Effects of rooting powder and soil salt stress on the growth and physiological characteristics of Tamarix chinensis cuttings

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Abstract

Background: Vegetation restoration is a main ecological remediation technology for greening saline and alkaline soils. The objectives of this study were to determine whether aminobenzotriazole (ABT), a rooting powder, can be used to improve the physiological regulatory abilities of Tamarix chinensis under salt stress; to reveal the physiological regulatory pattern by which T. chinensis pre-treated with ABT adapts to salt stress.

Results: (1) As the salt stress level increased, the cutting survival rate, height, and root length of T. chinensis gradually decreased, whereas their biomass first decreased and then increased. At salt content $S > 0.9\%$, cutting propagation of T. chinensis was difficult, and there was a considerable decrease in its biomass. The effectiveness of ABT in improving the survival rate and growth of T. chinensis cuttings became increasingly pronounced as the salt stress level increased. (2) T. chinensis was found to adapt to salt stress through increased Chl content. However, excess salt stress inhibited Chl synthesis. ABT can be used to widen the range of tolerance of T. chinensis seedlings to salt stress during Chl synthesis. (3) T. chinensis can eliminate excess reactive oxide species (ROS) by enhancing SOD and POD activities. An excess accumulation of ROS will impede the increase in enzyme activities. ABT can help improve T. chinensis seedling enzyme system regulation and was found to be most effective at a concentration of 100 mg·L$^{-1}$ . (4) ABT can reduce MDA accumulation and damage caused by membrane lipid peroxidation (MLP). ABT at a concentration of 100 mg·L$^{-1}$ was found to be highly effective in reducing MDA content.

Conclusions: ABT was effective in improving the survival rate and the growth and
physiological regulatory abilities of T. chinensis cuttings under salt stress. ABT enhanced the resistance of T. chinensis to salt stress. However, under high S c (>0.9%) and ABT concentration (>100 mg·L⁻¹) conditions, the physiological regulatory ability of T. chinensis seedlings exposed to salt stress weakened. At S c of 0.9%, T. chinensis seedlings pre-treated with ABT at 100 mg·L⁻¹ exhibited the most vigorous growth, highest biomass, and highest physiological and biochemical regulatory abilities.

**Background**

Soil salinization exerts a significant impact on sustainable agricultural development and environmental quality. Crop losses caused by salinization in irrigated areas around the world are estimated at USD 11 billion and continue to rise[1]. Soil salinization is a major environmental risk resulting from natural or human activities. Currently, more than one billion ha of land worldwide is salinized, accounting for 30% of the total land area[2]. According to the Second National General Survey conducted by the Ministry of Agriculture of China[3], approximately 36 million ha of land in China is salinized, accounting for 4.88% of China’s usable land area. Additionally, 9.209 million ha of farmland is salinized, accounting for 6.62% of China’s total farmland area. In China, salinized soils are distributed across a vast area, primarily in its northwestern, northern, northeastern, and coastal regions. Soil salinization will lead to an increase in the osmotic pressure of the soil solution and decreases in the air and water permeability and the nutrient availability in soil. Moreover, soil salinization can also hinder normal plant growth and cause severe vegetation degradation[4]. Conventionally, there are two main approaches for ameliorating saline and alkaline soils. One approach is to directly ameliorate soils.
Engineering measures, such as constructing ditches to drain salts, pumping freshwater to reduce soil salinity (Sc), and creating raised fields, are primarily implemented to reduce Sc and improve the physical and chemical properties of soils to make them suitable for development of agricultural and forestry industries. However, these measures are costly and have low land-use efficiency. Moreover, it is difficult to implement these measures in areas that lack freshwater resources. The other approach is to employ conventional breeding methods and modern bioengineering measures to breed salt-tolerant crop varieties and to use advanced biotechnologies to improve the salt tolerance of plants. Vegetation restoration measures focusing on planting of local halophytic or salt-tolerant plants have become an important approach for ameliorating saline and alkaline soils[5].

Researchers in China and elsewhere have investigated the use of halophytic plants to improve saline and alkaline soils. Some halophytic plants have been found to be capable of removing salts from soil by absorbing and accumulating the salts[6,7]. Halophytic plants can improve the physical and chemical properties of a soil by reducing its bulk density and improving its porosity. Improvements in the physical and chemical properties of a soil can in turn lead to an increase in its permeability and therefore facilitate salt leaching[8]. However, a main issue in implementing vegetation measures to improve saline and alkaline soils is the difficulty associated with adaptation of the planted seedlings to salt-alkali stress during the initial growth stage, resulting in slow root system growth of the seedlings and a relatively low survival rate. Hence, there is an urgent need to develop methods to improve the survival rate of halophyte seedlings during the initial planting stage and to study their physiological adaptability.

As global soil salinization becomes increasingly prominent, an increasing number of
studies are being conducted to examine the physiological and ecological mechanisms by which plants respond to salt stress. These studies focus mainly on crops, vegetables, and specific halophytic plants[4, 9, 10]. The results of these studies are of important guidance value to the breeding of halophytic plants and their application in saline and alkaline soil amelioration and vegetation restoration.

