



Effects of a heavy metal (cadmium) on the responses of subtropical coastal tree species to drought stress

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Abstract

With global climate change and increased industrialization, drought and heavy metals have become common abiotic stress factors for coastal vegetation. In this study, we investigated the ecophysiological responses of the seedlings of three subtropical coastal tree species (*Barringtonia racemosa*, *Hibiscus tiliaceus*, and *Terminalia neotaliala*) to drought stress (D), cadmium addition (Cd), and their combined effects (Cd + D). The results showed that, for all three plant species, treatment D significantly decreased A_{\max} , Y(II), qP, and ETR; increased the concentrations of PRO, soluble sugars, ABA, MDA, and O_2^- ; and increased the activity of Rubisco. The concentrations of soluble sugars, MDA, and O_2^- were similar for treatments D and Cd; the only difference was that qP, A_{\max} , and ETR values of *B. racemosa* and the A_{\max} value of *H. tiliaceus* were significantly lower in treatment Cd than in control. The concentrations of PRO, soluble sugars, ABA, and MDA were significantly lower for treatment Cd + D than for treatment D. The O_2^- concentration was positively correlated with the concentrations of soluble sugars and PRO, indicating that osmoregulation was important for the responses of the plants to oxidative stress. ABA was positively correlated with MDA, indicating that ABA was involved in the response to oxidative stress. These results, which show that Cd may weaken the physiological responses of coastal plants to drought stress by increasing ABA accumulation, may provide guidance for coastal ecosystem management in South China.

Keywords Coastal sandy land · Climate change · Industrial pollution · Subtropical forest

Introduction

Coastal sandy lands are transition zones between land and ocean. In addition to supporting economic and other human activities, such areas are environmentally fragile and environmentally important (Wang et al., 2017). Coastal sandy lands

not only reduce flooding from storm surges, but also support coastal tourism (Ewel et al., 1998). With the change in global climate and the excessive development in some areas, however, coastal sandy lands are increasingly experiencing erosion, vegetation degradation, and a reduction in the ecological services that they provide (Osland et al., 2018).

Coastal sandy lands are usually formed on aeolian sandy soil dominated by mud, sediment, or sand-mud. The soils in such areas have a loose structure, a poor water-storage capacity, and a poor nutrient-retention capacity; in tropical and subtropical regions including South China; sandy coastal shores receive little or uneven rainfall and periods of high temperature, making coastal afforestation difficult (Barbier et al., 2011; Chou et al., 2013). Plants that grow on coastal sandy lands are valuable resources and are often unique to that environment (Landry and Golden, 2018). These plants include obligate halophytes and facultative halophytes, which have low transpiration rates, high cell osmotic pressures, and high water-holding capacities, i.e., they are adapted to growing on the saline soil in coastal areas (Huang et al., 2020).

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Although the annual precipitation in South China has not changed during recent decades, the region is now wetter in the wet season and drier in the dry season, and the frequency of extreme drought events has increased (Chou et al., 2013). Drought stress has been well documented to be a serious threat to plant growth, productivity, and survival (Hui et al., 2018; Kaya et al., 2020; Kosar et al., 2021; Raja et al., 2020). Previous research has indicated that drought can reduce organic carbon storage and carbon sequestration in coastal ecosystems (Sanderman et al., 2018). Therefore, the extensive degradation of coastal vegetation caused by extreme drought warrants further study (Lovelock et al., 2009).

The contents of heavy metals have substantially increased in the soils of South China because of industrialization, urbanization, and the inadequate treatment of industrial, agricultural, and domestic sewage (Luo et al., 2020). Industrial wastewater containing heavy, ecologically persistent metals are discharged without treatment into waterways and soil, which poses a serious threat to the stability of estuarine and coastal ecosystems (Zheng et al., 2020). As the flow of water slows in estuaries and coastal zones, large amounts of heavy metals are deposited and accumulate in the soil (Liu et al., 2014). The toxic effects of high concentrations of cadmium (Cd) and other heavy metals on plants mainly include oxidative stress, growth inhibition, metabolic abnormalities, and even death (Arif et al., 2021). Most heavy metals reduce plant growth, but appropriate concentrations of some heavy metals (such as Mn and Zn) can promote plant growth (Azevedo and Lea, 2005). Studies have shown that drought can reduce the absorption of Cd by castor bean (*Ricinus communis*) and Indian mustard (*Brassica juncea*), but other studies have reported that drought can increase the concentration of Cd in the roots and seeds of mature peanut plants (Baudhdh and Singh, 2012; Shi et al., 2015; Xia et al., 2015).

Although previous studies have revealed the physiological and ecological responses of plants to drought and heavy metal stress (Jiang et al., 2019; Sharma and Zheng, 2019), there is still a lack of understanding of the effects of drought and heavy metals alone or in combination on subtropical coastal vegetation and semi-mangrove plants. In the current greenhouse study, we therefore investigated the effects of the following four treatments on the seedlings of three tree species that grow on sandy coastal land in subtropical areas: Cd stress, extreme drought, Cd stress plus extreme drought, and a control without Cd stress or drought stress. Our main objective was to determine the effects of these treatments, especially the combination of Cd stress and extreme drought, on the physiological and ecological properties of the three tree species. The results of this study should inform managers of sandy coastal ecosystems about how to reduce the detrimental effects of extreme drought and heavy metal pollution in South China.

Materials and methods

Plant materials

Three tree species, *Barringtonia racemosa*, *Hibiscus tiliaceus*, and *Terminalia neotaliala*, were selected for this research. *B. racemosa* and *H. tiliaceus* are semi-mangrove plants that are highly adapted to the intertidal zone and are important components of coastal vegetation communities (Huang et al., 2020). *T. neotaliala* is highly salt-tolerant and is a common tree species along the subtropical coast of China (Huang et al., 2018). Seedlings of *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* were purchased from a nursery in Guangzhou, Guangdong Province, China. The seedlings were maintained in a greenhouse at the South China Botanical Garden, Guangzhou, Guangdong Province, China.

Treatments

The seedlings of each species were divided into four treatment groups: a Cd-application group (Cd), a drought group (D), a Cd-application plus drought group (Cd + D), and a control group (CT, without Cd application or drought). Each treatment for each species was represented by 12 replicate seedlings in pots. All seedlings were fully watered and allowed to acclimate to the greenhouse environment for 7 days before the experiment began. The potted plants were randomly placed on a greenhouse bench, and the experiment lasted for 10 days (day 0 to day 10). CT seedlings were watered (35 mL water per pot) every other day from day 0, and Cd seedlings were treated with a Cd solution (35 mL of 30 mg/L CdCl₂ per pot) every other day from day 0. D seedlings were not watered or treated with Cd. Cd + D seedlings were treated with a Cd solution (35 mL 30 mg/L CdCl₂ per pot) on day 0 and were not subsequently watered or treated with Cd. The treatment schedule is shown in Table 1. Leaf photosynthetic parameters were measured on days 0, 1, 2, 5, 8, and 10. After photosynthesis measurement, the same leaf pieces were collected and frozen at –80 °C for determination of physiological indexes.

