Journal of Environmental Management 360 (2024) 121126

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article

Species selection as a key factor in the afforestation of coastal salt-affected lands: Insights from pot and field experiments

Tzu-Hao Su [a], Yang Shen [b], Yao-Yu Chiang [a], Yu-Ting Liu [b], Han-Ming You [a], Hung-Chih Lin [a], Kuan-Ning Kung [c], Yao-Moan Huang [d], Chih-Ming Lai [a,*]

[a] Silviculture Division, Taiwan Forestry Research Institute, Taipei City, 100060, Taiwan
[b] Department of Forestry, National Chung Hsing University, Taichung City, 402202, Taiwan
[c] Chiayi Research Center, Taiwan Forestry Research Institute, Chiayi City, 600054, Taiwan
[d] Forest Ecology Division, Taiwan Forestry Research Institute, Taipei City, 100060, Taiwan

ARTICLE INFO

Keywords:
Saline-sodic soils
Woody plants
Cross-species salt tolerance indicators
Physiological and biochemical responses
MDA
Field growth performance

ABSTRACT

Soil salinization is a significant global issue that leads to land degradation and loss of ecological function. In coastal areas, salinization hampers vegetation growth, and forestation efforts can accelerate the recovery of ecological functions and enhance resilience to extreme climates. However, the salinity tolerance of tree species varies due to complex biological factors, and results between lab/greenhouse and field studies are often inconsistent. Moreover, in salinized areas affected by extreme climatic and human impacts, afforestation with indigenous species may face adaptability challenges. Therefore, it is crucial to select appropriate cross-species salinity tolerance indicators that have been validated in the field to enhance the success of afforestation and reforestation efforts. This study focuses on five native coastal tree species in Taiwan, conducting afforestation experiments on salt-affected soils mixed with construction and demolition waste. It integrates short-term controlled experiments with potted seedlings and long-term field observations to establish growth performance and physiological and biochemical parameters indicative of salinity tolerance. Results showed that *Heritiera littoralis* Dryand. exhibited the highest salinity tolerance, accumulating significant leaf proline under increased salinity. Conversely, *Melia azedarach* Linn. had the lowest tolerance, evidenced by complete defoliation and reduced biomass under salt stress. Generally, the field growth performance of these species aligns with the results of short-term pot experiments. Leaf malondialdehyde content from pot experiments proved to be a reliable cross-species salinity tolerance indicator, correlating negatively with field relative height growth and survival rates. Additionally, parameters related to the photosynthetic system or water status, measured using portable devices, also moderately indicated field survival, aiding in identifying potential salt-tolerant tree species. This study underscores the pivotal role of species selection in afforestation success, demonstrating that small-scale, short-term salinity control experiments coupled with appropriate assessment tools can effectively identify species suitable for highly saline and degraded environments. This approach not only increases the success of afforestation but also conserves resources needed for field replanting and maintenance, supporting sustainable development goals.

1. Introduction

Soil salinization is a global issue, with approximately 424 million hectares of surface soil (0–30 cm) and up to 833 million hectares of subsoil (30–100 cm) affected worldwide (FAO, 2021). In coastal areas, excessive groundwater extraction can lead to subsidence, resulting in seawater backflow or intrusion, and high groundwater levels may also elevate soil salinity to the surface, with the additional influence of salt spray further limiting plant growth and consequently leading to vegetation degradation and a loss of ecological function (Du and Hesp, 2020; El Shinawi et al., 2022; Li and Zhang, 2021). Afforestation or reforestation of lands degraded by salinity is increasingly recognized as vital for ecological protection, biodiversity conservation, carbon sequestration, and climate change mitigation (Gupta et al., 2016; Shan et al., 2018; Zhang, 2020). However, a wide range of salt tolerance exists among different plant species: most crops, known as glycophytes, are sensitive

* Corresponding author.
E-mail address: ljm8829@tfri.gov.tw (C.-M. Lai).

https://doi.org/10.1016/j.jenvman.2024.121126
Received 21 February 2024; Received in revised form 3 May 2024; Accepted 8 May 2024
Available online 17 May 2024

to salinity; in contrast, halophytes, which include species such as mangroves, are naturally adapted woody plants capable of thriving in saline environments. These halophytes possess significant potential for research into their robust salt tolerance mechanisms and for sustainable applications in agriculture and forestry (Llanes et al., 2021). Choosing species with high salt tolerance is crucial for enhancing survival rates in degraded coastal areas, which is a critical determinant in the success of afforestation/reforestation efforts (Schachtsiek et al., 2014). Additionally, previous research has indicated that the selection of species in mangrove reforestation impacts both the quantity and quality of long-term carbon sequestration and storage in forests, thereby affecting the efficacy of carbon sinks (Wu et al., 2020).

Salt stress primarily affects plants through two pathways: firstly, by reducing soil water potential, which hinders water absorption by roots, and secondly, through ion toxicity and nutritional disorders (Osman, 2018). Such stress damages the photosynthetic system, disrupts cell membrane stability, and compromises the structure and functionality of proteins, ultimately leading to cell death (Shams and Khadivi, 2023). Plant salinity tolerance involves the regulation of multiple complex biological mechanisms. Researchers have proposed several physiological indicators that exhibit high correlations with salt tolerance, such as plasma membrane permeability (Mansour, 2013), ion accumulation (Hussain et al., 2012), osmolyte accumulation (Shahid et al., 2019), antioxidant defenses (Al Kharusi et al., 2019), and photosystem responses (Bordenave et al., 2019). To our knowledge, most experiments on plant salt tolerance have primarily involved the artificial application of sodium chloride (NaCl) in pots or laboratory/greenhouse settings and have focused on physiological studies of specific species, including analyses of genotypes with varying salt tolerances. These studies encompass research on food crops (Quan et al., 2021; Rasel et al., 2021), herbaceous plants (Cheng et al., 2020; Javed et al., 2022), and woody plants (Huang et al., 2020; Pompelli et al., 2021). However, research examining salt tolerance across multiple tree species is relatively rare. Furthermore, experimental results often vary due to differing background conditions, and outcomes from greenhouse experiments may not align with field performance (Poorter et al., 2016). It is important to note that the physiological responses to salt stress are influenced by the type of salt, species-specific traits, environmental conditions, and interactions with other abiotic stresses. This variability contributes to the lack of universally accepted indicators of salt tolerance in plants (Pirasteh-Anosheh et al., 2016; van Zelm et al., 2020). Therefore, developing indicators of cross-species salinity tolerance specifically for local plants is crucial for effectively screening tree species that exhibit enhanced field growth performance on salt-affected lands.

Taiwan is characterized by its varied climatic zones and ecological niches, contributing to its significant botanical diversity. It boasts over 4200 vascular plant species, including 588 trees and 426 shrubs, with approximately 26% endemic to the region (Hsieh, 2002). The diverse geomorphological features of Taiwan's coast, such as algal reefs, rocky shores, mudflats, dunes, coral reefs, mangroves, coastal shrublands, and forests, contribute significantly to its biological diversity (Li et al., 2021). Coastal vegetation provides essential ecosystem services, including wind prevention, sand fixation, carbon sequestration, and biodiversity enhancement, and plays a crucial role in environmental protection and disaster mitigation (Arkema et al., 2017; Feagin et al., 2015; Rudianto et al., 2016). However, anthropogenic activities have severely reduced lowland vegetation covers including mangroves, and research into their dynamics is limited, especially when compared to the more extensively studied vegetation on hillsides (Chen and Shih, 2019; Lee, 2005). A 60-year study on tropical coastal afforestation demonstrated that native tree species mixtures offer greater restoration benefits than *Eucalyptus* monoculture, particularly in terms of soil biodiversity and functionality (Wu et al., 2021). Traditionally, the selection of tree species for afforestation and reforestation in degraded coastal areas has been based on traditional practices and the unique characteristics of the coastal ecological landscape. However, with the worsening impact of human interference and extreme climate conditions, many local plants may struggle to survive. Therefore, by conducting environmental monitoring at afforestation sites and developing and applying indicators of cross-species salt tolerance, we can identify a greater number of potentially suitable native plants. This approach will enhance the success of afforestation/reforestation on salt-affected lands and lead to the development of more effective forest restoration strategies.

This study employed both pot and field experiments, focusing on five native coastal woody species in Taiwan, to examine the effects of salt stress. The objectives are: (1) To establish the growth, physiological, and biochemical responses of these species to salt stress through gradient salt experiments on potted seedlings; (2) To clarify the growth performance of these native tree species in salt-affected environments; (3) To analyze the correlation between the seedlings' field growth performance and responses to short-term salt stress in pot experiments, with the goal of identifying indicators for future screening of tree species suited for afforestation in salt-affected environments.

2. Materials and methods

2.1. Species selection and seedling materials

Five native tree species that are common in coastal areas of Taiwan, namely *Heritiera littoralis* Dryand., *Calophyllum inophyllum* L., *Pittosporum pentandrum* (Blanco) Merr., *Podocarpus costalis* Presl, and *Melia azedarach* Linn., were selected as the experimental materials. Among them, *H. littoralis*, a tropical coastal mangrove associate, is a medium-sized evergreen tree. It is characterized by coriaceous leaves with silvery scales on their undersides and possesses buttress roots. *C. inophyllum* is a slow-growing, evergreen, large tree with thick, coriaceous leaves. *P. pentandrum* is an evergreen small tree or shrub with coriaceous leaves, rich in epidermal wax on both the upper and lower sides. *P. costalis* is an evergreen small tree or shrub with coriaceous leaves, native to the coastal cliffs of Lanyu, an offshore island of Taiwan. It is extensively cultivated throughout various regions of Taiwan, primarily for its aesthetic benefits. *M. azedarach* is a deciduous large tree with papery leaves, a heliophilous species with rapid growth. These species were generally suggested for coastal afforestation/reforestation in Taiwan. We used the same batch of one to two-year-old seedlings for both pot and field experiments. The seedlings were planted in typical sandy loam soil in 1-L containers and cultivated in an open-air nursery in a coastal area, with meteorological conditions similar to the field area of this study.