Some researchers have found a significant increase in the superoxide dismutase (SOD) and peroxidase (POD) activities and malondialdehyde (MDA) content in the leaves of bean seedlings[11] and Jerusalem artichoke[12] with Sc. Hu et al. [13] reported an increase in the MDA content and SOD and POD activities of Panicum virgatum L. with the salt-alkali stress level. Li et al.[14] found that salt stress inhibited the growth of the branches and roots of Salix matsudana Koidz. Additionally, they also found that low-level salt stress induced an increase in the SOD, POD, and catalase (CAT) activities, whereas high-level salt stress inhibited the activities of antioxidant enzymes. Moreover, they reported that low-level salt stress led to an increase in the MDA content and that the MDA content increased rapidly as the salt stress level increased. Hong et al. found that as the sodium chloride (NaCl) concentration increased, there was a decrease in the relative water content, chlorophyll (Chl)-a (Chla) content, total Chl (ChlT) content, and Chla/Chlb ratio in the leaves of Salix spp., but an increase in their Chlb, proline (Pro), and MDA contents[15]. Additionally, they detected an increase in the SOD activity and soluble protein content in the leaves of Salix spp. under mild salt stress and a significant decrease in these two parameters under moderate and severe salt stress. However, Zhu et al. found that as the salt stress level increased, the SOD and POD activities and MDA content in the leaves of T. chinensis cuttings first increased and then decreased[16]. Evidently, the physiological and biochemical indices of plants vary
relatively significantly with the plant species and salt stress level.

*T. chinensis* is a shrub or small tree species belonging to the genus *Tamarix* in the family Tamaricaceae. *T. chinensis* has a developed root system and a relatively high capacity to break winds, fix sand, preserve water and soil, and ameliorate soil. Owing to its relatively high tolerance to salts, alkalis, and droughts, *T. chinensis* is often used as a primary vegetation restoration tree species for restoring and rebuilding degraded ecosystems in China’s western arid and desert regions, Yellow River Basin, and coastal saline and alkaline soil regions[17]. *T. chinensis* shrubs are the main protective shrubs for muddy coastal zones in saline and alkaline soil regions in the Yellow River Delta. These shrubs play a vital role in maintaining ecosystem stability and improving saline and alkaline soils in coastal zones. In recent years, as a result of global warming, there has been a decrease in precipitation and an increase in evaporation in the Yellow River Delta. Additionally, seawater intrusion caused by natural factors (e.g., ocean current movements) and human activities (overexploitation of underground brine resources) has intensified soil salinization and degraded the *T. chinensis* shrub ecosystem in the Yellow River Delta. Therefore, there is an urgent need to develop saline and alkaline soil amelioration measures that focus on *T. chinensis* shrub restoration. Determining the physiological and biochemical regulation processes by which *T. chinensis* tolerates salts is a key link and essential precondition for *T. chinensis* shrub restoration.

Currently, Chinese researchers study *T. chinensis* in areas such as morphology and taxonomy[18], ecological characteristics[19], cytogenetics[20], and physiological and ecological characteristics under salt[17], salt-alkali[21], and salt-drought intercross stress[16]. By contrast, researchers elsewhere, mostly treating *T. chinensis* as an invasive species, investigate its role in ecosystems as well as
biological control and physical removal methods for controlling its growth and propagation[22–24]. The physiological adaptability of T. chinensis to salt stress and its role in ameliorating saline and alkaline soils in some regions have also been examined[25].

Aminobenzotriazole (ABT), a rooting powder, is an efficient, broad-spectrum plant growth regulator. By enhancing and regulating the endogenous hormone contents and important enzyme activities of plants, ABT can regulate their metabolism intensity, improve the activity of their root systems, promote their growth, and enhance their tolerance, thereby increasing their survival rate and productivity. ABT has been extensively used in afforestation, seedling transplantation, and cutting propagation. Paradikovic et al. found that a commercial rooting powder played an active role in the rooting and development of Salvia officinalis L. and Rosmarinus officinalis L. cuttings and significantly improved their morphological properties (e.g., plant height, number of leaves, root length, fresh weight, and dry weight)[26]. Song et al. found that Patrinia rupestris cuttings pre-treated with 2,685 and 5,370 μm naphthalene acetic acid or 4,920 μm indole-3-butyric acid (IBA) exhibited the best rooting traits (rooting percentage, number of adventitious roots, root length, and fresh weight)[27]. Jamal et al. found the best survival rate and growth conditions in stem cuttings of Clerodendrum splendens pre-treated with 20% IBA[28]. Some researchers have also examined the use of rooting powders in vegetative propagation. Research has shown that prior to cutting propagation, treating current-year low-lignified branches with a rooting powder can significantly improve their survival rate. Tan found that treating T. chinensis shoot cuttings with ABT at 200 mg·L⁻¹ for 1 hour could increase their rooting percentage (to 84.44% on average) and biomass[29]. A combination of a rooting powder and fertilizer was
found to significantly improve root activities in *T. ramosissima* in various soil layers[30]. However, the available studies focused primarily on propagation under single-salt or salt-free conditions, and consequently their results cannot be satisfactorily applied under field conditions. Relatively few studies have been conducted to examine vegetative propagation of *T. chinensis* under various salt stress conditions. Moreover, the effects of rooting powders at various concentrations on the growth and physiological and biochemical characteristics of *T. chinensis* cuttings under salt stress have yet to be investigated. As a result, it is difficult to determine the rooting powder concentrations for *T. chinensis* cuttings under various salt stress conditions in practice.