Determination of metal content

Leaf samples harvested at the end of the experiment were oven dried and subjected to microwave wet digestion in 10 mL of concentrated HNO₃. The ashes were then dissolved in 1.5% HNO₃ to a total volume of 25 mL for the subsequent determination of the metal content by inductively coupled plasma mass spectrometry (ICP-MS). The concentrations of Cd in the sample were measured.

Table 1 Timing of water and Cd application for the four treatments in the experiment. CT (control), Cd (Cd addition), Cd + D (Cd addition + drought), and D (drought)

Day	Treatment			
	CT	Cd	D	Cd + D
0	Water	CdCl ₂	–	CdCl ₂
1	–	–	–	–
2	Water	CdCl ₂	–	–
3	–	–	–	–
4	Water	CdCl ₂	–	–
5	–	–	–	–
6	Water	CdCl ₂	–	–
7	–	–	–	–
8	Water	CdCl ₂	–	–
9	–	–	–	–
10	Water	CdCl ₂	–	–

Determination of photosynthetic parameters

Photosynthesis and chlorophyll fluorescence were measured using a portable photosynthesis system (LI-6800F, LI-COR, USA) fitted with a fluorometric sheet chamber (6800-01A). The leaf gas exchange parameters, including the net light saturated photosynthetic rate (A_{max}), were determined at 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic flux density, 400 $\mu\text{mol mol}^{-1} \text{CO}_2$ concentration, and 25 °C.

Determination of chlorophyll fluorescence parameters

The chlorophyll fluorescence endpoints were measured using a chlorophyll fluorescence imaging system (Imaging-PAM-MAXI, Walz, Germany). The fluorescence parameters included the actual photochemical efficiency ($Y(II)$), the apparent electron transfer rate (ETR), and the photochemical quenching coefficient (qP). Before measurement, areas of interest were randomly selected on each leaf sample. The chlorophyll fluorescence parameters were measured in saturated pulse mode; the saturation pulse light was 2700 $\text{mmol m}^{-2} \text{s}^{-1}$ (duration 0.8 s, interval 20 s), the measured light intensity was 0.5 $\text{mmol m}^{-2} \text{s}^{-1}$, and the actinic light intensity was 185 $\text{mmol m}^{-2} \text{s}^{-1}$.

Determination of the MDA concentration

MDA concentration was determined by the thiobarbituric acid method. Leaf materials (0.2 g) were mixed with 5 mL of 10% TCA. The preparation was then centrifuged at 10,000 $\times g$ for 20 min. A 2-mL volume of the supernatant was added to 2 mL of 6% 2-thiobarbituric acid. The absorption values were measured at 450, 532, and 600 nm with a spectrophotometer (UV-3802, Unico, China). MDA concentration was calculated as follows (Cakmak and Horst, 1991): MDA concentration ($\mu\text{mol L}^{-1}$) = $6.45 (A_{532} - A_{600}) - 0.56 A_{450}$.

Determination of the ABA concentration

Abscisic acid (ABA) concentration was determined by high-performance liquid chromatography (HPLC) as previously described (Murakamimizukami et al., 1991) with minor modification. One 0.5-g leaf sample was homogenized with 80% cold methanol. The homogenate was filtered, and the filtrate was suspended in 80% methanol, incubated in the dark for 1 h, and then filtered again. The two filtrates were mixed, evaporated, and dried with gaseous nitrogen and mixed with PVPP. The suspension was adjusted to pH 3.0 and was washed three consecutive times with the same volume of petroleum ether. ABA was detected by HPLC with a UV detector.

Determination of the soluble sugar concentration

The concentration of soluble sugars in leaves was determined by anthrone-sulfuric acid colorimetry. The leaf sample (0.5 g) was mixed with 7 mL of distilled water and placed in a boiling water bath for 30 min. The extract was then centrifuged, and a 2-mL volume of the supernatant was then added to 12 mL of anthrone-sulfuric acid reagent with a concentration of 0.2 mg/mL; the preparation was then placed in a boiling water bath for 12 min. After the preparation had cooled, its absorbance was measured at a wavelength of 625 nm. The concentration of soluble sugars was determined according to a standard curve.

Determination of the PRO concentration

For each combination of tree species and treatment, a 0.5-g leaf sample was placed in 5 mL of an aqueous 3% sulfosalicylic acid solution to extract proline (PRO) from the leaves (as indicated earlier, this was done with leaf samples collected on even-numbered days). After filtration, anhydride and glacial acetic acid were added, and the preparation was placed in a 100 °C water bath for 1 h. The mixture was then extracted with toluene, and the absorbance of the extract was measured at 520 nm. The concentration of PRO was determined according to a standard curve. The PRO results were the average of five repeated measurements.

Determination of Rubisco activity

Rubisco activity was assayed by the NADH-coupled enzyme assay (Kubien et al., 2011). A 0.5-g sample of leaves was added to 10 mL of pre-cooled (to 4 °C) extraction buffer (Tris-HCl pH 7.8 100 mmol/L, KCl 20 mmol/L, EDTA 1 mmol/L). The preparation was then homogenized and centrifuged at 15,000 $\times g$ for 10 min. A 100- μL volume of the supernatant was then treated

with 2.7 mL of reaction solution (Tris–HCl pH 8.2 100 mmol/L, NaHCO₃ 10 mmol/L, MgCl₂ 20 mmol/L, DTT 1 mmol/L NADH 0.5 mmol/L, and ATP 5 mmol/L), and the change in light absorption at 340 nm was then immediately measured at 15-s intervals.

Determination of the O₂⁻ concentration

The concentration of O₂⁻ in plant leaves was determined by the hydroxylamine oxidation method (Ke et al., 2002). A 0.5-g quantity of frozen leaf sample was ground to a powder in liquid nitrogen. The powder was immediately mixed with the extraction solution (250 mmol·L⁻¹ phosphate buffer, pH 8.0, containing 10 μmol·L⁻¹ pyridoxal phosphate, 1 mmol L⁻¹ EDTA, and 5 mmol·L⁻¹ DTT), and the preparation was centrifuged at 10,000×g for 25 min at 4 °C. The supernatant was then collected and treated with 1 mmol·L⁻¹ NH₄Cl (1 mL) and 50 mmol·L⁻¹ phosphate buffer (pH 7.8) (0.5 mL). A 0.5-mL volume of the crude enzyme solution was incubated at 25 °C for 60 min before 17 mmol·L⁻¹ *p*-aminobenzenesulfonic acid (1 mL) and 7 mmol·L⁻¹ α-naphthylamine (1 mL) were added. The preparation was then incubated at 25 °C for 20 min, and the absorbance was measured at 530 nm. The content of O₂⁻ was calculated according to a standard curve.