2.2. Field experiments

In February 2022, a field experiment was conducted using 630 seedlings, which included 126 individuals from each of five tree species with similar appearances. The experiment was carried out in Qigu District, Tainan City, Taiwan (23°09′13″ N, 120°05′18″ E), covering an area of approximately 3 ha (Fig. 1). The study area, encircled by an interchange exit of an expressway, had soil heavily contaminated with various types of construction waste, including steel bars, cement, bricks, rubble, and plastic bags, from the expressway's construction. The study area, approximately 2 km from the sea, was characterized by high groundwater levels and considerable soil salinization. Before the initiation of afforestation, the area was predominantly covered with unevenly distributed annual herbaceous plants, and woody plants were challenging to grow. The western side of the study area, elevated due to anthropogenic earthworks and waste accumulation, contrasts with the eastern side, which is characterized by its lower terrain. This topographical disparity results in the leaching of salts from the higher ground to the lower areas, culminating in the formation of a lowland salinity pool on the eastern side. At the boundary between the planting area and the salinity pool, an artificially shaped, arcuate slope has been constructed, featuring a gradient of 15–20° and a vertical difference of

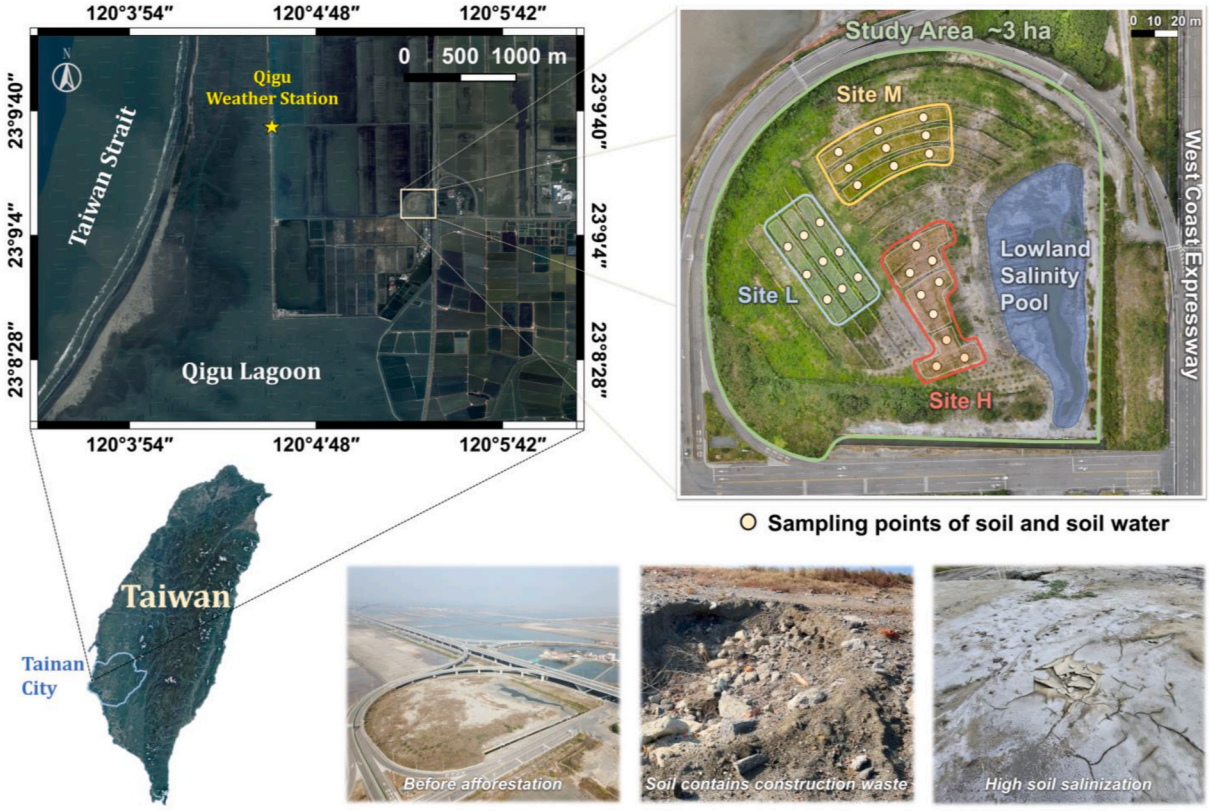

Fig. 1. Locations of the study area, soil salinity sites, and sampling points; the sites are denoted as Site L (low salinity), Site M (medium salinity), and Site H (high salinity); each site consists of three blocks, with each block comprising three soil and soil water sampling points.

about 4 m. The pool, accumulating at 0.8 m below sea level, contrasts with the planting area, where elevations range from a high of approximately 5.5 m above sea level on the west to northwest side, to a low of about 3.3 m on the southeast side. This variation in terrain contributes to distinct salinity zones within the afforestation area. In February 2022, preliminary trials assessing the soil electrical conductivity of the saturated extract (ECe) delineated the study area into three distinct planting zones based on soil salinity levels. These zones were identified with mean ECe values of 0.75 dS m^{-1} for Site L (low salinity), 4.21 dS m^{-1} for Site M (medium salinity), and 10.49 dS m^{-1} for Site H (high salinity). Also in February, due to the Northeast monsoon, the daily average wind speed in this area was recorded at 8.9 m s^{-1}, and the daily maximum reached 23.9 m s^{-1}. Consequently, bamboo windbreak fences measuring 1–2 m in height were employed to segregate the sites into multiple rows to protect the seedlings, particularly at Sites L and M, which are characterized by their elevated terrain. Each site consisted of three blocks, and each block was planted with 70 seedlings, representing the five tree species ($n = 14$). The planting was randomized with a row spacing of 3 m and a plant spacing of 2 m. Planting holes measuring approximately 50 cm in length, width, and depth were excavated and backfilled with a mixture of native soil, sandy loam, and organic fertilizer in a 4:1:1 ratio (v/v/v). The native soil was sieved through a 1 cm mesh to eliminate impurities. The organic fertilizer comprised rice bran, rice husks, and sugarcane bagasse. A sprinkler irrigation system was installed between the rows, and tap water was used for irrigation on days without rain (~3.5 mm d^{-1}). Each block at the sites had three soil and soil water sampling points for ongoing environmental monitoring ($n = 9$). Soil samples from a 0–30 cm depth were collected quarterly to assess the soil's ECe and sodium adsorption ratio (SAR). Soil water samples were extracted monthly using lysimeters (Irrometer Company, Inc. Riverside, CA, USA) positioned at a 20–30 cm depth for electrical conductivity (EC) analysis. Meteorological data was sourced from the Qigu Weather Station, located approximately 1.3 km from the study area.

2.2.1. Soil salinity determination

To evaluate soil ECe and SAR, 50 g of air-dried, 2 mm sieved soil was saturated with deionized water, followed by a 24-h shaking extraction at 140 rpm. Post-extraction, the mixture underwent centrifugation at 6000 rpm for 5 min, after which the supernatant was collected for ECe analysis using a conductivity meter (Cond 3310; WTW, Weilheim, Germany). Additionally, the supernatant was filtered through a 0.45 μm filter (GN-6, Pall Corporation, East Hills, NY, USA) for sodium (Na^+), magnesium (Mg^{2+}), and calcium (Ca^{2+}) concentration analysis using ion chromatography (DX-120, Dionex, Sunnyvale, CA, USA). The SAR is calculated based on the following formula according to Richards (1954):

$$SAR = \frac{Na^+}{\sqrt{\frac{1}{2}\left(Mg^{2+} + Ca^{2+}\right)}}$$

Where Na^+, Mg^{2+}, and Ca^{2+} are the ion concentrations in the saturated soil paste extract (meq L^{-1}). Soil salinity is classified into four categories: normal soil (ECe <4 dS m^{-1}; SAR <13), saline soil (ECe >4 dS m^{-1}; SAR <13), sodic soil (ECe <4 dS m^{-1}; SAR >13), and saline-sodic soil (ECe >4 dS m^{-1}; SAR >13) (Weil and Brady, 2016). Soil water is similarly tested for EC using a conductivity meter to assess the salinity conditions of the in-situ soil solution.

2.2.2. Growth responses and survival rates

From May 2022 to August 2023, the seedling height, root collar diameter (RCD), and survival rate across different sites and tree species were monitored quarterly, including assessments at 90, 180, 270, 360, 450, and 540 days after transplanting (DAT). The relative growth rate (RGR) of seedling height and RCD was calculated using the following equation (Hunt, 1982):

$$RGR = \frac{\ln S_2 - \ln S_1}{t_2 - t_1}$$

where S_2 is the measurement of seedling height or RCD at t_2 DAT, and S_1 is the measurement at the preceding t_1 DAT. The RGR for height is expressed in cm cm^{-1} day^{-1}, and for RCD in mm mm^{-1} day^{-1}. The sample size for each DAT varied with the number of surviving seedlings. Survival rates of different species for each site were calculated as the average of the survival rates from its three blocks.