Considering these findings, in this study, a rooting powder, ABT, was used at four concentrations to facilitate the growth of *T. chinensis* cuttings at four simulated Sc levels. *T. chinensis* cuttings under no salt stress were selected as the control. The *T. chinensis* cuttings were analysed to determine their growth indices (e.g., survival rate, height, root length, and biomass) and their physiological and biochemical indices (e.g., Chl content, SOD and POD activities, and MDA content). The growth conditions and physiological and biochemical characteristics of the *T. chinensis* seedlings pre-treated with ABT at various concentrations under salt stress were investigated. The present results can provide technical support for vegetative propagation techniques for *T. chinensis* and greening of saline and alkaline soils.

**Materials and Methods**

**Experimental materials and design**

Branch cuttings were harvested from the *T. chinensis* shrub obtained from the wild in the Shandong Changyi National Marine Ecology Special Reserve; the provenance
originates from Changyi City, Shandong Province, China. We comply with the Convention on the Trade in Endangered Species of Wild Fauna and Flora. In mid-February 2018 before *T. chinensis* began to sprout, *T. chinensis* branches with a diameter of approximately 1 cm were cut and harvested. The branches were then sectioned into 15-cm-long cuttings. Each cutting was sectioned obliquely at the base and flat at the top. Four Sc stress levels were studied, namely, mild (0.3%), moderate (0.6%), and severe (0.9% and 1.2%). An Sc of ≤0.1% was selected as the control (CK). Each soil Sc was prepared based on the dry soil weight. The Sc was monitored once every 7 days, and additional salt was added to maintain the previously established Sc. An 8-cm-deep tray was placed beneath each pot. The water that leaked from each pot into the tray was poured back into the pot. Additionally, the tray was washed, and the washing water was also poured into the pot. This procedure prevented salt loss. The bases of the cuttings were soaked at a depth of 2–3 cm in ABT solutions of various concentrations (0, 50, 100, and 200 mg·L⁻¹). Subsequently, the cuttings were planted in pots filled with soil at each Sc level. Ten cuttings were planted in each pot. Three repeats were performed for each treatment. A total of 600 cuttings were planted in 60 pots. During the initial cutting propagation stage, the pots were watered with freshwater twice a day to maintain a soil water content at 60%–70% of the field capacity. After 90 days of propagation, the growth (e.g., biomass), physiological, and biochemical indices of the *T. chinensis* cuttings were measured and analysed.

**Measurement of indices**

Measurement of growth indices: Three pots were selected for each treatment. Five *T. chinensis* cuttings were selected from each pot to measure their growth indices. The height of each plant was measured using a metre ruler. The aboveground and
underground biomass of each *T. chinensis* seedling was measured by harvesting the whole plant. Each whole seedling was dug out and cleaned. Then, the branches, trunk, and root system of each seedling were identified. Each seedling was subsequently fixed at 105°C for 30 minutes and then dried in an oven at 80°C until a constant weight was achieved.

Measurement of physiological and biochemical indices: Three pots were selected for each treatment. Three *T. chinensis* cuttings were randomly selected from each pot. Normally grown, mature leaves of the *T. chinensis* cuttings in the same area were collected and tested to determine their physiological and biochemical indices. The photosynthetic pigment content in each leaf was measured per unit fresh weight using the ethanol-acetone soaking procedure[31]. SOD activity was measured by nitroblue tetrazolium photoreduction[32]. POD activity was measured by guaiacol colorimetry[33]. The MDA content was measured by thiobarbituric acid colorimetry[34]. At least three repeated measurements of each index were obtained and subsequently averaged.

**Data processing**

The experimental data were calculated in Microsoft Excel 2010. Analysis of variance was performed using SPSS 17.0 statistical software to determine the significance of the difference between the experimental data. Multiple comparisons were performed using the least significant difference method.