Determination of the T-AOC

The total antioxidant capacity (T-AOC) of plant leaves was determined by the ferric ion reducing antioxidant power (FRAP) method (Bates et al., 1973). A 0.5-g sample of leaves was ground with 5 mL distilled water. The mixture was centrifuged at 4 °C for 10,000×g for 10 min. A 100-μL supernatant was added to 2.4 mL of working solution (300 mmol/L phosphate buffer (pH 3.6), 10 mmol/L TPTZ in 40 mmol/L HCL, and 20 mmol/L FeCl₃·6H₂O solution in the volume ratio of 10:1:1), and the absorbance at 593 nm was measured after water bath at 37 °C for 10 min. The T-AOC of the sample was determined according to the standard curve.

Data analysis

One-way ANOVAs with Fisher's LSD tests were used to assess the effects of treatment, tree species, and their interaction on A_{max}, Y [II], ETR, qP, PRO concentration, soluble sugar concentration, ABA concentration, MDA concentration, Rubisco activity, and O₂⁻ concentration. The relationships between paired variables were determined by the Pearson correlation analysis (two-tailed) and logistic regression. Statistical significance was set at *P* < 0.05. IBM SPSS Statistics 22.0 was used for data analyses.

Results

Leaf Cd contents and plant overall appearance

The contents of Cd in the leaves of each species were significantly higher with treatment Cd (Cd contents in *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* were increased by 498%, 548%, and 1328%, respectively) and treatment D (Cd contents in *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* were increased by 761%, 289%, and 1735%, respectively) than with treatments CT or D (Fig. 1), indicating that Cd metal ions were absorbed and accumulated in plants. As the experiment progressed from day 0 to day 8, the overall appearance of the three species with treatment Cd gradually changed (Figs. S1–S3). The leaves of *B. racemosa* began to wilt on day 8 with treatment Cd + D and began to wilt on day 4 with treatment D (Fig. S1). The appearance of *H. tiliaceus* leaves was not changed by the treatments (Fig. S2). The leaves of *T. neotaliala* began to wilt on day 8 with treatments Cd + D and D (Fig. S3). It was obvious that treatments Cd + D and D had greater effects than treatment Cd on the appearance of *B. racemosa* and *T. neotaliala* leaves.

Leaf photosynthetic parameters

Most photosynthetic parameters of the three species were affected by treatment D. The chlorophyll fluorescence parameters of *H. tiliaceus* and *T. neotaliala* but not of *B. racemosa* were less affected by treatment Cd than by treatment CT (Fig. 2). Y[II] of *B. racemosa* was significantly lower with treatments Cd + D (Y[II] was reduced by 49%) and D (Y[II] was reduced by 42%) than with treatment CT (Fig. 2A). Y[II] of *H. tiliaceus* was significantly lower with treatment D (Y[II] was reduced by 51%) than with treatment CT, but Y[II] of *T. neotaliala* did not significantly differ among the treatments (Fig. 2B, C). qP of all three species was significantly lower with treatments Cd + D (qP of *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* was reduced by 62%, 47%, and 32%, respectively) and D (qP of *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* was reduced by 77%, 66%, and 56%, respectively) than with treatment CT (Fig. 2D–F). A_{max} of *B. racemosa* and *H. tiliaceus* was significantly lower with treatments Cd (A_{max} of *B. racemosa* and *H. tiliaceus* was reduced by 61% and 47%, respectively), Cd + D (A_{max} of *B. racemosa* and *H. tiliaceus* was reduced by 93% and 86%, respectively), and D (A_{max} of *B. racemosa* and *H. tiliaceus* was reduced by 95% and 86%, respectively) than with treatment CT (Fig. 3A, B). A_{max} of *T. neotaliala* was significantly lower with treatments Cd + D (A_{max} was reduced by 63%) and D (A_{max} was reduced by 88%) than with treatment CT (Fig. 3C). ETR of *B. racemosa* was significantly lower with

Fig. 1 Cd content in the leaves of the three tree species (*Barringtonia racemosa*, *Hibiscus tiliaceus*, and *Terminalia neotaliala*) as affected by CT (control), Cd (Cd addition), Cd+D (Cd addition + drought), and D (drought) treatments. Values are means \pm SE; for each tree species, means with different letters are significantly different ($P < 0.05$) based on one-way ANOVAs with Fisher's LSD tests