2.3. Pot experiments

In June 2022, seedlings of each tree species underwent a process of original media removal, root pruning, and repotting to ensure uniform underground growth. The new media consisted of a mixture of sandy loam soil and peat moss (1:1, v/v) with the ECe estimated to be 1.25 dS m^{-1}, and the seedlings were then planted in 2.5-L polypropylene pots. After three months of acclimatization, a salinity gradient experiment was initiated. For each of the five tree species, 20 visually similar seedlings were selected and randomly assigned to four groups: control (CK), low salinity (L), medium salinity (M), and high salinity (H), with five seedlings from each species in each treatment group ($n = 5$). The experiment followed a completely randomized design and was conducted in a net house environment free from pest interference and with approximately 40% shading. The seedlings were irrigated with tap water with an EC of approximately 0.35 dS m^{-1}. Saucers were placed underneath the pots to prevent salt leaching, maintaining the media's moisture content between 25% and 30%. In September 2022, the salinity treatment commenced, with 500 mL of 2%, 3%, and 4% NaCl solutions being introduced into the pots of the L, M, and H groups, respectively. This 15-week experiment involved the application of saline water during the 1st, 5th, 9th, 12th, and 14th weeks, simulating the gradual increase in salinity typically encountered in the field environment. The average temperature during the experiment was 27.1 °C. Upon conclusion of the trial, the average ECe of media in the CK, L, M, and H groups was measured at 1.03, 13.08, 20.42, and 40.06 dS m^{-1}, respectively.

2.3.1. Growth and portable device measurement of physiological responses

In the final week of the experiment (15th week), portable instrument assessments of the photosynthetic system and water physiology were performed. The third fully expanded leaf from each plant was selected for these measurements, with random sampling conducted across different tree species and salinity treatments. Net photosynthetic rate (Pn) was measured on sunny days from 9 a.m. to 12 p.m. using the LI-6400 portable photosynthetic system (LI-COR Inc., Lincoln, Nebraska, USA). The maximum photochemical efficiency of photosystem II (Fv/Fm) was assessed at 9 p.m. using the MINI-PAM photosynthesis yield analyzer (Walz Company, Effeltrich, Germany). Midday leaf water potential (WP) was determined between 10 a.m. and 1 p.m. using the PSYPRO water potential system (Wescor Inc., Logan, Utah, USA). To conduct this measurement, a 6 mm diameter leaf disc was excised and placed in a C-52 sample chamber, and after a stabilization period of 15 min, the water potential reading was recorded. At the end of the experiment, seedling height and RCD were measured. After harvesting, the root media was carefully removed, and root length was measured. A portion of fresh mature leaves was weighed and stored at −80 °C for further physiological and biochemical analysis. Subsequently, the plants were segmented into roots, stems, and leaves and dried at 70 °C to a constant weight, after which the dry weights of the roots, stems, leaves, and the total plant biomass were recorded.

2.3.2. Leaf biochemical and physiological responses

Biochemical and physiological parameters in leaf tissue, including electrolyte leakage (EL), relative water content (RWC), hydrogen peroxide (H_2O_2), malondialdehyde (MDA), proline, carotenoids (Cars), and chlorophyll *a* and *b* (Chl *a* and Chl *b*) content, were analyzed. EL was measured using a conductivity meter (Cond 3310; WTW, Weilheim, Germany). Specifically, this involved placing 0.2 g of fresh leaf discs (non-frozen) in tubes with 10 mL deionized water, followed by a 24-h room temperature incubation with shaking. The conductivity (EC1) of the solution was then measured. The same samples were subsequently heated at 100 °C for 30 min, cooled to room temperature, and the conductivity (EC2) was measured again. Leaf EL (%) was calculated as EC1/EC2 (Mihailova et al., 2018). RWC was determined using 20 fresh leaf discs by measuring the fresh weight (FW), soaking them in 10 mL of deionized water at 4 °C in the dark for 4 h, measuring the turgid weight (TW) after removing the discs from water, and finally drying the samples at 70 °C to a constant dry weight (DW). RWC (%) was calculated as (FW−DW)/(TW−DW) (Bastam et al., 2012). H_2O_2 (Alexieva et al., 2001), MDA (Esterbauer and Cheeseman, 1990), proline (Bates et al., 1973), and Cars, Chl *a*, and Chl *b* (Lichtenthaler, 1987) were all quantified using fresh leaf with spectrophotometric methods (V730 spectrophotometer, Jasco Co., Tokyo, Japan), as described by previous research.

2.3.3. Nutrient and antioxidant responses

The soluble sugars in the leaf and root were determined using the phenol-sulphuric acid method (DuBois et al., 1956). A 0.1 g sample of dried, ground plant material was extracted with 80% ethanol in a 75 °C water bath. The supernatant from two extractions was then treated with phenol and sulphuric acid, and the absorbance was measured at 485 nm. Starch content in the leaf and root was determined using the anthrone method (Hansen and Møller, 1975). The residue remaining after soluble sugar extraction was extracted with 35% perchloric acid, followed by the addition of anthrone reagent and a reaction at 100 °C for 11 min. The absorbance was then measured at 630 nm. Total soluble protein and free amino acids (FAA) in the leaves were extracted from 0.1 g of fresh leaf tissue ground in liquid nitrogen and mixed with 4 mL of phosphate buffer (pH 7.0). The mixture was centrifuged at 4 °C for 20 min at 12,000 g to obtain the supernatant. Protein concentration was measured using the Bradford protein assay (Bradford, 1976) at a wavelength of 595 nm. FAA content was determined using the ninhydrin method (Moore and Stein, 1954), with absorbance measured at 570 nm. The antioxidant enzymes, including superoxide dismutase (SOD; EC 1.15.1.1), peroxidase (POD; EC 1.11.1.7), and catalase (CAT; EC 1.11.1.6), were extracted from the leaves. This was done by taking 0.1 g of fresh leaf tissue, grinding it in liquid nitrogen, and then mixing it with 5 mL of phosphate buffer (pH 7.8; 1% Triton X-100; 1 mM EDTA-Na_2; 0.8% polyvinylpyrrolidone). The mixture was then centrifuged at 4 °C for 20 min at 12,000 g to obtain the supernatant. The assays for SOD (Giannopolitis and Ries, 1977), POD (Chance and Maehly, 1955), and CAT (Aebi, 1984) were conducted in accordance with the spectrophotometric methods previously described. Absorbance was measured at wavelengths of 560 nm for SOD, 470 nm for POD, and 240 nm for CAT. The specific activities of these enzymes were expressed in units per milligram of protein (U mg^{-1} protein). One unit of SOD activity is defined as the amount of enzyme required to inhibit the rate of nitro blue tetrazolium reduction by 50%. POD activity was quantified based on the amount of tetraguaiacol formed, using its extinction coefficient (26.6 mM^{-1} cm^{-1}); one unit of POD activity is defined as the amount of enzyme that forms 1 nmol of tetraguaiacol per minute. CAT activity was determined by the consumption of H_2O_2, using its extinction coefficient (43.6 M^{-1} cm^{-1}); one unit of CAT activity is defined as the amount of enzyme that consumes 1 μmol of H_2O_2 per minute.

2.4. Statistical analysis

In the pot experiment, the leaf results were adjusted from FW to DW using the data from RWC to avoid hydration influence. Growth, physiological, and biochemical responses were analyzed using one-way analysis of variance (ANOVA) to test for differences among tree species under different salinity treatments, with post-hoc testing performed using the Tukey method ($\alpha = 0.05$). In the field experiment, the RGR was evaluated for differences among salinity sites using one-way ANOVA,

and across DATs using repeated measures ANOVA, with post-hoc testing employing the Tukey and Šidák method, respectively ($\alpha = 0.05$). Additionally, differences in seedling height and RCD at the initial (90 DAT) and final (540 DAT) stages were assessed using paired t-test ($\alpha = 0.05$). We performed Spearman correlation analysis (represented as ρ) using data from salinity treatments CK, L, and H in our pot experiments, corresponding to observations at field Sites L, M, and H for the same species. Parameters from pot experiments were selected for analysis only if they exhibited significant differences in salinity treatments across more than one species. Notably, *M. azedarach* was not included in the correlation analysis due to the absence of tested parameters for its leaves (defoliation). Further, we analyzed the results of field measurements, including seedling height, RCD, and survival rate, all recorded 540 DAT. All correlation analysis data were standardized separately for each tree species using the z-score method, eliminating unit discrepancies and reducing the influence of species-specific characteristics. Statistical analyses and graphing were performed using R (v. 4.3.2; R Development Core Team, 2023) and Sigmaplot 14.0 (Systat Software Inc., San Jose, CA, USA).

3. Results

3.1. Environmental conditions of the study area

In the study area, the total annual rainfall for 2022 was only 950 mm, characterized by an uneven distribution primarily concentrated in the summer months, driven by the southwest monsoon and typhoons. The year 2022 also marked a significant drought in Taiwan, exacerbated by the absence of typhoons in the region. Data from the Qigu Weather Station indicated that the annual precipitation for that year was the lowest since the station's establishment in 2015, amounting to merely 52% of the historical average. Notably, significant rainfall occurred only from May through August. From September 2022 through April 2023, an extended dry season persisted for eight months, with monthly rainfall below 15 mm. Significant rainfall resumed in June 2023, with July and August each recording monthly totals of 300 mm. Temperature extremes during the study period peaked in July and were lowest in January. The average monthly temperature in July 2022 was 29.5 °C, with a daily maximum of 32.7 °C; in January 2023, the average monthly temperature was 17.0 °C, with a daily minimum of 8.8 °C (Fig. 2).

Soil measurements in May 2022 (90 DAT) at Sites L, M, and H revealed average ECe values of 0.8, 5.2, and 12.3 dS m^{-1}, respectively, and SAR values of 1.6, 8.0, and 16.4, respectively. Site M met the saline soil standard (ECe >4 dS m^{-1}; SAR <13), while Site H met the saline-sodic soil standard (ECe >4 dS m^{-1}; SAR >13). Initially, soil properties differed significantly between Sites L and M, but post-rainy season leaching in 2022 significantly reduced these differences. During the study period, soil ECe and SAR showed two declining trends in August and February, associated with rainfall leaching and reduced evaporation due to cooler temperatures, respectively. However, a prolonged dry season and rising temperatures in May 2023 led to the highest soil ECe and SAR values at Site H, averaging 17.8 dS m^{-1} and 24.1, respectively. Additionally, monthly variations in soil water conductivity mirrored those in the soil, with differences between Sites L and M diminishing during the rainy season and increasing in the dry season. In contrast, the soil water at Site H exhibited dramatic fluctuations, peaking at 63.0 dS m^{-1} in May 2023 (Fig. 2).