**Results and analysis**

**Growth characteristics of *T. chinensis* cuttings**

**Survival rates of *T. chinensis* cuttings**

Salt stress exerted a significant impact on the survival rate of *T. chinensis* cuttings
pre-treated with various concentrations of ABT (Figure 1). With increasing salt stress, there was a significant decrease in the survival rate of T. chinensis cuttings pre-treated with ABT at each concentration. The survival rate of T. chinensis cuttings with each concentration of ABT was 100% in the CK group. The survival rate of T. chinensis cuttings pre-soaked in water at Sc of 0.3% was significantly lower than that in the CK group (P<0.05). However, there was no significant difference in the survival rate between T. chinensis cuttings with each concentration of ABT at Sc of 0.3% and those in the CK group (P>0.05). At Sc of 0.3%, there was also no significant difference in the survival rate among T. chinensis cuttings with various concentrations of ABT (P>0.05). These findings demonstrate that the ABT concentration had no significant impact on the survival of T. chinensis in the absence of salt stress and had a relatively minor impact on the survival of T. chinensis under mild salt stress. At Sc of 0.6%, the survival rates of T. chinensis cuttings with ABT at 0, 50, 100, 200 mg·L⁻¹ were 40.00%, 20.00%, 23.40%, and 36.70% lower than in the CK group, respectively. Additionally, at Sc of 0.6%, the survival rates of T. chinensis cuttings with ABT at 50 and 100 mg·L⁻¹ were significantly higher than T. chinensis cuttings with ABT at 0 mg·L⁻¹ (i.e., water) (P<0.05). This result suggests that salt stress significantly inhibits and that ABT can significantly increase the survival rate of T. chinensis. At Sc of 0.9%, the survival rate was highest for T. chinensis cuttings with ABT at 200 mg·L⁻¹ (53.30%). By comparison, the survival rate of T. chinensis cuttings pre-soaked in water was only 20.00%, which was significantly lower than that of T. chinensis cuttings with ABT at 50 and 200 mg·L⁻¹ (P<0.05). At Sc of 1.2%, the survival rate was 0% for T. chinensis cuttings pre-soaked in water and only 6.7% for cuttings treated with various
concentrations of ABT.

Biomass of *T. chinensis* cuttings

As the salt stress level increased, the biomass of *T. chinensis* cuttings with each concentration of ABT first decreased, then increased, and then decreased again (Figure 2A). At Sc of 0.9%, the biomass of individual *T. chinensis* cuttings with ABT at 100 mg·L\(^{-1}\) reached a peak value (16.70 g). The biomass of *T. chinensis* cuttings with ABT at 0, 50, and 200 mg·L\(^{-1}\) was 48.57%, 48.59%, and 54.69% lower than that of *T. chinensis* cuttings with ABT at 100 mg·L\(^{-1}\), respectively. At the same Sc, there was a significant difference in biomass among *T. chinensis* seedlings with various concentrations of ABT (*P*<0.05). The difference in biomass among *T. chinensis* seedlings with various concentrations of ABT was nonsignificant (*P*>0.05) under mild salt stress (Sc≤0.3%) but significant under moderate and severe salt stress (Sc≥0.6%). At Sc of 1.2%, there was a significant decrease in the biomass of *T. chinensis* cuttings with each concentration of ABT (*P*<0.05).

The difference in height between *T. chinensis* seedlings became significant as Sc increased (*P*<0.05). Overall, the height of *T. chinensis* seedlings decreased as Sc increased (Figure 2B). Under mild (0.3%) and moderate (0.6%) salt stress, there was no significant difference in height between *T. chinensis* seedlings with ABT at 100 and 200 mg·L\(^{-1}\). At Sc of 0.9%, the height of *T. chinensis* seedlings with ABT at 0, 50, 100, and 200 mg·L\(^{-1}\) was only 60.45%, 62.61%, 52.66%, and 52.42% of that in the CK group. The root length of *T. chinensis* seedlings with ABT at 50 and 100 mg·L\(^{-1}\) first decreased and then increased as Sc increased, reaching their respective minimum values at Sc of 0.6%. At Sc of 0.3% and 0.6%, the root length of *T. chinensis* seedlings with ABT at 0 mg·L\(^{-1}\) was significantly greater than that of *T.
*chinensis* seedlings with any other concentration of ABT (Figure 2C).

**Chl content in *T. chinensis* cuttings**

The differences in Chla (Figure 3A), Chlb (Figure 3B), and ChlT (Figure 3C) contents between *T. chinensis* seedlings with ABT at various concentrations became significant (*P*<0.05) as the salt stress level increased. At Sc of 0.3%, the Chla, Chlb, and ChlT contents of the leaves of *T. chinensis* seedlings pre-soaked in water were lower than those in the CK group, although the differences were nonsignificant (*P*>0.05). At Sc of 0.6%, the Chla, Chlb, and ChlT contents all reached their respective peak values. At Sc of 0.9%, the Chla and ChlT contents of the leaves of the *T. chinensis* seedlings reached their respective maximums, whereas their Chlb content began to decrease. As the salt stress level continued to increase, the Chl content in the leaves of *T. chinensis* seedlings began to decrease, suggesting that *T. chinensis* photosynthesis is enhanced by increases in Chl content to adapt to salt stress within a certain range.

At Sc≤0.3%, there was no difference in Chl content among *T. chinensis* seedlings. At Sc of 1.2%, the Chla, Chlb, and ChlT contents of the leaves of *T. chinensis* seedlings all first decreased and then increased. At Sc of 0.9%, the Chla, Chlb, and ChlT contents of the leaves of *T. chinensis* seedlings all first increased and then decreased as the ABT concentration increased. Additionally, the ChlT content in *T. chinensis* seedlings with ABT at 50, 100, and 200 mg·L⁻¹ was 26.05%, 23.04%, and 11.75% higher than that of *T. chinensis* seedlings pre-soaked in water, respectively. This result suggests that under severe salt stress, ABT at suitable concentrations (50 and 100 mg·L⁻¹) improves Chl synthesis in *T. chinensis* and reduces the inhibitory effects of salt stress on Chl synthesis.
SOD activity in *T. chinensis* cuttings