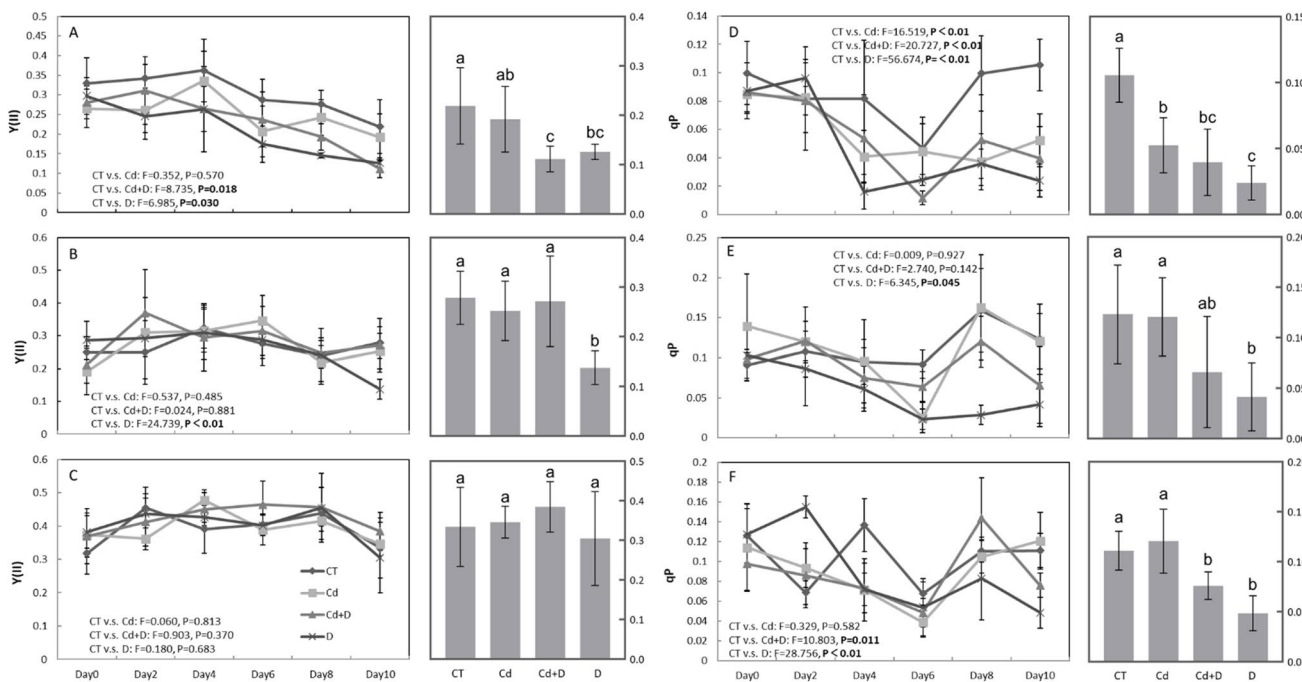
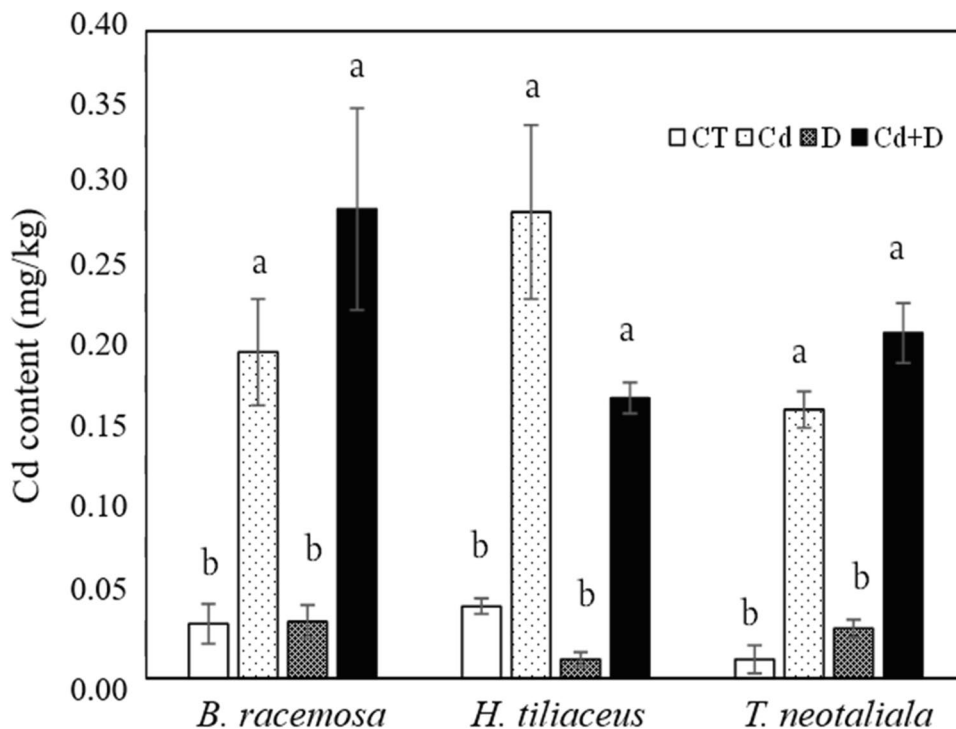


Fig. 2 Changes in Y(II) (A, B, C) and qP (D, E, F) of the three tree species as affected by CT (control), Cd (Cd addition), Cd+D (Cd addition + drought), and D (drought) treatments. (A, D *B. racemosa*;

B, E *H. tiliaceus*; C, F *T. neotaliala*). Values are means \pm SE. Means with different letters are significantly different ($P < 0.05$) based on one-way ANOVAs with Fisher's LSD tests

treatments Cd (ETR was reduced by 50%), Cd + D (ETR was reduced by 56%), and D (ETR was reduced by 73%) than with treatment CT (Fig. 3D). ETR of *H. tiliaceus* and *T.*

neotaliala was significantly lower with treatment D (ETR of *H. tiliaceus* and *T. neotaliala* was reduced by 74% and 56%, respectively) than with treatment CT (Fig. 3E, F).

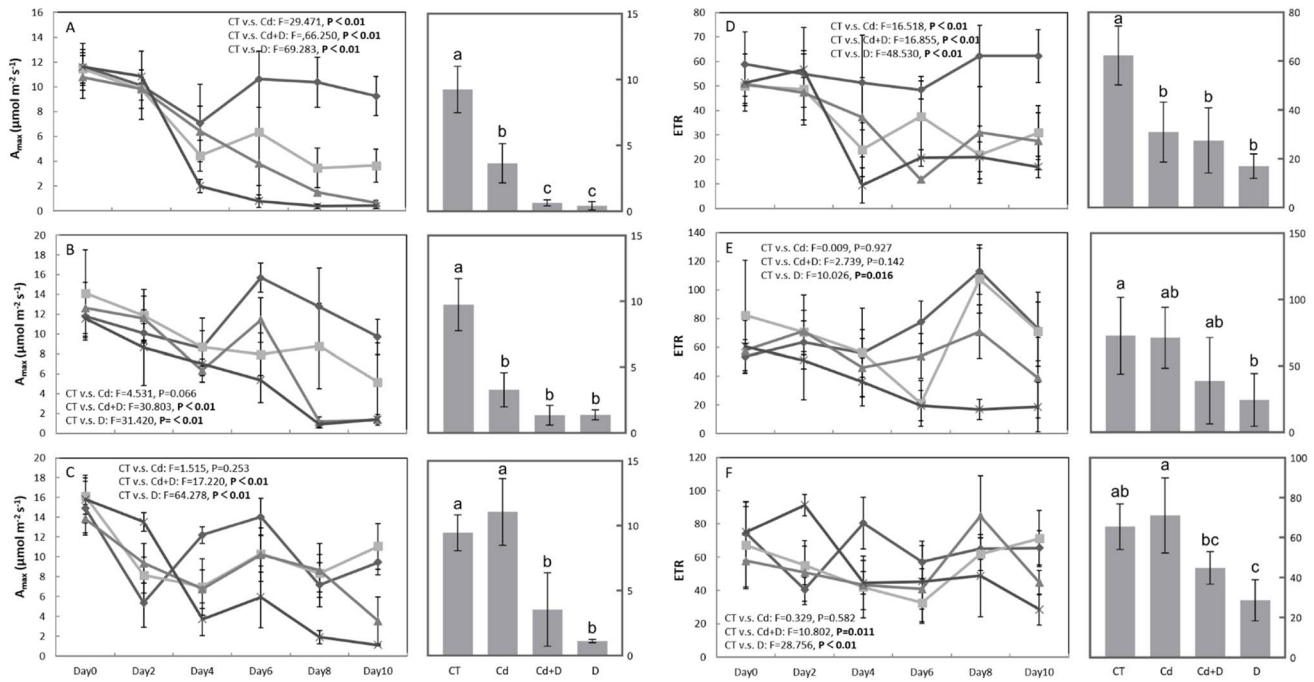


Fig. 3 Changes in A_{max} (maximum photosynthetic rate) (A, B, C) and ETR (D, E, F) of the three tree species as affected by CT (control), Cd (Cd addition), Cd+D (Cd addition+drought), and D (drought) treatments. (A, D *B. racemosa*; B, E *H. tiliaceus*; C, F *T. neotaliala*).