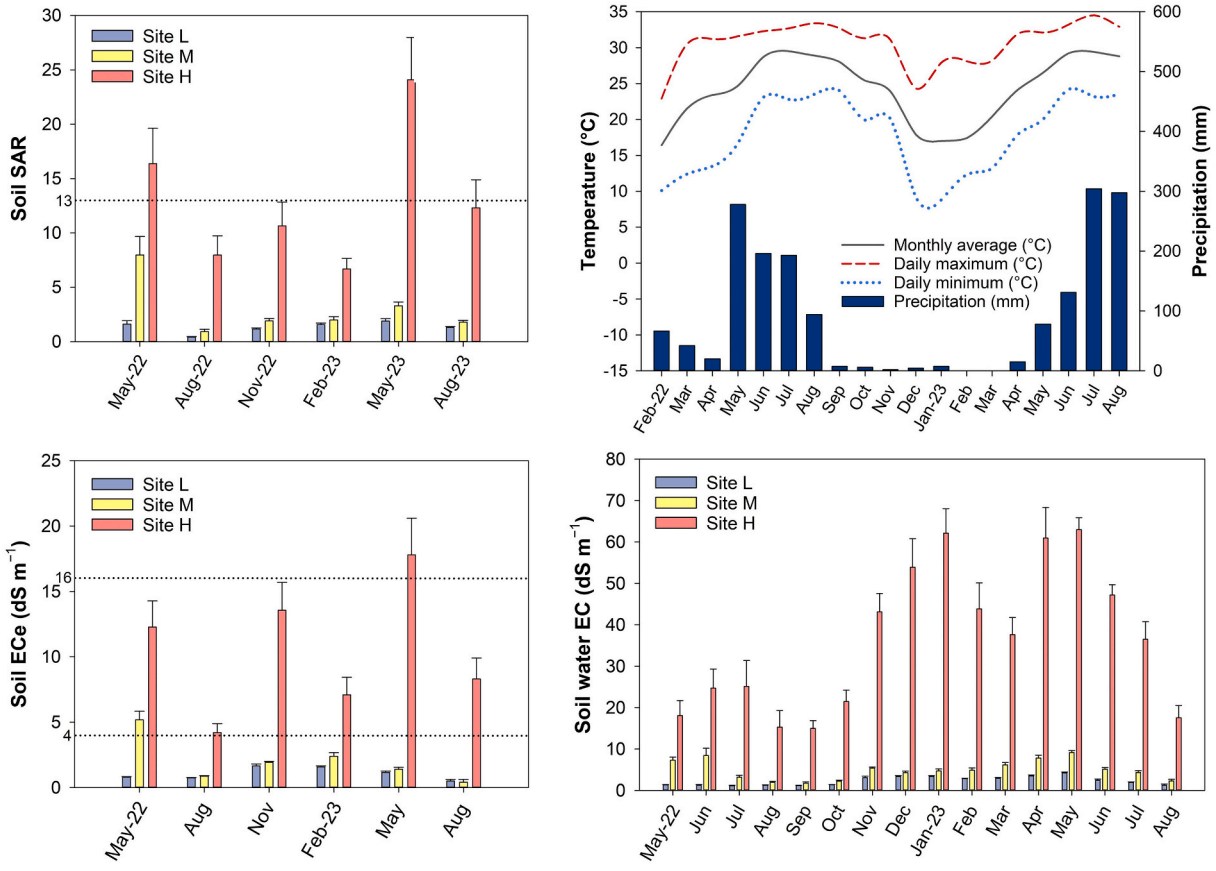

Fig. 2. Meteorological data for the study area and soil conditions at different salinity sites (low salinity [Site L], medium salinity [Site M], and high salinity [Site H]); temperature and precipitation data were obtained from Qigu Weather Station located 1.3 km away; soil and soil water samples were collected at depths of 0–30 and 20–30 cm, respectively ($n = 9$). Abbreviations: *ECe*, electrical conductivity (EC) of saturated paste extract; *SAR*, sodium absorption ratio.

3.2. Growth and survival rates in field experiments

Field RGR results of this study revealed that seedling height and RCD trends exhibited a distribution with higher values at the beginning and end, aligning with the rainy season (May–August); however, results varied among the tree species. In particular, the *H. littoralis* and *C. inophyllum* demonstrated relatively higher RGR, with tree height at Site H exhibiting lower results in the early phase of the experiment (180 DAT) (Fig. 3a and b). In terms of RCD, no significant difference was observed between Sites L and H at 180 DAT, but at the end of the experiment (540 DAT), RCD at Site H was significantly higher than the other two sites (Fig. 3f and g). The shrub types *P. pentandrum* and *P. costalis* exhibited slow growth in height across all sites (Fig. 3c and d), with RCD at Site H initially suppressed by salinity but significantly increased during the second growing season (450 & 540 DAT) (Fig. 3h and i). Moreover, the fast-growing species *M. azedarach* had the highest RGR measurements; however, both seedling height and RCD were noticeably constrained by salinity (Fig. 3e–j).

Regarding absolute growth records, at 540 DAT, both *H. littoralis* and *C. inophyllum* showed no significant differences in seedling height or RCD across the three sites (Fig. 3k and l). Additionally, the seedling height and RCD of *P. pentandrum* and *P. costalis* were significantly lower at Site H. Notably, the height of *P. costalis* exhibited no significant difference from planting initiation (90 DAT) at Sites M and H, indicating stagnation in seedling elongation (Fig. 3m and n). *M. azedarach* exhibited a gradient decrease in growth with increasing salinity across sites, reflecting its relative sensitivity to salinity, with significant reductions in seedling height and RCD at Site H compared to Site L, reaching up to 52% (Fig. 3o).

Survival rate results for the transplanted seedlings of each species showed that *H. littoralis* had the highest survival rate, followed by *P. pentandrum* and *C. inophyllum*, maintaining over 90% at Sites L and M. At Site H, the rates for the three species as mentioned above were 88%, 76%, and 66%, respectively. In the case of *P. costalis*, survival rates gradually decreased over time, maintaining 79% at Site L but dropping to 48% at Site H. From as early as 90 DAT, *M. azedarach* displayed noticeable survival rate gradients across sites, with minimal variation over time. By 540 DAT, the survival rates at Sites L, M, and H were 57%, 43%, and 17%, respectively (Fig. 4).

3.3. Growth, biochemical, and physiological responses in pot experiments

The growth results of potted seedlings indicated that, aside from *M. azedarach,* which experienced a significant height reduction under high salinity, no notable differences occurred in height, RCD, and root length for all tree species across various salinity treatments. Regarding biomass, a significant decline in root or leaf biomass was observed in most species under high salinity, especially in *M. azedarach*, which exhibited a pronounced reduction in all plant parts and complete leaf loss in all salinity treatments (resulting in the exclusion of leaf-related physiological and biochemical parameter assessments). In contrast, *H. littoralis* maintained a stable biomass across different treatments, with its stem biomass increasing significantly under high salinity. Additionally, neither *H. littoralis* nor *C. inophyllum* exhibited significant changes in the total biomass in response to salinity treatments. In physiological measurements conducted using portable devices, a significant decrease in Pn and Fv/Fm was observed in all species under salt stress, except for *H. littoralis*, which sustained a level of net photosynthesis and showed no significant impact on photosystem II (PSII). Regarding WP, no significant differences were observed for *H. littoralis* and *C. inophyllum* across the treatments; in contrast, the other species exhibited their lowest WP under medium or high salinity conditions (Table 1).

For leaf physiological and biochemical responses, EL indicated no significant differences among salinity treatments for *H. littoralis*, in contrast to other species, which demonstrated significant increases under medium and high salinity. Compared to the control group, RWC was notably reduced in *H. littoralis* and *P. pentandrum* when exposed to high salinity. Within each species, H_2O_2 content exhibited no significant changes across salinity treatments, while both MDA and proline levels increased with increasing salinity. Specifically, *H. littoralis* exhibited a minor increase in MDA under elevated salinity, whereas its proline levels escalated by 10–30 times. Regarding photosynthetic pigments, most species maintained consistent levels under salt stress, except for *P. costalis*, which displayed significant reductions in Cars, Chl *a*, Chl *b*, and total chlorophyll (Table 2).

In nutritional and antioxidant response analysis, leaf FAA, proteins, and soluble sugars did not vary significantly across different salinity levels within each species. However, an exception was observed in *P. costalis*, where FAA significantly increased in the high-salinity group compared to the control. In salt-tolerant species such as *H. littoralis* and *C. inophyllum*, leaf starch content decreased significantly under high salinity. In roots, *H. littoralis* exhibited distinct responses to varying salinity levels, with a decrease in soluble sugar content and an increase in starch content as salinity increased. Further, diverse trends were observed in other species: *C. inophyllum* and *M. azedarach* remained unchanged, while *P. pentandrum* and *P. costalis* showed increased soluble sugars and decreased starch in the medium-salinity group, respectively. Regarding the activity of antioxidant enzymes,levels of SOD and CAT in leaves remained stable across species under different salinity treatments. POD levels, however, increased significantly in salt-tolerant species such as *H. littoralis* and *C. inophyllum* under high salinity, and decreased significantly in the salt-sensitive *P. costalis* when exposed to salt stress (Table 3).