As demonstrated in Figure 4, SOD activity in the leaves of *T. chinensis* seedlings with ABT at various concentrations first increased and then decreased with increasing salt stress. Additionally, under various salt stress conditions, SOD activity was higher in the leaves of ABT-pre-treated *T. chinensis* seedlings than in the CK group. At $Sc \leq 0.6\%$, SOD activity significantly decreased in the *T. chinensis* seedlings with an increasing ABT concentration. At $Sc \geq 0.9\%$, SOD activity first increased and then decreased as the ABT concentration increased. This finding suggested that under mild salt stress, ABT increased SOD activity. As the salt stress level increased, ABT at a suitable concentration (100 mg·L$^{-1}$) increased SOD activity in *T. chinensis* seedlings. However, under severe salt stress, a high ABT concentration led to a significant decline in SOD activity.

The $Sc$ corresponding to the peak SOD activity varied between the *T. chinensis* seedlings with ABT at various concentrations. The maximum SOD activity in the *T. chinensis* seedlings with ABT at 0 mg·L$^{-1}$ occurred at $Sc$ of 0.6% and was 5.96 times higher than in the CK group. The maximum SOD activity in *T. chinensis* seedlings with ABT at 50, 100, and 200 mg·L$^{-1}$ occurred at $Sc$ of 0.9% and was elevated 2.60, 4.19, and 4.29 times compared with the CK group, respectively. At $Sc$ of 0.9%, SOD activity was significantly different in *T. chinensis* seedlings with ABT at 50 and 100 mg·L$^{-1}$ ($P<0.05$) compared with the *T. chinensis* seedlings pre-soaked in water. Specifically, SOD activity was 20.85% lower and 14.72% higher in the *T. chinensis* seedlings with ABT at 50 and 100 mg·L$^{-1}$ than in the *T. chinensis* seedlings pre-soaked in water, respectively.

POD activity in *T. chinensis* cuttings
In *T. chinensis* seedlings with ABT at 50 and 200 mg·L⁻¹, POD activity first increased and then decreased with increasing salt stress and reached a respective maximum value at Sc of 0.9% (Figure 5). POD activity was relatively low in *T. chinensis* seedlings pre-treated with ABT at 50 and 200 mg·L⁻¹ in the CK group. As the salt stress level increased, there was a consistent increase in POD activity in *T. chinensis* seedlings with ABT at 100 mg·L⁻¹. However, there was no significant difference in POD activity under severe salt stress (*P* > 0.05). At Sc ≤ 0.9%, POD activity remained relatively high in the leaves of the *T. chinensis* seedlings pre-soaked in water. However, at Sc ≤ 0.6%, there was no significant difference in POD activity between *T. chinensis* seedlings (*P* > 0.05). At Sc of 0.3%, 0.6%, 0.9%, and 1.2%, POD activity was 37.20%, 77.52%, 125.35%, and 56.17% higher, respectively, in the leaves of *T. chinensis* seedlings with ABT at 200 mg·L⁻¹ than in the CK group. This finding suggests that salt stress significantly increased POD activity in the leaves of *T. chinensis* seedlings with ABT, whereas there was a relatively nonsignificant difference in POD activity between *T. chinensis* seedlings pre-soaked in water.

POD activity first decreased and then increased with an increasing ABT concentration at each salt stress level, except for severe salt stress (Sc = 1.2%), at which there was a gradual increase in POD activity. There was a significant decrease in POD activity in *T. chinensis* seedlings with ABT at suitable concentrations (50 and 100 mg·L⁻¹). By contrast, there was a significant increase in POD activity in *T. chinensis* seedlings with water or a high concentration of ABT. These findings suggest that a suitable concentration of ABT can significantly reduce POD activity, whereas an overly low or high concentration of ABT can easily lead to
an increase in POD activity. At Sc of 0.6%–0.9%, there was no significant difference in POD activity between *T. chinensis* seedlings with water and ABT at 200 mg·L⁻¹ (*P* >0.05), whereas there was a significant difference in POD activity between *T. chinensis* seedlings with various concentrations of ABT (*P*<0.05). At Sc of 0.6%, POD activity was 60.86% and 40.03% higher in *T. chinensis* seedlings with ABT at 200 mg·L⁻¹ than in those pre-treated with ABT at 50 and 100 mg·L⁻¹, respectively. At Sc of 0.9%, POD activity was 63.12% and 53.12% higher in *T. chinensis* seedlings with ABT at 200 mg·L⁻¹ than in those pre-treated with ABT at 50 and 100 mg·L⁻¹, respectively.