Values are means \pm SE. Means with different letters are significantly different ($P < 0.05$) based on one-way ANOVAs with Fisher's LSD tests

Leaf physiological indicators

The PRO concentrations in *B. racemosa* and *H. tiliaceus* under the four treatments initially increased and then decreased during the experiment (Fig. 4A, B). PRO concentrations in all three species were significantly higher with treatment Cd + D (the concentration increased by 50% for all three species) and treatment D (the concentration in *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* increased by 116%, 120%, and 124%, respectively) than with treatment CT (Fig. 4A–C), but PRO concentrations were not significantly affected by treatment Cd in *B. racemosa* or *T. neotaliala* (Fig. 4A, C). The soluble sugar concentration of the three species initially increased and then decreased during the experiment (Fig. 4D–F). The soluble sugar concentration in the three species was significantly higher with treatments Cd (concentrations in *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* increased by 93%, 97%, and 53%, respectively), Cd + D (concentrations in *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* increased by 139%, 142%, and 95%, respectively), and D (concentrations in *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* increased by 198%, 192%, and 124%, respectively) than with treatment CT (Fig. 4E, F). The ABA concentration in *B. racemosa* was significantly higher with treatment Cd (the concentration increased by 59%),

treatment Cd + D (the concentration increased by 88%), and treatment D (the concentration increased by 135%) than with treatment CT (Fig. 5A). With all treatments, the ABA concentrations increased and then remained stable (Fig. 5A–C). The MDA concentrations of the three species tended to initially increase and to then remain stable (Fig. 5D–F). In all three species, the MDA concentration in leaves tended to increase more with treatments Cd (the concentration in *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* increased by 85%, 23%, and 56%, respectively), Cd + D (the concentration in *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* increased by 120%, 55%, and 89%, respectively), and D (the concentration in *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* increased by 151%, 97%, and 131%, respectively) than with treatment CT (Fig. 5D–F).

With all four treatments, the Rubisco activities in *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* initially increased and then decreased to different degrees (Fig. 6A, B). Rubisco activities of the three species were higher with treatments Cd (the activities in *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* increased by 31%, 68%, and 80%, respectively), Cd + D (the activities in *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* increased by 56%, 117%, and 135%, respectively), and D (the activities in *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* increased by 75%,

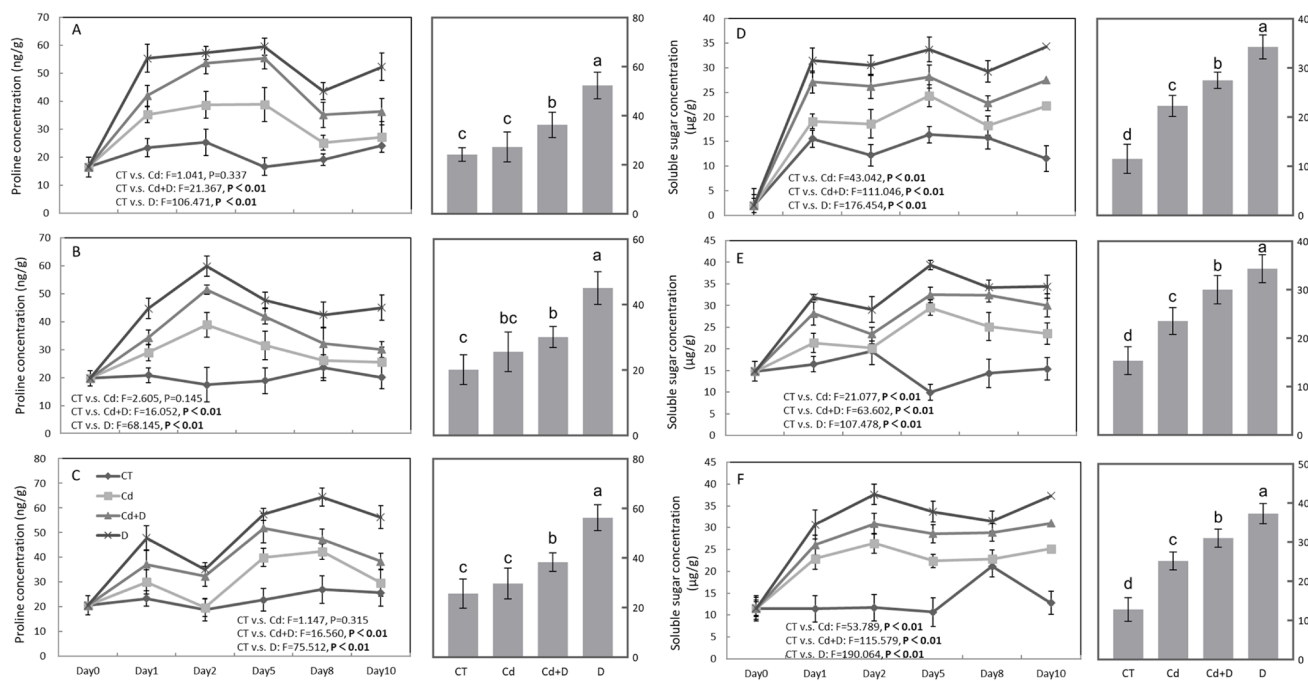


Fig. 4 Changes in the proline concentration (A, B, C) and soluble sugar concentration (D, E, F) of three tree species as affected by CT (control), Cd (Cd addition), Cd+D (Cd addition+drought), and D (drought) treatments. (A, D B. *racemosa*; B, E *H. tiliaceus*; C, F *T.*

neotaliala). Values are means ± SE. Means with different letters are significantly different ($P < 0.05$) based on one-way ANOVAs with Fisher's LSD tests