3.4. Relationships between parameters from pot and field experiments

The correlation analysis revealed a significant strong negative correlation between seedling height from the field experiment and proline and MDA from the pot experiment ($\rho = -0.64$ and -0.62, respectively; $p < 0.001$), and a moderate positive correlation with WP and leaf DW ($\rho = 0.55$; $p < 0.001$). In contrast, field seedling RCD did not demonstrate significant correlations with most pot experiment measurements, except for a weak positive correlation with total DW ($\rho = 0.34$; $p < 0.05$). Regarding the survival rate of field seedlings, significant moderate to strong negative correlations were found with proline, MDA, and EL ($\rho = -0.63$, -0.77, and -0.54, respectively; $p < 0.001$), along with moderate positive correlations with Pn, WP, leaf DW, and Fv/Fm, where ρ values ranged from 0.51 to 0.60 ($p < 0.01/0.001$) (Fig. 5).

4. Discussion

4.1. Short-term effects of salt stress on seedlings

In the pot experiment, the *H. littoralis* exhibited the best salt tolerance, particularly in maintaining leaf and total biomass under salinity treatments, while sustaining stable leaf water potential and photosynthetic efficiency. The substantial increase in proline levels in the leaves of *H. littoralis* under salt treatments compared to other species indicates its potential for higher tolerance to salinity and drought conditions. Proline aids in osmotic regulation, protein stability, and scavenging of ROS (Hayat et al., 2012). It has also been confirmed to buffer cytoplasmic pH, balance cellular redox states, and act as a component in signaling pathways regulating stress response genes, thereby enhancing salt tolerance (Hossain et al., 2014). High proline content, known to maintain membrane stability (Reddy et al., 2015), suggests a potential role in the minimal variation of MDA levels in *H. littoralis* under salt treatments. Therefore, the observed salt tolerance of *H. littoralis* in the pot experiment may be attributed to the synthesis of large amounts of proline. Notably, root soluble sugar content is generally considered related to osmotic regulation during physiological drought and a crucial physiological indicator of plant salt tolerance (Liang et al., 2018). However, most species did not show significant changes in soluble sugar

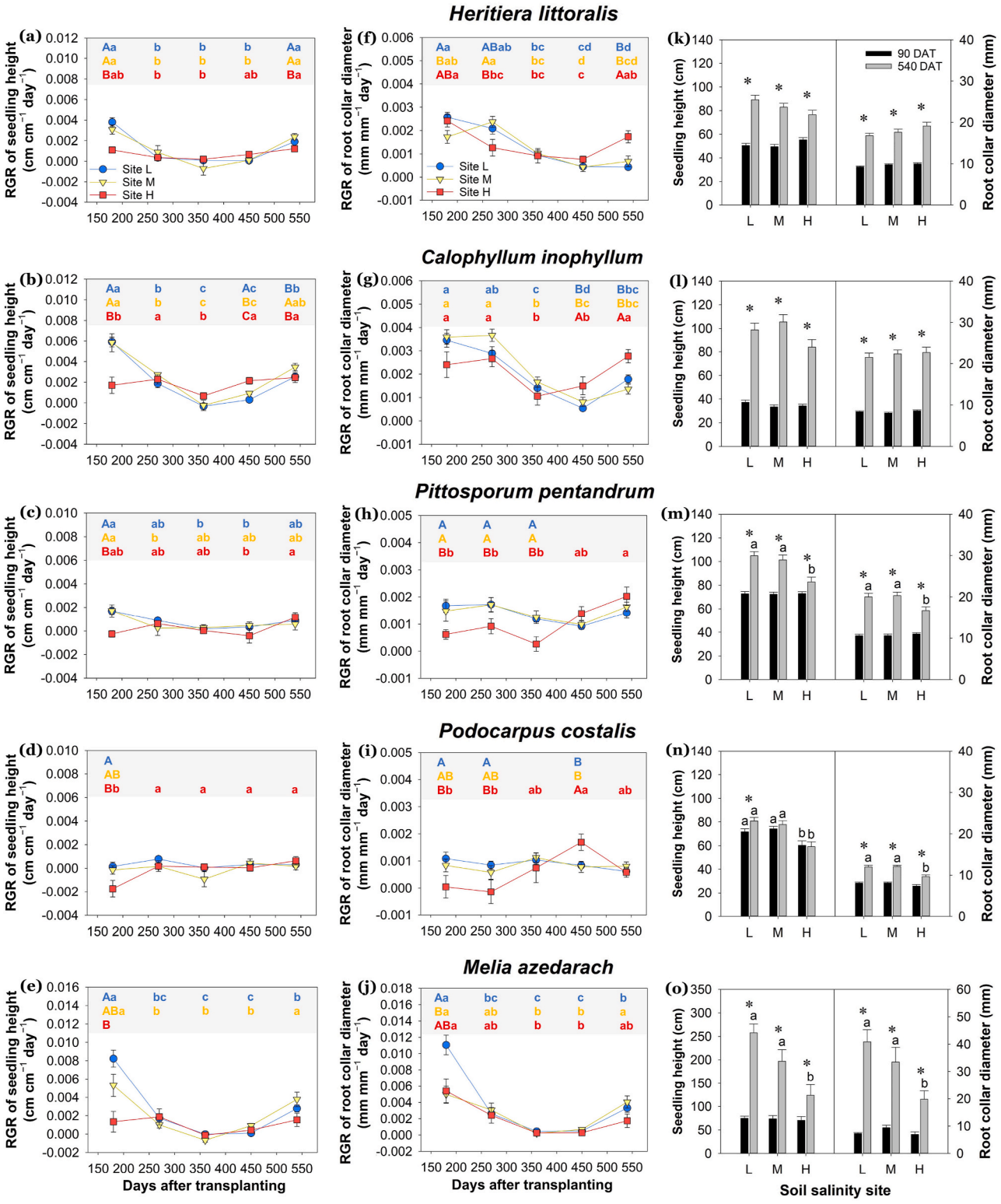

Fig. 3. Relative growth rates (RGR) of seedling height (a–e) and root collar diameter (f–j) of five tree species, and their measurements recorded at 90 and 540 days after transplanting (DAT) (k–o), in field experiments under different soil salinity sites (low salinity [Site L], medium salinity [Site M], and high salinity [Site H]); data represent the mean and standard error; in panel a–j, the capital letters indicate significant differences between different salinity sites (one-way analysis of variance [ANOVA], Tukey method, $\alpha = 0.05$), the lowercase letters indicate significant differences between different DATs (repeated measures ANOVA, Šidák method, $\alpha = 0.05$), and the colors blue, yellow, and red represent Site L, M, and H, respectively; in panel k–o, the lowercase letters indicate significant differences between different salinity sites on each transplanting date (one-way ANOVA, Tukey method, $\alpha = 0.05$), and the asterisk (*) indicates significant difference between 90 and 540 DAT in each salinity site (paired t-test, $\alpha = 0.05$); seedlings were transplanted in February 2022. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

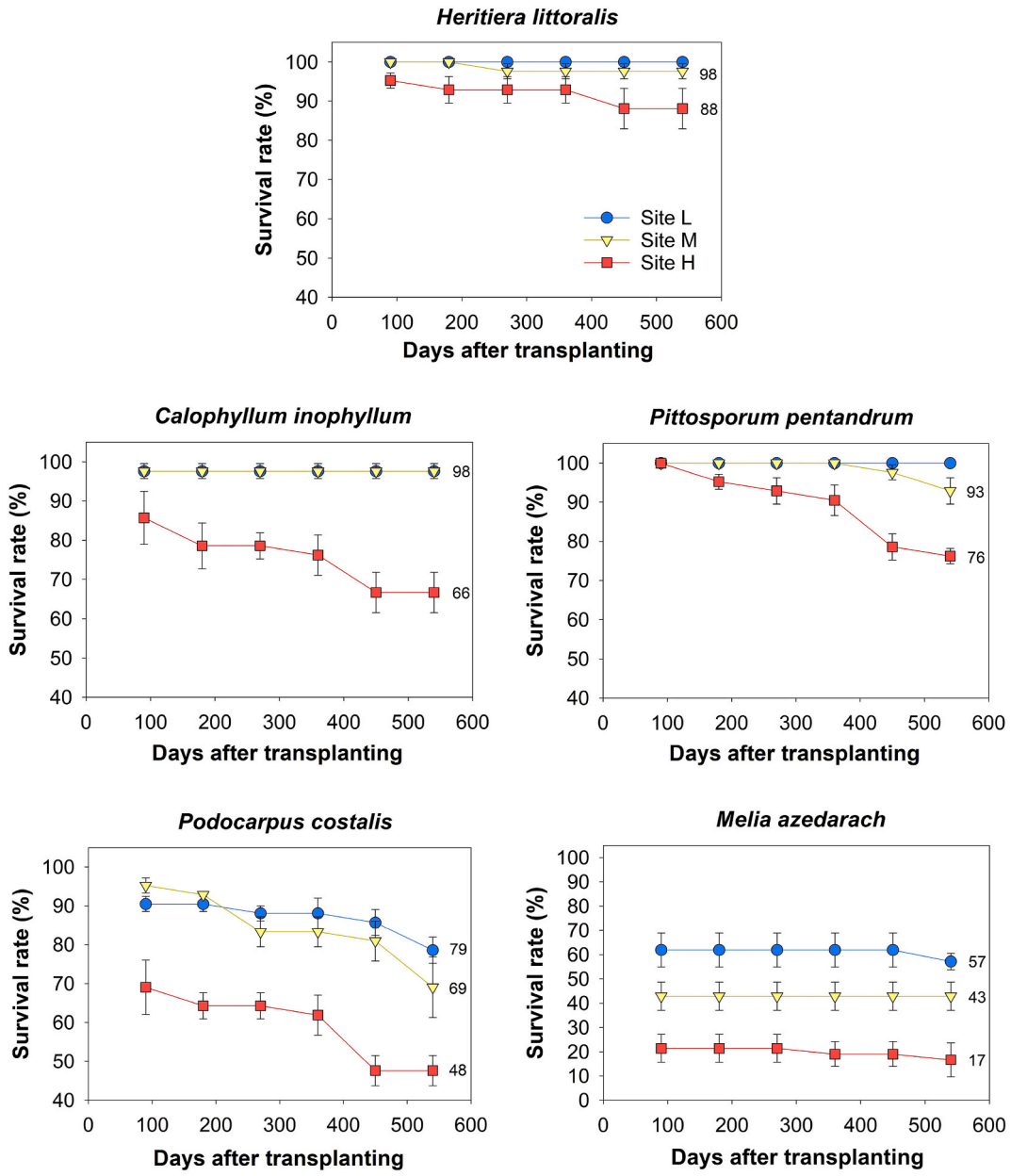

Fig. 4. Survival rates of five tree species at different days after transplanting in field experiments under different soil salinity sites (low salinity [Site L], medium salinity [Site M], and high salinity [Site H]); data represent the mean and standard error; seedlings were transplanted in February 2022.