**MDA content in *T. chinensis* cuttings**

As the salt stress level increased, the MDA content first increased and then decreased in *T. chinensis* cuttings with ABT at 0, 50, and 200 mg·L⁻¹. In comparison, as the salt stress level increased, there was a gradual increase in the MDA content in *T. chinensis* cuttings with ABT at 100 mg·L⁻¹ (Figure 6). This result may be a consequence of enzyme system regulation. Owing to this regulation, there was an increase in activities of relevant antioxidant enzymes. These enzymes, in turn, reduced the cell membranes damage caused by salt stress. The MDA content in leaves of *T. chinensis* cuttings pre-soaked in water reached a maximum (30.21 nmol·mg⁻¹prot) at Sc of 0.6%. At this Sc, the leaves of the *T. chinensis* cuttings sustained significant damage caused by membrane lipid peroxidation (MLP). At the same Sc, the MDA content in ABT-pre-treated *T. chinensis* seedlings exhibited various patterns at different ABT concentrations. At Scs of 0.6% and 0.9%, the MDA content first decreased and then increased. Additionally, at these two Scs, the MDA content was significantly higher in *T. chinensis* seedlings pre-soaked in water than
in *T. chinensis* seedlings pre-treated with ABT. At Sc of 1.2%, the MDA content first increased and then decreased, suggesting that at a suitable concentration (50 and 200 mg·L⁻¹), ABT prevented *T. chinensis* seedlings from being damaged by severe salt stress and led to a significant decrease in their MDA content.

discussion

**Effects of salt stress on growth conditions of *T. chinensis***

The survival rate of *T. chinensis* cuttings under mild salt stress (Sc≤0.3%) was relatively high and differed nonsignificantly from that of *T. chinensis* cuttings in the CK group. This difference suggests that *T. chinensis* is tolerant to salt to a certain extent. As the salt stress level increased, the survival rate of *T. chinensis* cuttings became relatively low or even zero (Sc>1.2%). Increasing salt stress also caused increasing damage in *T. chinensis* cuttings and significantly affected the normal growth of their root systems. The effects of growth regulator concentrations on cutting growth vary relatively significantly. An increase in the growth regulator concentration will prevent gymnosperms from rooting. Some research has also found that increasing the growth regulator concentration will not increase the rooting percentage but can improve the quality of the root system. This phenomenon is related to the difference in the type and concentration of hormones needed and the hormone sensitivities among tree species[35]. A rooting powder (e.g., ABT) can be used to facilitate growth of the root system of *T. chinensis* cuttings. By increasing and regulating the content of endogenous hormones and the activities of important enzymes in *T. chinensis* seedlings, ABT stimulates cell division and growth in the inner root sheath, strengthens root system development,
facilitates vigorous growth, significantly reduces cell membrane damage caused by salt stress, and increases salt stress adaptability. In this study, under mild salt stress (Sc≤0.3%), the ABT concentration showed no significant impact on the survival rate of *T. chinensis* cuttings. As Sc increased, ABT at a suitable concentration increased the survival rate. However, as the salt stress level continued to increase, ABT became ineffective. A relatively high soil salinity generally causes osmotic stress in plants and disrupts their nutrient ion balance, thereby affecting physiological and biochemical processes such as growth, photosynthesis, osmotic adjustment substance synthesis, and lipid metabolism[36], ultimately limiting their growth rate and biomass accumulation. In this study, there was a significant decrease in the biomass, root length, and height of *T. chinensis* under salt stress. *T. chinensis* may reduce biomass accumulation and utilize more resources and energy to respond to high salinity-induced damage[36], which suggests that plants under stress are able to respond to adverse external conditions by altering their biomass allocation pattern. By reducing the proportion of biomass allocated to root systems, some plants reduce salt absorption and salt transport to their aboveground portions[37]. Some plants acquire more water and nutrients by increasing the proportion of biomass allocated to their root systems. This mechanism increases plant growth ability and salt dilution in plant cells[38]. In this study, *T. chinensis* seedlings pre-treated with ABT at 100 mg·L⁻¹ had relatively long root systems and the highest biomass at Sc of 0.9%, and their aboveground and belowground portions showed consistent growth.

**Effects of salt stress on Chl contents in *T. chinensis* cuttings**

Chl is an important substance in plant photosynthesis. The Chl content can reflect
the ability of plants to assimilate substances. Under salt stress, plant Chl contents gradually decreased as Sc increased. Some research has shown that as Sc increases, the Chl content in plants either first increases and then decreases or gradually increases, and the plants exhibit relatively high salt tolerance[39]. In this study, as Sc increased, Chla, Chlb, and ChlT contents in the leaves of *T. chinensis* cuttings pre-treated with ABT at various concentrations all initially decreased, then increased, and then decreased again. This pattern may result from the low Scs, which was conducive to *T. chinensis* growth and did not activate its resistance mechanism to salt stress. As the salt stress level increased, the Chl content began to increase. Because Chl synthesis requires Pro, under low salt stress, a large amount of Pro accumulated in the leaf cells of *T. chinensis*, facilitating Chl synthesis. *T. chinensis* photosynthesis in leaves is enhanced by increases in Chl synthesis to adapt to salt stress. Under high salt stress, a decrease in the Chl content was observed herein, suggesting an increase in the inhibitory effects of salt stress on *T. chinensis*. This phenomenon resulted in a decrease in the content of glutamic acid, the precursor for the synthesis of 5-aminolevulinic acid (5-ALA), in leaves and consequently in 5-ALA content. These changes ultimately limited Chl synthesis, for which 5-ALA is the precursor and, to some extent, damaged the Chl synthesis system. Additionally, salt stress facilitated the decomposition of Chl by chlorophyllase[40], resulting in a decrease in Chl content. These alterations were similar to the changes in Chl content in *T. chinensis* seedlings[16] and in *Rhaphiolepis umbellata, Rosa chinensis*, and *Morus alba*[41] under salt stress. The Scs corresponding to the peak Chl content differed in leaves of *T. chinensis* pre-treated with ABT at various concentrations. The higher the ABT concentration was, the higher the Sc corresponding to the peak Chl content in *T. chinensis* leaves,
which suggested that applying ABT at a specific concentration could reduce the effects of salt stress on Chl synthesis in *T. chinensis* cuttings, potentially because ABT can increase the *T. chinensis* rooting rate and activity and thereby allows its relatively early adaptation to salt stress.