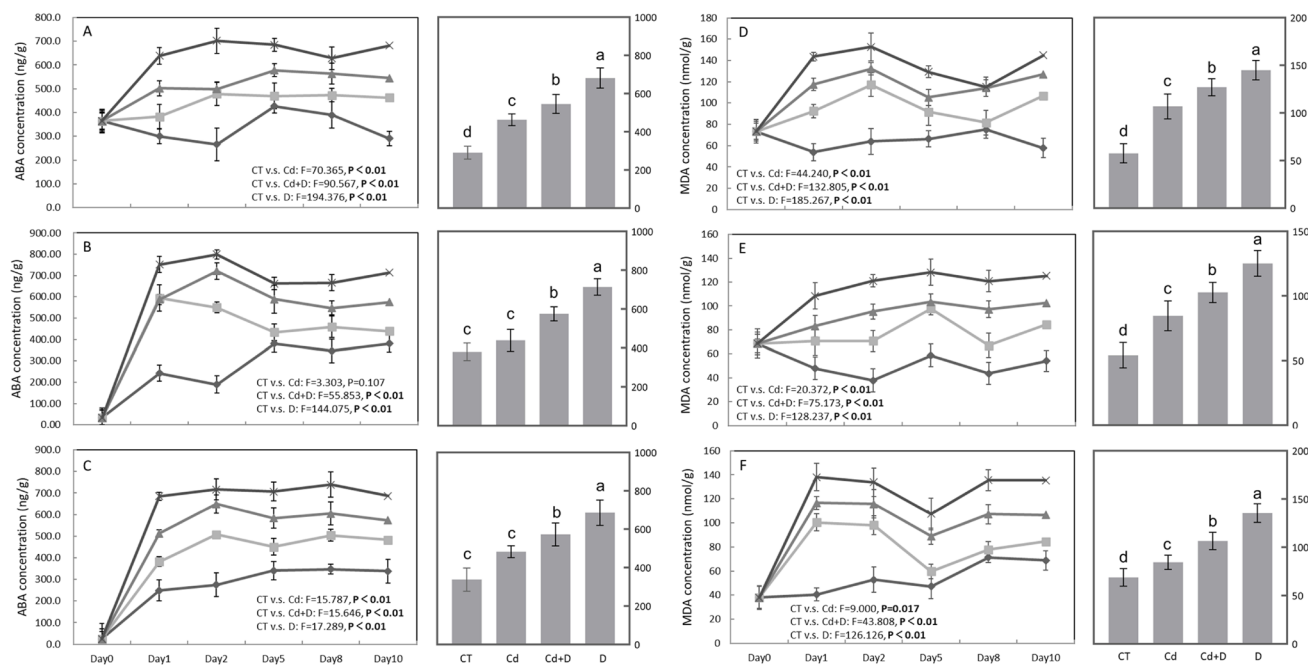


Fig. 5 Changes in the ABA concentration (A, B, C) and MDA concentration (D, E, F) of the three tree species as affected by CT (control), Cd (Cd addition), Cd+D (Cd addition+drought), and D (drought) treatments. (A, D B. *racemosa*; B, E *H. tiliaceus*; C, F *T.*

neotaliala). Values are means ± SE. Means with different letters are significantly different ($P < 0.05$) based on one-way ANOVAs with Fisher's LSD tests

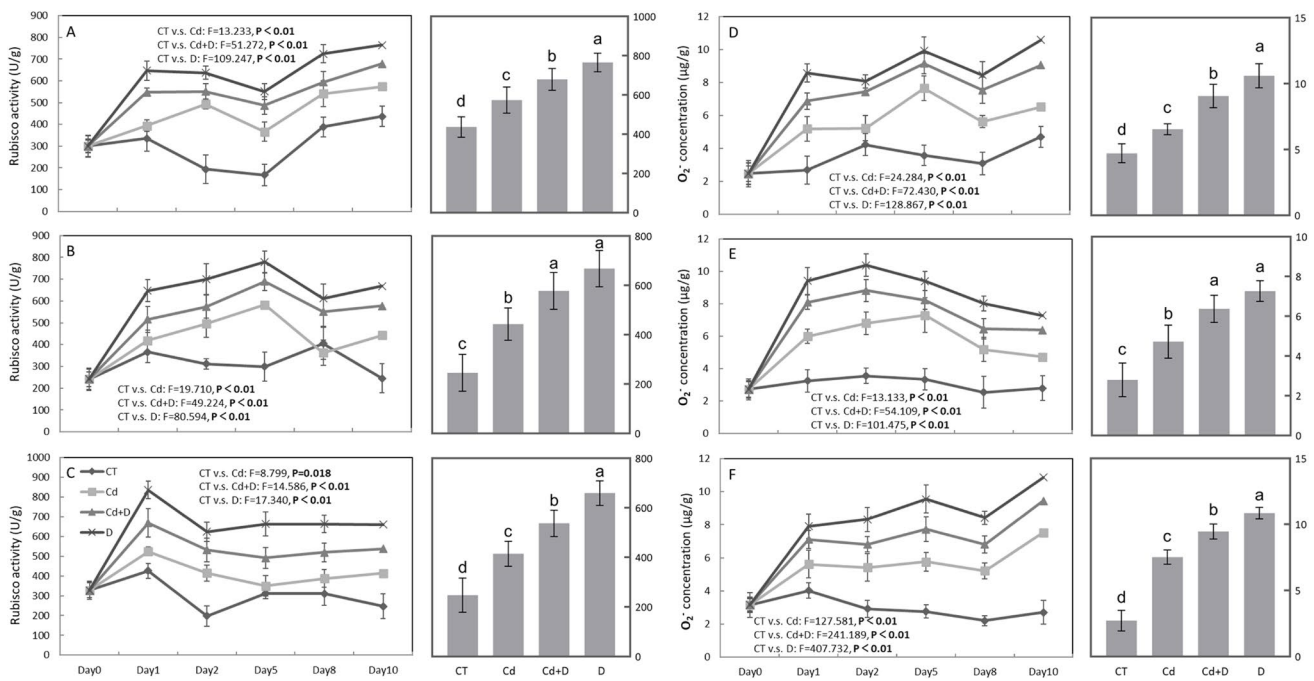


Fig. 6 Changes in Rubisco activity (A, B, C) and O_2^- concentration (D, E, F) in the three tree species as affected by CT (control), Cd (Cd addition), Cd + D (Cd addition + drought), and D (drought) treat-

ments. (A, D *B. racemosa*; B, E *H. tiliaceus*; C, F *T. neotaliala*). Values are means \pm SE. Means with different letters are significantly different ($P < 0.05$) based on one-way ANOVAs with Fisher’s LSD tests

167%, and 172%, respectively) than with treatment CT (Fig. 6A, C). The O_2^- concentration of the three species was significantly higher in treatments Cd (the concentrations in *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* increased by 39%, 69%, and 177%, respectively), Cd + D (the concentrations in *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* increased by 92%, 128%, and 2485, respectively), and D (the concentrations in *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* increased by 125%, 160%, and 300%, respectively) than in treatment CT (Fig. 6D–F). Toward the end of the experiment, the O_2^- concentration increased in *B. racemosa* and *T. neotaliala* (Fig. 6D, F) but decreased in *H. tiliaceus* (Fig. 6E). Only T-AOC of *B. racemosa* was significantly lower (it was 14% lower) in treatment CD + D than in treatment CT. T-AOC of *H. tiliaceus* and *T. neotaliala* did not significantly differ among the four treatments (Fig. 7).