content in our experiment. Instead, leaf starch and root soluble sugars were decreased under high salinity in the *H. littoralis*, accompanied by significant root starch accumulation. Under abiotic stress, starch is vital in enhancing plant stress adaptability (Thalmann and Santelia, 2017). The significant accumulation of root starch under salt stress was commonly observed, indicating enhanced source-to-sink assimilate allocation. Thitisaksakul et al. (2017) suggested that starch accumulation in roots could reduce sugar accumulation in source leaves to improve photosynthesis and promote root growth by enhancing gravitropic response. A study on salt-tolerant common reed indicated that higher root starch content facilitates the trapping of Na^+ in starch granules, mitigating ionic toxicity (Kanai et al., 2007). Nevertheless, research on plant salt tolerance has generally focused on herbaceous plants, particularly economic crops, with few studies on woody species. Llanes et al. (2021) pointed out that carbohydrate accumulation in woody plants can enhance salt tolerance, but results may vary with the duration of stress. In addition, proline plays multiple essential roles in responding to abiotic stress, but research on its role in woody plants warrants further exploration.

In contrast, *M. azedarach* exhibited a high sensitivity to salinity, showing complete defoliation under various salt treatments and a progressive decline in biomass across all parts as salinity increased, clearly indicating growth inhibition by salt. Salt stress visibly causes leaf chlorosis, necrosis, and bud dehydration, leading to leaf fall under prolonged exposure (Vita et al., 2022). Generally, plants experience two phases under salt stress: an initial rapid response triggered by osmotic pressure inhibiting young leaf growth, and a slower response due to Na^+ accumulation causing ionic toxicity, accelerating senescence in mature leaves (Munns and Tester, 2008). Necrosis in older leaves is also associated with plant salt sensitivity (Gil-Muñoz et al., 2020). Our results suggest that *M. azedarach* is highly sensitive to osmotic challenges posed by salinity and less tolerant to ionic toxicity. This leads to complete defoliation, making it unsuitable for long-term high-salinity environments. Previous studies have indicated that while *M. azedarach* is

Table 1
Growth and portable device measurement of physiological responses of seedlings in pot experiments under different soil salinities.

Species	Salinity	Height (cm)	RCD (mm)	Root length (cm)	Root DW (g)	Stem DW (g)	Leaf DW (g)	Total DW (g)	Pn (μmol m^{-2} s^{-1})	Fv/Fm	WP (MPa)
Heritiera littoralis	CK	53.67 ± 1.78	9.71 ± 0.34	31.97 ± 3.25	17.93 ± 1.34	13.72 ± 0.34b	6.90 ± 0.27	38.56 ± 1.68	6.19 ± 0.86a	0.71 ± 0.01	−1.35 ± 0.02
	L	48.00 ± 0.62	12.11 ± 0.24	32.43 ± 0.19	17.48 ± 0.72	14.83 ± 0.38b	7.59 ± 0.67	39.91 ± 1.71	3.71 ± 0.03ab	0.72 ± 0.01	−2.05 ± 0.13
	M	49.33 ± 6.06	12.00 ± 1.42	32.93 ± 1.20	16.51 ± 1.47	10.26 ± 0.94b	5.78 ± 0.58	32.56 ± 2.48	1.55 ± 0.29b	0.72 ± 0.01	−1.93 ± 0.19
	H	51.33 ± 1.19	11.95 ± 0.48	27.60 ± 2.77	21.67 ± 1.58	21.74 ± 1.94a	5.03 ± 0.59	48.43 ± 4.09	1.46 ± 0.19b	0.71 ± 0.02	−2.22 ± 0.17
Calophyllum inophyllum	CK	70.17 ± 0.49	16.73 ± 0.14	20.00 ± 1.39	40.92 ± 1.58	32.76 ± 1.49	33.03 ± 0.48a	106.71 ± 3.13	3.82 ± 0.77a	0.76 ± 0.01a	−1.32 ± 0.01
	L	71.33 ± 2.42	15.38 ± 0.60	19.73 ± 0.57	40.09 ± 4.11	31.32 ± 1.35	18.69 ± 1.56b	90.09 ± 6.55	0.09 ± 0.05b	0.62 ± 0.03b	−1.88 ± 0.21
	M	70.00 ± 1.70	14.52 ± 0.43	22.57 ± 2.52	34.67 ± 5.35	30.35 ± 3.16	15.42 ± 1.46b	80.44 ± 9.49	0.11 ± 0.01b	0.56 ± 0.02b	−2.09 ± 0.12
	H	69.00 ± 4.24	14.87 ± 0.19	21.97 ± 1.34	34.50 ± 4.76	31.99 ± 3.81	16.34 ± 1.75b	82.83 ± 10.16	0.01 ± 0.01b	0.52 ± 0.02b	−2.48 ± 0.38
Pittosporum pentandrum	CK	66.33 ± 1.44	16.55 ± 1.28	30.37 ± 1.51	46.59 ± 5.21a	49.20 ± 6.42	5.37 ± 0.63a	101.15 ± 12.25a	6.30 ± 0.69a	0.74 ± 0.01a	−1.63 ± 0.09a
	L	63.00 ± 0.82	15.20 ± 1.07	26.33 ± 1.91	34.59 ± 1.26ab	41.81 ± 1.95	4.10 ± 0.29ab	80.50 ± 1.74ab	1.30 ± 0.45b	0.72 ± 0.02a	−2.65 ± 0.09b
	M	65.33 ± 1.78	15.88 ± 1.60	29.17 ± 0.91	35.36 ± 1.01ab	37.70 ± 2.78	4.30 ± 0.21ab	77.36 ± 3.64ab	0.53 ± 0.22b	0.63 ± 0.04b	−3.02 ± 0.2bc
	H	60.00 ± 1.03	14.67 ± 0.59	21.33 ± 5.39	26.91 ± 0.77b	30.77 ± 1.18	2.12 ± 0.26b	59.80 ± 1.81b	0.18 ± 0.07b	0.63 ± 0.01b	−3.62 ± 0.12c
Podocarpus costalis	CK	101.67 ± 0.54	11.11 ± 0.29	22.20 ± 1.39	26.69 ± 2.26	41.98 ± 2.02	42.02 ± 4.19a	110.69 ± 7.91a	1.37 ± 0.29a	0.71 ± 0.01a	−1.32 ± 0.02a
	L	98.33 ± 1.36	11.39 ± 0.33	20.67 ± 3.31	26.21 ± 1.03	42.41 ± 0.16	28.51 ± 2.15ab	97.13 ± 2.93ab	0.20 ± 0.11b	0.73 ± 0.02a	−2.22 ± 0.13b
	M	100.00 ± 1.25	11.19 ± 0.24	18.47 ± 1.09	21.40 ± 1.51	38.28 ± 2.17	24.77 ± 1.39ab	84.45 ± 4.57b	0.10 ± 0.01b	0.48 ± 0.04b	−3.27 ± 0.18c
	H	96.00 ± 3.09	11.41 ± 0.06	22.53 ± 0.53	23.22 ± 1.48	39.20 ± 1.72	22.81 ± 4.49b	85.23 ± 4.39b	0.11 ± 0.01b	0.44 ± 0.02b	−2.41 ± 0.21b
Melia azedarach	CK	91.33 ± 1.19a	9.96 ± 0.19	29.33 ± 1.58	40.80 ± 3.80a	18.18 ± 0.83a	1.22 ± 0.12	60.20 ± 3.73a	NA	NA	NA
	L	90.87 ± 0.88a	10.38 ± 0.70	20.77 ± 1.16	32.67 ± 5.32ab	18.90 ± 1.49a	*	51.57 ± 4.25a	NA	NA	NA
	M	82.33 ± 1.52a	10.61 ± 0.30	17.93 ± 1.48	25.44 ± 1.80ab	17.95 ± 0.30a	*	43.39 ± 1.85ab	NA	NA	NA
	H	68.00 ± 3.56b	8.80 ± 0.49	16.30 ± 3.09	17.12 ± 4.01b	11.46 ± 1.46b	*	28.58 ± 5.37b	NA	NA	NA

Data represent the mean and standard error; the lowercase letters indicate significant differences between different soil salinities (control [CK], low [L], medium [M], and high [H]) in each species (one-way analysis of variance, Tukey method, $\alpha = 0.05$, $n = 5$). Abbreviations: *RCD* (root collar diameter), *DW* (dry weight), *Pn* (net photosynthetic rate), *Fv/Fm* (maximum quantum efficiency of PSII), *WP* (midday leaf water potential), *(completely defoliated), *NA* (no analysis due to defoliation).

considered one of the tall trees among halophytes, its salt tolerance is moderate. Consequently, it is not the preferred species for planting in high-salinity environments (Tomar et al., 2003; Zhang et al., 2020). Additionally, *P. costalis* was the only species in the pot experiment significantly affected by photosynthetic pigments content. Salt stress leads to a decline in pigments such as Chl *a* and Chl *b*, mainly due to weakened binding in the pigment-protein-lipid complex and increased activity of chlorophyllase, thereby impairing plant light absorption and photoreaction efficiency (Duarte et al., 2013; Lu et al., 2021). The reduction in Cars also impedes the transfer of excited-state chlorophyll energy, generating highly oxidative singlet oxygen, causing oxidative stress, and further reducing PSII photosynthetic efficiency (Telfer, 2014). Therefore, the noticeable decrease in Fv/Fm in *P. costalis* under medium to high salt treatments relative to other species indicates poor photosynthetic performance under salt stress, which could impact its long-term growth.