**Effects of salt stress on the activities of antioxidant enzymes in *T. chinensis* cuttings**

Salt stress leads to an increase in reactive oxide species (ROS) levels in plants. ROS affect many cell functions by damaging nucleic acids, oxidizing proteins, and causing lipid peroxidation[42]. Plants have an ROS removal system consisting of antioxidant enzymes as key components. SOD and POD are the primary antioxidant enzymes in plants under salt stress and play a vital role in removing superoxide ions, preventing MLP, and reducing plasma membrane damage[11]. Under normal conditions, there is a dynamic balance between the production and removal of ROS in cells. Under stress, this balance is disrupted, and ROS start to accumulate. Plants remove excess ROS by increasing SOD activity. POD and SOD collectively remove ROS. SOD converts the ROS formed in the oxidation process into oxygen and H$_2$O$_2$ through disproportionation reactions. Subsequently, POD decomposes and removes the formed H$_2$O$_2$ [11]. Under salt stress, there is a threshold for the ROS level tolerable to plant cells. Below this threshold, plants are able to remove ROS by increasing the activities of antioxidant enzymes. Beyond this threshold, the activities of antioxidant enzymes will be inhibited, resulting in an excess accumulation of ROS and leading to plant tissue damage[28]. In this study, as the salt stress level increased, SOD activity first increased and then decreased in the leaves of the *T. chinensis* cuttings pre-treated with ABT at various concentrations. This result suggested that as the salt stress level increased, ROS began to
accumulate in the leaf cells of \textit{T. chinensis}, and \textit{T. chinensis} removed excess ROS by increasing the SOD activity to adapt to salt stress. However, under relatively high salt stress, the ROS that formed exceeded the regulation ability of SOD. Consequently, SOD activity was inhibited and therefore decreased. This SOD pattern is consistent with that in \textit{T. austromongolica} and \textit{T. chinensis}\cite{21} in saline and alkaline habitats and in the leaves of \textit{Pennisetum alopecuroides} (L.) Spreng\cite{43} under NaCl stress.

Plants reduce salt stress-induced damage by increasing POD activity. The causes of the increase in POD activity include not only ROS production but also cell membrane damage and changes in the calcium ion concentration. At various Scs, POD activity in the leaves of \textit{T. chinensis} cuttings pre-soaked in water was relatively high, suggesting that the relatively large amount of \( \text{H}_2\text{O}_2 \) produced in leaf cells of \textit{T. chinensis} seedlings that were not pre-treated with ABT resulted in increased POD activity to remove \( \text{H}_2\text{O}_2 \). Evidently, the damage (MLP) induced by salt stress was three times greater in \textit{T. chinensis} seedlings that were not pre-treated with ABT than in \textit{T. chinensis} seedlings in the three ABT pretreatment groups. Li et al. found that as the salt stress level was increased, POD activity in \textit{T. austromongolica} and \textit{T. chinensis} first increased and then decreased\cite{21}. They also found that POD activity in the leaves of \textit{T. austromongolica} and \textit{T. chinensis} reached a maximum at Sc of 1.2\%, which was 3.5 and 3.6 times greater than in the control group, respectively. A similar pattern was also found in this study. POD activity in the leaves of \textit{T. chinensis} seedlings pre-treated with ABT at 200 mg·L\(^{-1}\) first increased and then decreased with increasing salt stress. At Scs of 0.3\%–0.9\%, there was a significant increase in POD activity in the leaf cells. The antioxidant enzyme system
decomposed the $H_2O_2$ produced by SOD through disproportionation reactions by increasing POD activity. Under high salt stress ($S_c\geq1.2\%$), excess ROS were produced in leaf cells, exceeding the removal threshold of POD. As a result, the accumulating ROS damaged the enzyme system, resulting in a decline in POD activity. Compared with pretreatment with ABT at 50 and 100 mg·L$^{-1}$, the sensitivity of POD activity was relatively low in the leaves of $T.\ chinensis$ seedlings pre-treated with ABT at 200 mg·L$^{-1}$, and the ability of POD in these $T.\ chinensis$ seedlings to regulate salt tolerance was also relatively low.

