibited inhibitory effects. (3) Antioxidant enzyme activities also showed an initial increase followed by a decrease with increasing lead and cadmium concentrations, indicating that low concentrations of heavy metals (lead $600 \text{ mg} \cdot \text{kg}^{-1}$, cadmium $5 \text{ mg} \cdot \text{kg}^{-1}$) activated the antioxidant stress response in *D. involucrata*, effectively reducing heavy metal damage, whereas high concentrations inhibited antioxidant enzyme activity. (4) Correlation and principal component analyses demonstrated that antioxidant enzymes and free proline could effectively reflect the response patterns of *D. involucrata* seedlings to both heavy metal stresses.

Keywords: *Davidia involucrata*; lead; cadmium; antioxidant enzymes; membrane lipid peroxidation

Introduction

Accelerated urbanization and intensified human activities have increased the release of pollutants into the atmosphere, water, and soil, degrading natural resource quality and endangering the health of animals, plants, and humans (Ewa et al., 2009; Lin et al., 2012; Wang et al., 2015). As a critical medium for material and energy exchange and the fundamental basis for terrestrial plant growth and reproduction, soil has experienced aggravated contamination due to anthropogenic interference. Heavy metal pollution in soil is characterized by low degradability, high mobility, and long latency periods, with lead (Pb) and cadmium (Cd) being the two most severely polluting heavy metals in China (Yang et al., 2016; Hu et al., 2018). For plants, lead and cadmium are non-essential elements that are absorbed through root systems and translocated into plant tissues. Excessive lead and cadmium inhibit plant cell enzyme activities and functions, interfere with respiration and photosynthesis, hinder plant growth and development, and cause cumulative toxicity (Zhou et al., 2014; Zhuang, 2015).

Plant antioxidant enzymes serve as important indicators of plant resistance to heavy metal stress. Heavy metals stimulate stress responses in plants, generating increased superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) to autonomously scavenge excess oxygen free radicals (Jin et al., 2013; Yang et al., 2014). Therefore, increased enzyme activity indicates enhanced plant capacity to withstand adverse environments. Additionally, free proline accumulation represents an important detoxification mechanism under unfavorable conditions. Soluble proteins primarily undergo denaturation and degradation under heavy metal toxicity, leading to metabolic dysfunction in enzyme-mediated processes (Yang et al., 2013; Tang et al., 2015). Conversely, malondialdehyde accumulation indicates severe stress damage, particularly the degree of membrane structural destruction.

Davidia involucrata, commonly known as the dove tree, belongs to the family Davidiaceae and is a tertiary relict species endemic to China, listed as a key protected wild plant (Spongberg, 1993; Zhang et al., 1995; Wu et al., 2000). Currently, wild populations are distributed only in southwestern Sichuan Province and central Hubei Province. Due to its high ornamental, economic, and medicinal value, *D. involucrata* has been widely introduced in nature reserves and scenic areas (Wang et al., 2011). Previous research has focused on artificial propagation, introduction ecology, and cytology (Zhu et al., 2007). He et al. (1995) studied the natural distribution characteristics and environmental conditions of *D. involucrata* habitats, while Tang et al. (2017) used species distribution models to predict future climate-suitable ranges. Liu et al. (2009) conducted

RNA-Seq-based gene expression analysis of *D. involucrata* seedlings under 42°C heat treatment. Such studies are crucial for improving survival rates and planning conservation measures.

Heavy metal pollutants enter soil through atmospheric deposition and wastewater irrigation, where they are retained and subsequently absorbed by plants, hindering normal growth and reducing biomass (Han et al., 2020). *Davidia involucrata* has strict environmental requirements, and soil quality significantly impacts its growth. However, few studies have examined the effects of soil heavy metal pollution on the physiological and biochemical indexes of *D. involucrata* seedlings, with limited available data. Therefore, this study analyzed the activity or concentration changes of antioxidant enzymes, MDA, soluble protein, and free proline in *D. involucrata* seedlings under different soil concentrations of lead and cadmium pollution. The objectives were to explore the response mechanisms and potential influencing factors of *D. involucrata* to heavy metal pollution, provide research data for further studies on its survival ability under stress, and offer reference bases for conservation efforts, survival improvement, and rational protection planning.