Furthermore, *C. inophyllum* and *P. pentandrum* exhibited moderate salt tolerance in the pot experiment. *C. inophyllum*'s thick, coriaceous leaves and substantial cuticular and/or waxy layers play a crucial protective role by effectively preventing water loss and regulating biosynthesis under abiotic stress (Shaheenuzzamn et al., 2021; Shepherd and Wynne Griffiths, 2006). Our results also noted the stability of WP and RWC under salt treatments in *C. inophyllum*. As for *P. pentandrum,* it exhibited significant accumulation of soluble sugars and proline under moderate to high salinity, indicating an advantage in osmotic adjustment. The accumulation of soluble sugars and proline within plant tissues is a vital drought resistance strategy in dominant species in subtropical forests (Kuang et al., 2017). Moreover, while salt tolerance is associated with antioxidative capacity in plants, effective antioxidative activity does not necessarily imply an upregulation of all antioxidative enzymes, and vice versa (Abogadallah, 2010). Although H_2O_2 levels across different salt treatments did not vary significantly within each tree species in our study, the more salt-tolerant *H. littoralis* and *C. inophyllum* significantly increased POD activity under high salinity. This aligns with previous research findings that in salt-stressed conditions, POD activity significantly increases in salt-tolerant plants, acting as the primary scavenger of H_2O_2. In contrast, CAT activity is mainly upregulated in salt-sensitive plants, while SOD shows less sensitivity to salinity variations (Abogadallah et al., 2010; Chakraborty et al., 2016). Similarly, a genetic analysis of poplar trees revealed that 41 genes in the POD superfamily were regulated under salt stress, while only one member of the SOD and CAT families was differentially expressed (Zheng et al., 2015). Besides ROS scavenging, the stability and strength of plant cell walls become crucial in response to osmotic pressure

Table 2
Leaf biochemical and physiological responses of seedlings in pot experiments under different soil salinities.

Species	Salinity	EL (%)	RWC (%)	H_2O_2 (μmol g^{-1})	MDA (nmol g^{-1})	Proline (μg g^{-1} DW)	Cars (mg g^{-1} DW)	Chl *a* (mg g^{-1} DW)	Chl *b* (mg g^{-1} DW)	Chl *a*+*b* (mg g^{-1} DW)	Chl *a*/*b*
Heritiera littoralis	CK	23.42 ± 2.52	82.01 ± 0.24a	1.46 ± 0.08	655.26 ± 35.28b	42.00 ± 11.36b	0.36 ± 0.01	0.96 ± 0.08	0.36 ± 0.09	1.32 ± 0.17	3.04 ± 0.44
	L	23.91 ± 1.48	81.36 ± 0.85a	1.84 ± 0.22	748.12 ± 15.16ab	412.82 ± 83.81b	0.38 ± 0.02	1.08 ± 0.10	0.36 ± 0.06	1.43 ± 0.16	3.18 ± 0.29
	M	24.08 ± 3.95	74.99 ± 2.33ab	1.54 ± 0.14	726.91 ± 19.65ab	1254.64 ± 174.74a	0.41 ± 0.04	1.19 ± 0.13	0.36 ± 0.04	1.55 ± 0.17	3.38 ± 0.10
	H	22.84 ± 2.98	65.82 ± 4.46b	1.92 ± 0.08	806.66 ± 17.75a	1389.89 ± 183.46a	0.40 ± 0.02	1.08 ± 0.15	0.35 ± 0.10	1.43 ± 0.24	3.48 ± 0.42
Calophyllum inophyllum	CK	28.33 ± 1.07b	76.16 ± 0.52	2.61 ± 0.29	640.64 ± 6.98b	18.61 ± 2.03b	0.37 ± 0.02	1.00 ± 0.06	0.29 ± 0.03	1.29 ± 0.09	3.48 ± 0.16
	L	30.58 ± 3.66b	73.02 ± 0.71	3.34 ± 0.34	888.32 ± 5.07ab	31.94 ± 7.28ab	0.40 ± 0.01	0.89 ± 0.05	0.24 ± 0.01	1.12 ± 0.06	3.78 ± 0.16
	M	38.41 ± 8.42ab	73.27 ± 2.00	2.90 ± 0.07	1068.92 ± 19.33ab	36.94 ± 1.25ab	0.44 ± 0.02	1.11 ± 0.07	0.30 ± 0.03	1.41 ± 0.10	3.67 ± 0.13
	H	59.95 ± 6.89a	70.77 ± 2.57	3.18 ± 0.05	1272.54 ± 24.64a	41.80 ± 0.56a	0.38 ± 0.02	0.92 ± 0.06	0.30 ± 0.02	1.21 ± 0.07	3.11 ± 0.11
Pittosporum pentandrum	CK	14.67 ± 0.91b	91.23 ± 0.38a	29.29 ± 1.57	66.81 ± 0.02c	19.37 ± 6.93b	0.42 ± 0.01	0.93 ± 0.05	0.20 ± 0.02	1.13 ± 0.07	4.79 ± 0.25
	L	13.79 ± 0.09b	89.65 ± 0.22ab	35.89 ± 1.61	126.01 ± 1.34b	28.96 ± 3.94b	0.47 ± 0.04	1.05 ± 0.14	0.27 ± 0.07	1.32 ± 0.21	4.41 ± 0.69
	M	13.99 ± 0.58b	86.91 ± 1.98ab	34.27 ± 1.26	153.26 ± 5.93ab	16.21 ± 3.31b	0.47 ± 0.04	0.92 ± 0.06	0.18 ± 0.01	1.09 ± 0.06	5.23 ± 0.31
	H	21.77 ± 1.27a	77.69 ± 0.74b	32.17 ± 0.24	182.44 ± 8.65a	128.12 ± 20.23a	0.52 ± 0.03	1.00 ± 0.03	0.19 ± 0.01	1.19 ± 0.03	5.26 ± 0.28
Podocarpus costalis	CK	24.57 ± 2.50b	74.42 ± 3.04	2.43 ± 0.10	703.40 ± 5.51c	17.65 ± 0.45b	0.31 ± 0.01a	0.90 ± 0.01a	0.29 ± 0.01a	1.19 ± 0.02a	3.17 ± 0.01
	L	39.80 ± 4.81ab	74.83 ± 0.66	3.40 ± 0.17	664.84 ± 14.47c	24.03 ± 0.32b	0.25 ± 0.01b	0.65 ± 0.06b	0.19 ± 0.02b	0.84 ± 0.09b	3.35 ± 0.09
	M	48.83 ± 0.83a	68.03 ± 6.31	3.95 ± 0.74	901.15 ± 7.09b	42.35 ± 2.52a	0.25 ± 0.02b	0.58 ± 0.05b	0.16 ± 0.01b	0.73 ± 0.07b	3.71 ± 0.31
	H	39.53 ± 5.81ab	77.68 ± 0.93	3.54 ± 0.31	1089.67 ± 5.64a	41.87 ± 5.48a	0.26 ± 0.01b	0.62 ± 0.01b	0.16 ± 0.01b	0.79 ± 0.02b	3.82 ± 0.20
Melia azedarach	CK	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	L	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	M	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	H	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Data represent the mean and standard error; the lowercase letters indicate significant differences between different soil salinities (control [CK], low [L], medium [M], and high [H]) in each species (one-way analysis of variance, Tukey method, $\alpha = 0.05$, $n = 5$). Abbreviations: *EL* (electrolyte leakage), *RWC* (relative water content), *MDA* (malondialdehyde), *DW* (dry weight), *Cars* (carotenoids), *Chl* (chlorophyll), *NA* (no analysis due to defoliation).

induced by salinity. Class III PODs participate in cell wall synthesis and repair through lignin polymerization, forming irreversible covalent bonds with phenolic compounds or glycoproteins, thus enhancing the mechanical structure of the cell wall (Francoz et al., 2015; Tenhaken, 2014). In our study, only POD activity among the antioxidative enzymes of various tree species was significantly affected by salt treatment, suggesting that POD activity in woody plants might be more critical for salt tolerance.