Correlations

For all three plant species, the concentration of soluble sugars was positively correlated with the ABA concentration (Fig. S4A), the concentration of O_2^- was positively correlated with the soluble sugar concentration (Fig. S4B) and with the PRO concentration (Fig. S4C), and the concentration of MDA was positively correlated with the ABA concentration (Fig. S4D).

Discussion

Heavy metals and drought are generally considered to be stress factors for plants (Mansoor et al., 2021). These two stress factors can reduce pigment content, destroy chloroplast and membrane structure, and cause oxidative and osmotic stress (Jin et al., 2008; Wehner et al., 2016). In the current study, we found that 10 days of drought resulted in severe leaf wilt in all three plant species. Adverse effects of Cd alone, however, were not obvious, probably due to the short duration of the exposure time and low concentration of the Cd added.

Drought and Cd stress can cause oxidative damage to plants by increasing the concentration of reactive oxygen species (ROS), resulting in plant growth stagnation or even death (Hoque et al., 2021; Sinha et al., 2016). High concentrations of ROS can destroy important molecules (such as photosynthetic pigments, proteins, and lipids) and cause plant metabolic disorders (Iqbal et al., 2019). In the current study, the concentrations of superoxide (O_2^-) and MDA in *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* were significantly higher with treatments D, Cd, and D + Cd than with the CT. These results are consistent with the recent finding that the concentrations of H_2O_2 and MDA in radish (*Raphanus sativus* L.) leaves increased under drought and Cd stress (Tuver et al., 2022). In addition, the O_2^- and MDA concentrations of these three plant species were significantly higher with treatment Cd + D

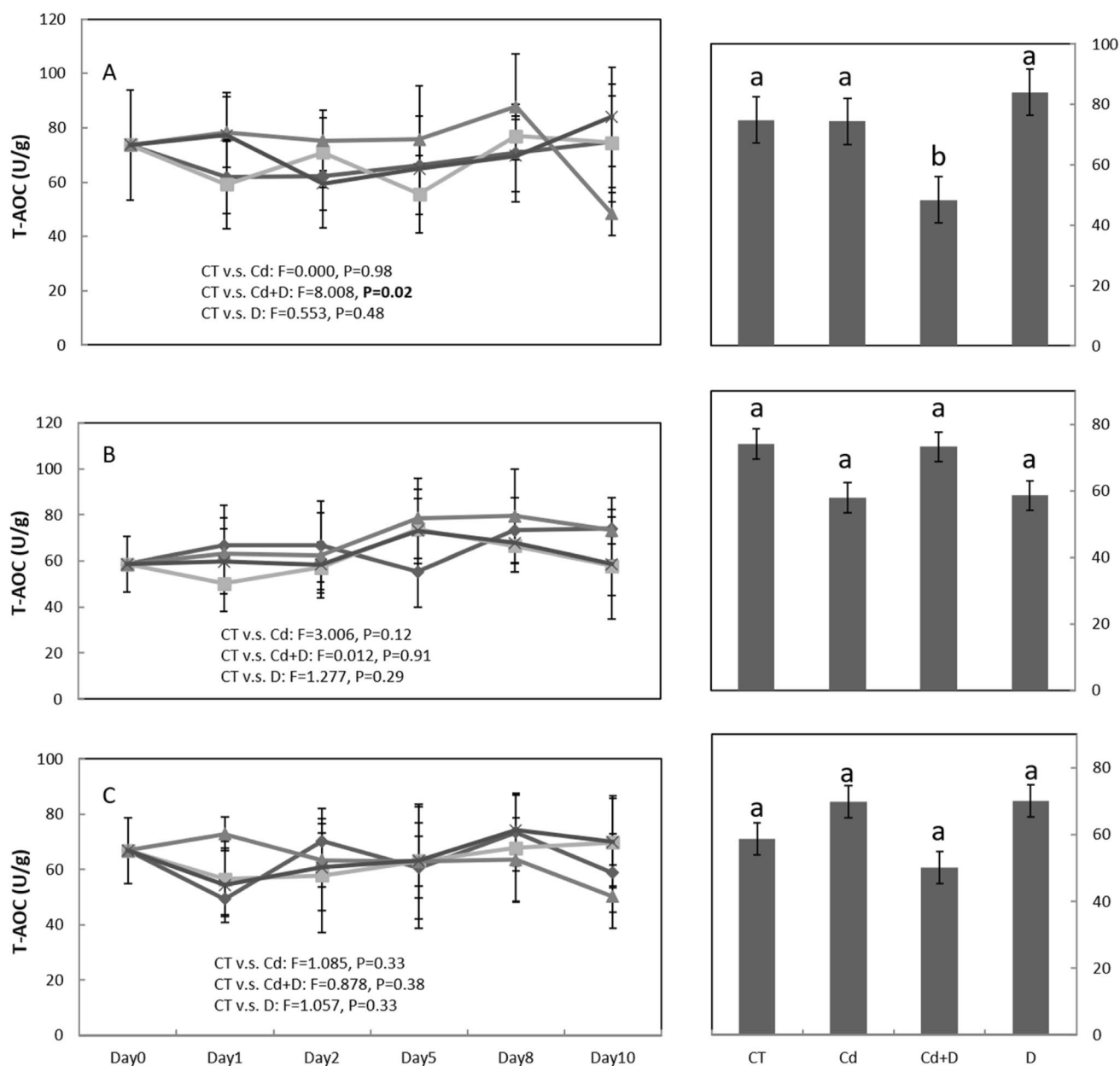


Fig. 7 Changes in T-AOC in the three tree species as affected by CT (control), Cd (Cd addition), Cd+D (Cd addition+drought), and D (drought) treatments. (**A** *B. racemosa*; **B** *H. tiliaceus*; **C** *T. neotalia*).