1.1 Experimental Materials

Three-year-old *D. involucrata* seedlings were obtained from Shifang City, Sichuan Province. The experimental soil had a pH of 7.67 ± 0.07 , with total nitrogen and phosphorus contents of $513.47 \text{ mg} \cdot \text{kg}^{-1}$ and $472.5 \text{ mg} \cdot \text{kg}^{-1}$, respectively. Background concentrations of Pb and Cd were $5.71 \text{ mg} \cdot \text{kg}^{-1}$ and $0.09 \text{ mg} \cdot \text{kg}^{-1}$, respectively.

1.2 Material Cultivation and Treatment

Based on soil environmental quality standards (GB15618-1995), heavy metal solutions were prepared using $\text{Pb}(\text{NO}_3)_2$ and $\text{CdCl}_2 \cdot 2.5\text{H}_2\text{O}$ to simulate low, medium, and high concentration stress environments (see Table 1). The prepared solutions were added to soil and thoroughly mixed. Pot cultivation experiments were conducted at the China West Normal University experimental base for 90 days (June 2018 to August 2018), with three replicates per treatment group.

1.3 Measurement Methods

1.3.1 Plant Height Before heavy metal treatment, plant height of each *D. involucrata* seedling was measured using a tape measure (three replicates). After 90 days of heavy metal treatment, plant height was measured again for each seedling (three replicates). Height increment was calculated as post-treatment height minus pre-treatment height.

1.3.2 Malondialdehyde, Free Proline, and Soluble Protein Three to five leaves from the same functional area were collected, placed in an ice box,

and immediately transported to the laboratory for analysis. Malondialdehyde was determined using the thiobarbituric acid method (AbdElgawad et al., 2019), free proline was measured using the sulfosalicylic acid method (Jin et al., 2019), and soluble protein was quantified using the Coomassie brilliant blue method (Cheng et al., 2016).

1.3.3 Antioxidant Enzyme Activities SOD, POD, and CAT activities were measured using spectrophotometric methods. Leaf samples (0.2 g) were ground in a mortar with 2 mL phosphate buffer on ice, then centrifuged at $10,000 \text{ r} \cdot \text{min}^{-1}$ for 15 min at 4°C . The supernatant was collected for analysis. SOD activity was measured as the enzyme amount required to inhibit 50% nitroblue tetrazolium (NBT) reduction rate at 560 nm wavelength according to Donahue et al. (1997). POD activity was determined via guaiacol oxidation method (Merey et al., 2018) by measuring absorbance increase at 470 nm. CAT activity was quantified by measuring absorbance decrease at 240 nm due to H_2O_2 substrate consumption (Jing et al., 2018).

1.4 Statistical Analysis

Experimental data were statistically analyzed using SPSS 23.0 (IBM Inc., USA), including mean and standard deviation calculations, significance testing among treatment groups, and Pearson correlation analysis. Principal component analysis was performed using Origin 2018.

Results

2.1 Characteristics of Plant Height Changes in *D. involucrata* Seedlings

As shown in Figure 1 [Figure 1: see original paper], plant height of *D. involucrata* seedlings increased after 90 days of lead and cadmium stress. With increasing lead concentration, height increment initially increased then decreased. Lead concentrations of $200\text{--}800 \text{ mg} \cdot \text{kg}^{-1}$ showed relatively low inhibition on *D. involucrata* growth, while $1,000 \text{ mg} \cdot \text{kg}^{-1}$ exhibited strong inhibition. Height increments under 600 and $800 \text{ mg} \cdot \text{kg}^{-1}$ treatments were significantly higher than the control group. With increasing cadmium concentration, height increment also showed an initial increase followed by a decrease, with the most pronounced increment occurring at $5 \text{ mg} \cdot \text{kg}^{-1}$ cadmium, though overall differences were not significant.