**Effects of salt stress on MDA content in $T.\ chinensis$ cuttings**

Plants produce MDA as a result of MLP under stress. MDA is the main indicator of cell membrane damage and free radical formation in plants. As MDA increasingly accumulates, membrane damage increases and the resistance of the plant declines. Thus, MDA can be used as an important index for evaluating the extent of membrane system damage under stress[44]. The MDA content in plant leaves varies relatively significantly with their salt tolerance. As salt stress increases, there is a continuous increase in MDA content in the leaves of plants with relatively low salt tolerance, such as $T.\ chinensis$ tissue culture seedlings[45]. In comparison, with increasing salt stress, the MDA content in the leaves of plants with relatively high salt tolerance first decreases and then increases[32]. In this study, the MDA content in the leaves of $T.\ chinensis$ cuttings first increased and then decreased as the salt stress level increased. This finding is consistent with those reported by Li et al. showing the effects of MLP in the seedling leaves of six gramineous forages[46], but differs from the results of Qiu et al. investigating the MDA content in $Lagerstroemia$
indica ‘Pink Velour’ under salt stress[47]. This distinction may be related to the relatively significant differences in salt stress tolerance regulatory mechanisms among plants. Here, MDA content in the leaves of *T. chinensis* peaked at Sc of 0.6% and then decreased at Sc of 0.9%; SOD and POD activities were relatively high at Sc of 0.9%. These findings suggest that through inter-regulation, SOD and POD can effectively remove the excess ROS produced under salt stress and maintain the number of ROS in the organism at a low level, thereby essentially preventing ROS-induced MLP and other damaging processes. However, under severe salt stress (Sc = 1.2%), SOD and POD activities were both relatively low, and there was a significant decrease in MDA content, which might be related to the adaptive regulation of a certain dominant factor under the combined action of salt stress and ABT. The relevant internal mechanism requires further analysis.

conclusions

As the salt stress level increased, the survival rate, root length, and height of *T. chinensis* cuttings gradually decreased, whereas their biomass first increased and then decreased. At Sc≥1.2%, there was a significant decrease in *T. chinensis* cutting biomass, and the survival rate was zero. ABT, the rooting powder used in this study, enhanced the resistance of *T. chinensis* to severe salt stress (Sc>0.6%). ABT treatment exhibited a relatively high compensatory effect on *T. chinensis* cuttings under salt stress. ABT at a concentration of 100 mg·L⁻¹ exhibited a positive effect on the growth of *T. chinensis*. The effectiveness of ABT in improving the survival rate and growth of *T. chinensis* cuttings became increasingly pronounced as the salt stress level increased. ABT was most effective in improving the survival rate of *T. chinensis* when applied at 50 and 100 mg·L⁻¹.
*T. chinensis* seedling photosynthesis was enhanced by increasing the content of Chl to adapt to salt stress at suitable levels. However, under excessively high salt stress, Chl synthesis was disrupted, resulting in a decline in Chl content. Increasing the ABT concentration could strengthen the tolerance of *T. chinensis* seedlings to salt stress during Chl synthesis.

As the salt stress level increased, *T. chinensis* seedlings showed reduced ROS-induced damaged through increases in SOD and POD activities. Excess ROS accumulation inhibited the increase in enzyme activities. More significant changes in MLP in the cell membranes of *T. chinensis* seedlings resulted in higher MDA accumulation. ABT helped enhance the regulatory ability of the enzyme system of *T. chinensis* cuttings and significantly reduced the damage caused by low salt stress in cell membranes. The enzyme activities were highest in the *T. chinensis* seedlings pre-treated with ABT at 100 mg·L⁻¹, and the cell membranes in these seedlings sustained the least significant oxidative damage. The following conditions were found to be suitable for vegetative propagation of *T. chinensis*: Sc≤0.9% and ABT≤100 mg·L⁻¹. At Sc of 0.9%, *T. chinensis* seedlings pre-treated with ABT at 100 mg·L⁻¹ showed the most vigorous growth, had the highest biomass, and exhibited relatively high physiological regulatory ability and salt adaptability.

**abbreviations**

ABT, aminobenzotriazole; Sc, soil salinity; Chl, chlorophyll; SOD, superoxide dismutase; POD, peroxidase; MDA, malondialdehyde; ROS, reactive oxide species; MLP, membrane lipid peroxidation; CAT, catalase; Chla, chlorophyll-a; Chlb, chlorophyll-b; ChlT, total Chl; 5-ALA, 5-aminolevulinic acid.
declarations

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

Authors’ contribution
Jia Sun, the first author of the paper, had overall responsibility for the experimental design, data collection, analysis, writing and project management; Jiangbao Xia is the corresponding author, and made significant contributions to experimental arrangements and manuscript preparation; Ximei Zhao and Li Su made significant contributions to data collection and analysis; Chuanrong Li and Fanglei Gao made significant contributions to the interpretation of the data and manuscript preparation; Ping Liu made significant contributions to data collection and analysis and writing.

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The authors declare that they have no conflict of interest.

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Figures

Figure 1

Effects of salt stress on the survival rate of T. chinensis cuttings with various concentrations.
Figure 2

Effects of salt stress on the biomass of T. chinensis cuttings with various concentrations.
Figure 3

Effects of salt stress on the Chl content in the leaves of T. chinensis cuttings with
Figure 4

Effects of salt stress on SOD activity in the leaves of T. chinensis cuttings with va
Figure 5

Effects of salt stress on POD activity in the leaves of T. chinensis cuttings with va
Figure 6

Effects of salt stress on MDA content in leaves of T. chinensis cuttings with various concentrations.