Values are means \pm SE. Means with different letters are significantly different ($P < 0.05$) based on one-way ANOVAs with Fisher's LSD tests

than with Cd but were significantly lower with treatment Cd+D than with treatment D (except for the O_2^- concentration in *H. tiliaceus*). This showed that the oxidative damage to the three plant species was lower with treatment Cd+D than with treatment D, but was higher with treatment Cd+D than with treatment Cd. It is well known that the antioxidant system (antioxidant enzymes and antioxidants) in plants will be induced to deal with the damage of ROS caused by abiotic stress and will rapidly convert ROS into water and oxygen. However, related studies also showed that the stimulation

of the antioxidant system is directly affected by the concentration of Cd in the environment or the degree of drought (Jin et al. 2008; Iqbal et al. 2019; Raja et al. 2020). In the current study, the T-AOC was not significantly increased or decreased by drought or Cd addition, indicating that the antioxidant system of these three plants did not play a significant protective role under the stress conditions.

Drought and Cd stress lead to water imbalance in plants and to increases in the content of PRO with osmotic regulation function (Ahmed et al., 2020; Rady and Hemida,

2015). Previous studies showed that the PRO content of rice (*Oryza sativa* L.) increased with an increase of Cd concentration in the environment, and that the Cd tolerance of cucumber (*Cucumis sativus* L.) seeds was increased after soaking in PRO (Majumdar et al., 2018; Semida et al., 2018). In the current study, the PRO concentration of *B. racemosa*, *H. tiliaceus*, and *T. neotaliala* tended to increase but did not change significantly in the Cd treatment, perhaps because the quantity of added Cd did not exceed the tolerance threshold of the plants. Previous research has shown that in order to alleviate the adverse effects of drought, rice, safflower (*Carthamus tinctorius* L.), and other plant species accumulate PRO (Farooq et al., 2020; Lum et al., 2014). Our results are consistent with those of previous studies, i.e., all three plant species significantly increased their accumulation of PRO in response to drought stress. Soluble sugars can maintain normal plant metabolism by regulating cell water potential under environmental stress (Abd Allah et al., 2017; Zhang et al., 2018). Researchers found that the soluble sugar content in the leaves of *Spirodela polyrhiza* and *Robinia pseudoacacia* significantly increased in response to Cd stress (Jia et al., 2017; Zhang et al., 2018). We also found that the soluble sugar concentration of the three plant species increased significantly with Cd treatment. Under short-term drought stress, the soluble sugar content in the photosynthetic organs of hinoki cypress (*Chamaecyparis obtusa*) and in the stems and roots of citrus (*Citrus reticulata*) seedlings increased (Tsuji et al., 2022; Zaher-Ara et al., 2016). Our results are consistent with these previous studies in that the soluble sugar concentration of the three plant species increased significantly under drought. Similar to the concentrations of O_2^- and MDA, the concentrations of PRO and soluble sugar in the current study were significantly lower with the combination of Cd addition + drought than with drought alone, which also indicated that plants experienced less osmotic stress with the former than with the latter treatment. We found that the O_2^- concentration was positively correlated with PRO and soluble sugar concentration, which suggested that that PRO and soluble sugars may also be involved in the response to oxidative stress in these three plant species.

Many studies have shown that ABA can increase the drought resistance of plants (Awan et al., 2021; Yoshida et al., 2019). ABA is mainly involved in stomatal closure; by reducing transpiration, ABA reduces water loss and thereby increases the drought tolerance of plants (Kim et al., 2010; Li et al., 2020). Consistent with previous studies, we found that the ABA concentration in the three plant species was significantly higher with the drought treatment than with the control. We also found that the ABA concentration of the three plant species was significantly higher with the combination of Cd addition + drought than with the control or with Cd addition alone, but was significantly

lower with the combination of Cd addition + drought than with drought alone. This indicates that Cd addition reduces the accumulation of ABA in these three plants, which may enable them to maintain a certain degree of stomatal opening and photosynthetic carbon assimilation under drought stress, perhaps improving their performance under mild drought stress. This is consistent with a recent study that found that ABA is involved in the response of barley to Cd stress (Liu et al., 2022).

Drought and Cd stress generally reduce the content of Rubisco enzyme or inhibit its activity (Galmes et al., 2013). In the current study, Rubisco activity was not inhibited and instead was significantly increased by drought, Cd addition, or the combination of drought + Cd addition, perhaps because of the short treatment time or the low level of stress. In general, a higher level of Rubisco activity supports a higher photosynthetic capacity (Qu et al., 2021). However, A_{max} of three plant species was significantly decreased by drought, Cd addition, or the combination of drought + Cd addition (except for *T. neotaliala* in response to Cd addition alone). One likely explanation is that the accumulation of ABA leads to stomatal closure, which reduces the entry of CO_2 into leaf cells, resulting in the inhibition of photosynthesis (Chaves et al., 2009). Chlorophyll fluorescence parameters reflect the changes in photosynthesis of plants under different environmental conditions (Dai et al., 2009). Drought stress reduces the activity of PS II and blocks electron transfer, resulting in the decline of the photosynthetic rate (Zhang et al., 2019). In the current study, ETR and qP of the three plant species were significantly lower with the drought treatment than with the control, which was consistent with the results of previous studies (Iqbal et al., 2019). However, ETR and qP of *H. tiliaceus* and *T. neotaliala* did not change significantly in response to addition of Cd alone, probably because the concentration of Cd added was not very high for these coastal tree species.

Conclusion

The responses to drought and Cd treatments were mainly similar among *B. racemosa*, *H. tiliaceus*, and *T. neotaliala*. We found that a drought treatment significantly decreased A_{max} , Y(II), qP, and ETR; increased the concentrations of PRO, soluble sugars, ABA, MDA, and O_2^- ; and increased the activity of Rubisco in these three plant species. The contents of soluble sugars, MDA, and O_2^- were similar among the three species in response to drought and Cd addition, except that qP, A_{max} , and ETR of *B. racemosa* and A_{max} of *H. tiliaceus* decreased significantly. In addition, the concentrations of PRO, soluble sugars, ABA, and MDA were significantly lower with the combined treatment of drought and Cd addition than with the drought alone treatment. These

results show that Cd addition can inactivate the response of plants to the osmotic stress caused by drought mainly by increasing ABA accumulation. Finally, the findings increase our understanding of how plants respond to pollutants in the coastal areas of South China under the extreme drought conditions caused by global change and may provide guidance for the selection of species for vegetation restoration in coastal sandy land.

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Data availability All data generated and analyzed during this study are included in this article.

Declarations

Ethics approval Not applicable.

Consent of participate Not applicable.

Consent for publication All the authors agree for the publication.

Conflict of interest The authors declare no competing interests.

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