2.2 Characteristics of Malondialdehyde, Free Proline, and Soluble Protein

As shown in Figure 2 [Figure 2: see original paper] A, C, and E, concentrations of MDA, free proline, and soluble protein initially increased then decreased with increasing lead concentration. The control group showed significantly lower MDA concentration than other treatment groups ($P < 0.05$), with MDA concentration

significantly higher in the 400-800 mg · kg⁻¹ lead range. Free proline concentration peaked at 400 mg · kg⁻¹ lead (P<0.05) but decreased significantly at 800 and 1,000 mg · kg⁻¹ lead (P<0.05). Soluble protein concentration was significantly higher at 200 and 400 mg · kg⁻¹ lead than other treatments (P<0.05), with no significant differences observed above 400 mg · kg⁻¹. Cadmium stress effects on MDA, free proline, and soluble protein differed from lead stress (Figure 2 [Figure 2: see original paper]B, D, and F). MDA concentration was lowest at 10 mg · kg⁻¹ cadmium, followed by the control group, both significantly lower than other treatments (P<0.05). Free proline concentration was significantly lower than the control at 20 and 30 mg · kg⁻¹ cadmium (P<0.05). Soluble protein concentration was significantly higher than the control under all cadmium concentrations, with no significant differences among treatment groups.

2.3 Characteristics of SOD, POD, and CAT Activities

SOD, POD, and CAT activities initially increased then decreased with increasing lead concentration. SOD activity peaked at 400 mg · kg⁻¹ lead, while concentrations above 600 mg · kg⁻¹ showed significantly lower activity than the control (P<0.05). POD activity in the control group was significantly lower than all treatment groups (P<0.05), with higher activities observed at 200, 400, and 800 mg · kg⁻¹ lead. Except at 800 mg · kg⁻¹ lead, CAT activity in all treatment groups was significantly higher than the control (P<0.05), with the highest activity at 200 mg · kg⁻¹ lead.

Under cadmium stress, SOD activity was significantly higher at 1, 5, and 20 mg · kg⁻¹ than other treatments (P<0.05). POD and CAT activities peaked at 5 mg · kg⁻¹ and 1 mg · kg⁻¹ cadmium, respectively. CAT activity gradually decreased with increasing cadmium concentration, becoming significantly lower than the control at 10-30 mg · kg⁻¹ (P<0.05).

2.4 Correlation Analysis of Antioxidant Enzymes, Malondialdehyde, and Osmotic Adjustment Substances

As shown in Table 2, under lead stress, SOD activity was significantly positively correlated with free proline and soluble protein (P<0.01), POD activity was significantly positively correlated with MDA concentration (P<0.01), and CAT activity was significantly correlated with soluble protein (P<0.01). Table 3 reveals that under cadmium stress, SOD activity was significantly positively correlated with CAT activity and MDA concentration (P<0.01 and P<0.05, respectively). Additionally, POD activity showed significant positive correlations with both MDA and soluble protein (P<0.05). Different heavy metals differentially affected various physiological and biochemical indexes in *D. involucrata*. Under both lead and cadmium stress, SOD and POD production correlated with increased soluble protein concentration. Under lead stress, enhanced SOD activity correlated with increased free proline concentration, while under cadmium stress, elevated SOD activity was accompanied by enhanced CAT activity.

2.5 Principal Component Analysis of Antioxidant Enzymes, Malondialdehyde, and Osmotic Adjustment Substances

Figure 4 [Figure 4: see original paper]A shows that two principal components explained 75.49% of the information, with PC1 accounting for 45.63% and PC2 for 29.86%. Antioxidant enzymes, MDA, free proline, and soluble protein were the main indicators for PC1, with soluble protein showing the highest correlation. These results indicate that the three antioxidant enzymes, MDA concentration, free proline, and soluble protein can all reflect *D. involucrata*'s response to lead stress to varying degrees. Figure 4 [Figure 4: see original paper]B shows that PC1 and PC2 together explained 64.98% of the information (PC1: 39.98%, PC2: 25%). Except for free proline, all other indicators showed strong positive correlations with PC1. Free proline, CAT, and SOD showed strong correlations with PC2, while MDA and soluble protein showed strong negative correlations with PC2. The three antioxidant enzymes, MDA concentration, and soluble protein could effectively indicate *D. involucrata*'s response characteristics to cadmium stress.

Discussion

3.1 Effects of Lead and Cadmium on Membrane Lipid Peroxidation, Free Proline, and Soluble Protein in *D. involucrata* Seedlings

Membrane lipids and proteins are targets of reactive oxygen species under environmental stress and serve as indicators of oxidative stress regulation (Liu et al., 2015). Malondialdehyde is a product of free radical-lipid interactions in plants. Stress environments cause MDA accumulation, leading to cross-linking and polymerization of macromolecules like proteins and nucleic acids, reducing protein metabolic efficiency in plant cells and causing significant damage to membrane systems and photosynthesis (Yang et al., 2014). This study found that different lead concentrations significantly increased MDA concentration in *D. involucrata* seedlings, with stronger membrane lipid peroxidation occurring at higher lead concentrations below $800 \text{ mg} \cdot \text{kg}^{-1}$. This aligns with Wang et al. (2011), indicating that higher heavy metal concentrations exacerbate membrane lipid peroxidation in *D. involucrata*.

Free proline and soluble protein are important metabolic substances in plants. Free proline plays crucial roles in protecting membrane structure, maintaining macromolecular stability, and scavenging free radicals. Soluble protein can increase functional protein quantity to maintain normal physiological metabolism and enhance plant stress resistance (Qi, 1989; Chen et al., 2019). Under no heavy metal conditions, free proline was relatively high, but its concentration initially increased then decreased with increasing lead and cadmium concentrations. Previous studies reported that plant leaf free proline concentration increases with stress intensity (Jiang et al., 1997; Ding et al., 2006; Qin et al., 2006; Zhao and Xi, 2007), which differs from our findings. This suggests that within a certain range, *D. involucrata* can resist lead and cadmium stress by

increasing free proline and soluble protein, but excessive concentrations may further damage membrane systems and metabolic balance, reducing stress capacity and causing free proline concentration to decline (Qin et al., 2006). This is further supported by the observation that MDA was significantly higher than the control in all treatment groups (except $10 \text{ mg} \cdot \text{kg}^{-1}$ cadmium) and showed an initial increase followed by decrease, while also indicating that free proline is more sensitive to lead and cadmium stress.

At $10 \text{ mg} \cdot \text{kg}^{-1}$ cadmium, membrane lipid peroxidation was lowest, but *D. involucreta* seedling height increment was also lowest without significant differences from other groups. This may be related to reduced antioxidant enzyme activity under high cadmium concentration, inhibiting plant capacity to resist heavy metal damage. Under lead stress, soluble protein concentration initially increased then decreased but remained significantly higher than the control, similar to free proline patterns. This indicates that low lead concentrations can induce soluble protein production to mitigate damage, while high concentrations are inhibitory. This is associated with aggravated membrane lipid peroxidation reducing protein function and causing deactivation of protein synthesis systems, further confirming that heavy metal concentration increases inhibit *D. involucreta* seedling growth (Guo et al., 2009; Wang et al., 2010; Xu et al., 2016). Except for the control showing lowest soluble protein concentration, no significant differences were observed among cadmium treatments, suggesting different stress mechanisms for different heavy metals and consequently different soluble protein responses, similar to Tang et al. (2015).

3.2 Effects of Lead and Cadmium on Antioxidant Enzyme Activities in *D. involucreta* Seedlings

Heavy metals stimulate excessive reactive oxygen species production in plants, which react with lipids, proteins, and nucleic acids, causing lipid peroxidation, membrane damage, and enzyme inactivation that affect cellular performance and viability. When exceeding plant self-scavenging capacity, this can lead to plant death (Maleki et al., 2017; Zhang et al., 2019). SOD is a metalloenzyme that catalyzes dismutation of highly reactive superoxide radicals (O_2^-) into less reactive H_2O_2 , which is then decomposed by POD and CAT to prevent peroxidation (Tian et al., 2001; Liu and Liang, 2005; Zeng et al., 2019). This study found that under lead stress, SOD activity showed a “high-promotion, low-inhibition” pattern, while POD and CAT (except at $800 \text{ mg} \cdot \text{kg}^{-1}$) activities were significantly higher than the control but decreased at higher lead concentrations. This indicates that low lead concentrations activated the antioxidant response in *D. involucreta*, stimulating antioxidant enzyme production to remove oxygen free radicals, while high concentrations ($800\text{-}1,000 \text{ mg} \cdot \text{kg}^{-1}$) severely damaged plant cell function and reduced antioxidant system responsiveness, with SOD activity being most sensitive to lead stress. Li et al. (2007) reported similar findings in *Houttuynia cordata* under lead stress, where SOD, POD, and CAT activities initially increased then decreased, with POD and CAT activity reductions

related to decreased SOD activity.

At cadmium concentrations of 1, 5, and 20 $\text{mg} \cdot \text{kg}^{-1}$, POD activity also showed an initial increase then decrease with increasing cadmium concentration. Higher cadmium concentrations (10–30 $\text{mg} \cdot \text{kg}^{-1}$) also inhibited CAT activity, consistent with Liu et al. (2010) findings on cadmium effects on sorghum antioxidant regulation. This study also found that *D. involucrata*'s antioxidant system could cope with low cadmium concentrations ($\text{Cd } 5 \text{mg} \cdot \text{kg}^{-1}$), scavenging harmful substances like O_2^- and H_2O_2 to maintain normal free radical metabolism (Tian et al., 2001; Jia et al., 2011; Liu et al., 2019), while enhanced cadmium toxicity inhibited antioxidant system responsiveness (Yang et al., 2018). Plant height changes in *D. involucrata* seedlings were more sensitive to lead stress, with no significant growth effects from different cadmium concentrations.

3.3 Main Indicators of *D. involucrata* Seedlings Under Lead and Cadmium Stress

Under lead stress, SOD activity was significantly positively correlated with free proline and soluble protein, CAT activity was significantly positively correlated with soluble protein, and principal component analysis showed strong correlations between SOD, soluble protein and PC1, and between POD activity, free proline and PC2. This suggests that antioxidant enzymes SOD and POD, along with free proline, can serve as primary reference indicators for *D. involucrata* seedling responses to lead. Under cadmium stress, SOD activity may affect CAT activity, and the positive correlation between SOD, POD activities and MDA indicated that increased antioxidant capacity in *D. involucrata* was accompanied by increased membrane lipid peroxidation. SOD, POD, and MDA showed strong positive correlations with PC1, while CAT and free proline showed strong positive correlations with PC2, further demonstrating the important indicative roles of antioxidant enzymes, MDA, and free proline under cadmium stress.

Conclusion

- (1) Under low-concentration lead and cadmium stress ($\text{Pb } 600 \text{mg} \cdot \text{kg}^{-1}$, $\text{Cd } 5 \text{mg} \cdot \text{kg}^{-1}$), *D. involucrata* exhibited strong antioxidant responses and higher plant height increments, indicating effective self-defense mechanisms to alleviate heavy metal toxicity.
- (2) Lead and cadmium stress caused substantial MDA accumulation, demonstrating that both heavy metals readily induced membrane lipid peroxidation and damaged normal cellular metabolic functions in *D. involucrata* seedlings. Free proline concentration initially increased then decreased with increasing lead and cadmium concentrations, while soluble protein showed the same pattern under lead stress. However, high-concentration lead and cadmium stress reduced the stress response capacity of *D. involucrata* seedlings.

- (3) Antioxidant enzyme activities in *D. involucrata* seedlings were enhanced under low-concentration lead and cadmium stress, improving scavenging capacity for oxygen free radicals and other harmful substances. Furthermore, antioxidant enzyme activities and free proline could effectively indicate response patterns of *D. involucrata* seedlings to heavy metal stress. These findings enrich research data on *D. involucrata* and provide reference bases for investigating its adaptability to heavy metal stress environments.

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

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