4.2. Growth performance of different species in afforestation

In the Qigu area of Taiwan, remnants of early salt-making industries have left abandoned salt fields, which now coexist with the largest seawater fish farms in Taiwan, covering over 4750 ha. The soil at the experimental site, characterized by high salinity and alkalinity, also contains construction and demolition waste (CDW) from coastal expressway developments. Substantial CDW in the soil leads to groundwater and soil pollution, adversely affecting soil biology (Balali et al., 2023; Hou et al., 2018). The fines in CDW also elevate soil pH and EC, exacerbating saline conditions and inhibiting the growth of salt-sensitive plant species (Yun et al., 2019). Our experimental area experiences a concentrated rainy season of only approximately four months, with temperatures exceeding 30 °C at the end of this period. This leads to strong soil evaporation, causing capillary action that brings salts to the surface and results in highly saline and alkaline topsoil (Zhang et al., 2022). Under extreme weather conditions and prolonged drought, maintaining a low level of water supply for seedlings becomes unavoidable. However, leaching the salts under limited irrigation conditions is challenging, leading to high dissolved salt content in the soil water. In the high salinity site of our study, the soil water EC was higher than the regional seawater average (~50 dS m^{-1}) (Tyler et al., 2017). The high salinity of the soil water exacerbates physiological drought and ionic toxicity, harming plant growth and development (Tavakkoli et al., 2010). Due to intense human interference and uneven salt distribution in the study area, the soil in the high-salinity site met the highest standards of salinity and alkalinity. For up to nine months, the soil water EC exceeded 35 dS m^{-1}, significantly affecting the growth of potential native coastal tree species. The reclamation of salt-affected lands is challenging due to high costs and freshwater scarcity in coastal areas. Additionally, the effectiveness of natural leaching is limited by rainfall distribution and the impact of drainage properties on groundwater levels, which factors often lead to poor outcomes in managing salt-affected lands (Li et al., 2018; Li and Zhang, 2021). Enhancing afforestation success is possible by pre-selecting tree species with high salinity tolerance. This approach reduces the need for replanting and conserving reclamation resources, accelerating ecological recovery in salt-affected areas. Moreover, afforestation timing is crucial in this region; planting at the beginning of the rainy season not only fulfills the water requirements but also mitigates soil salinity, reducing the adverse effects on the initial growth of plants.

The RGR results indicate that most tree species experience more pronounced inhibition in height growth due to salinity than radial

Table 3
Nutrient and antioxidant responses of seedlings in pot experiments under different soil salinities.

Species	Salinity	Leaf FAA (mg g^{-1} DW)	Leaf protein (mg g^{-1} DW)	Leaf soluble sugar (mg g^{-1} DW)	Leaf starch (mg g^{-1} DW)	Root soluble sugar (mg g^{-1} DW)	Root starch (mg g^{-1} DW)	SOD (U mg^{-1} protein)	POD (U mg^{-1} protein)	CAT (U mg^{-1} protein)
Heritiera littoralis	CK	7.74 ± 0.64	22.75 ± 2.08	97.83 ± 2.48	182.40 ± 8.61a	162.35 ± 7.73a	230.84 ± 13.06b	55.06 ± 6.60	967.71 ± 40.41b	31.41 ± 3.47
	L	6.95 ± 0.16	21.67 ± 0.52	77.22 ± 8.30	170.48 ± 3.31 ab	151.26 ± 16.70a	200.80 ± 7.12b	56.58 ± 2.07	1077.79 ± 2.88ab	24.60 ± 5.24
	M	6.98 ± 0.62	19.41 ± 1.67	76.11 ± 3.54	155.22 ± 10.12ab	144.61 ± 2.39ab	224.95 ± 7.79b	64.65 ± 7.45	980.76 ± 85.52b	29.77 ± 2.16
	H	8.43 ± 1.33	20.92 ± 3.51	72.75 ± 6.83	139.19 ± 3.36b	89.80 ± 7.04b	287.37 ± 1.20a	65.13 ± 8.39	1339.12 ± 52.60a	18.06 ± 1.73
Calophyllum inophyllum	CK	3.17 ± 0.49	20.17 ± 1.22	167.79 ± 9.26	351.21 ± 22.13a	221.24 ± 12.62	178.80 ± 9.61	67.83 ± 3.89	2.66 ± 0.41b	21.30 ± 5.24
	L	3.06 ± 0.04	22.80 ± 2.45	182.42 ± 14.44	274.95 ± 1.02ab	234.01 ± 18.63	152.47 ± 6.29	61.53 ± 6.64	4.46 ± 0.71b	19.17 ± 2.09
	M	3.12 ± 0.14	21.87 ± 0.24	172.44 ± 13.19	251.15 ± 19.33b	220.76 ± 8.97	163.01 ± 13.83	66.73 ± 2.91	3.53 ± 0.37b	18.61 ± 6.41
	H	2.77 ± 0.57	21.00 ± 0.53	189.74 ± 8.39	267.03 ± 4.43b	196.03 ± 6.60	155.39 ± 14.17	66.60 ± 0.99	8.97 ± 0.61a	13.52 ± 5.16
Pittosporum pentandrum	CK	4.98 ± 0.89	25.14 ± 1.65	193.22 ± 23.75	277.79 ± 27.05	118.65 ± 2.21b	246.34 ± 7.03	33.74 ± 0.03	37.50 ± 1.96	10.61 ± 0.19
	L	2.89 ± 1.17	28.51 ± 2.85	182.31 ± 5.00	245.96 ± 22.21	126.26 ± 2.72b	200.24 ± 1.29	26.63 ± 1.27	24.52 ± 4.40	13.53 ± 1.49
	M	2.59 ± 0.77	27.46 ± 1.86	212.17 ± 26.19	210.72 ± 14.83	155.98 ± 1.90a	239.89 ± 13.93	26.75 ± 3.53	21.56 ± 2.38	13.41 ± 3.08
	H	2.51 ± 0.44	31.35 ± 0.59	202.04 ± 9.71	166.20 ± 9.54	126.96 ± 4.44b	216.97 ± 17.35	26.51 ± 3.54	28.65 ± 5.71	9.38 ± 1.05
Podocarpus costalis	CK	1.73 ± 0.03b	35.43 ± 0.37	164.04 ± 5.36	289.84 ± 9.21	136.36 ± 2.25	211.16 ± 4.33a	41.55 ± 0.23	6.50 ± 0.62a	8.33 ± 1.87
	L	2.61 ± 0.11ab	27.28 ± 0.51	171.81 ± 10.93	300.99 ± 20.30	187.34 ± 10.22	208.38 ± 6.78a	48.84 ± 2.88	4.59 ± 0.08b	10.78 ± 2.69
	M	2.28 ± 0.13ab	35.55 ± 2.30	215.22 ± 17.05	298.08 ± 13.99	162.73 ± 12.95	161.24 ± 3.32b	39.49 ± 3.56	4.46 ± 0.27b	12.21 ± 3.23
	H	2.78 ± 0.31a	39.01 ± 4.43	196.73 ± 23.16	309.29 ± 14.31	162.33 ± 17.99	187.12 ± 5.46ab	37.09 ± 4.66	3.61 ± 0.21b	9.38 ± 1.05
Melia azedarach	CK	NA	NA	NA	NA	208.57 ± 19.57	385.79 ± 20.10	NA	NA	NA
	L	NA	NA	NA	NA	220.16 ± 12.07	353.79 ± 16.41	NA	NA	NA
	M	NA	NA	NA	NA	253.41 ± 10.46	349.04 ± 12.17	NA	NA	NA
	H	NA	NA	NA	NA	220.04 ± 22.53	366.13 ± 6.60	NA	NA	NA

Data represent the mean and standard error; the lowercase letters indicate significant differences between different soil salinities (control [CK], low [L], medium [M], and high [H]) in each species (one-way analysis of variance, Tukey method, $\alpha = 0.05$, $n = 5$). Abbreviations: *FAA* (free amino acids), *DW* (dry weight), *SOD* (leaf superoxide dismutase), *CAT* (leaf catalase), *POD* (leaf peroxidase), *NA* (no analysis due to defoliation).

growth. Under saline conditions, cell walls thicken through hemicellulose and lignin deposition, forming secondary cell walls (Le Gall et al., 2015). This increased thickness adds rigidity and maintains appropriate turgor pressure (Muszyńska et al., 2014). Lignification of cell walls is considered a vital response of plants to environmental stress and mechanical challenges (Moura et al., 2010), aligning with the increased POD activity observed in our pot experiments. Field growth and survival performance of various tree species in this study align with salt tolerance results from pot experiments. *H. littoralis* showed the best performance and *M. azedarach* the worst, suggesting that short-term controlled salt experiments can reliably predict longer-term field performance. According to Yeh et al. (2013), the spatial and temporal distribution of evapotranspiration in Taiwan shows approximately 3 mm during the dry season (November to April) and 4.4 mm in the rainy season (May to August) in the study area. In our field experiment, water supply during the winter meets the evapotranspiration demand, while in autumn and spring, limited irrigation amidst reduced rainfall and high temperatures may lead to drought conditions for the seedlings. Additionally, the study area faces various abiotic stresses such as high temperatures, intense light, strong winds, and salt spray. Proline, positively correlated with tolerance to various abiotic stresses (Ghosh et al., 2022), was synthesized in large amounts by *H. littoralis* under saline conditions in pot experiments, aiding in resistance to diverse environmental stresses. Beyond physiological responses, the characteristics and adaptability of leaves are crucial factors in responding to various abiotic stresses in actual environmental conditions (Li et al., 2023). The waxy leaf surfaces of *H. littoralis* leaves effectively prevent water loss and salt spray damage, with their silvery scales on the back increasing reflection to mitigate damage to the photosynthetic system from intense light (Ye et al., 2011). Conversely, the leaves of *M. azedarach*, lacking a waxy layer or succulent features, are not conducive to water retention, with growth and survival rates decreasing with increasing salinity. This phenomenon, consistent with pot experiment results, indicates a high sensitivity of *M. azedarach* to environmental salinity. Similarly, the survival rates of *M. azedarach* across different sites were notably stable after transplantation. This reflects that individuals sensitive to high salinity levels quickly succumbed within the first three months post-transplantation, indicating an immediate maladaptation to the saline conditions. Overall, choosing tree species with good tolerance helps ensure stable growth under repeated abiotic stresses, enhancing the possibility of successful afforestation.

4.3. Key indicators in pot experiments linking to field performance

In afforestation activities on salt-degraded lands, selecting suitable

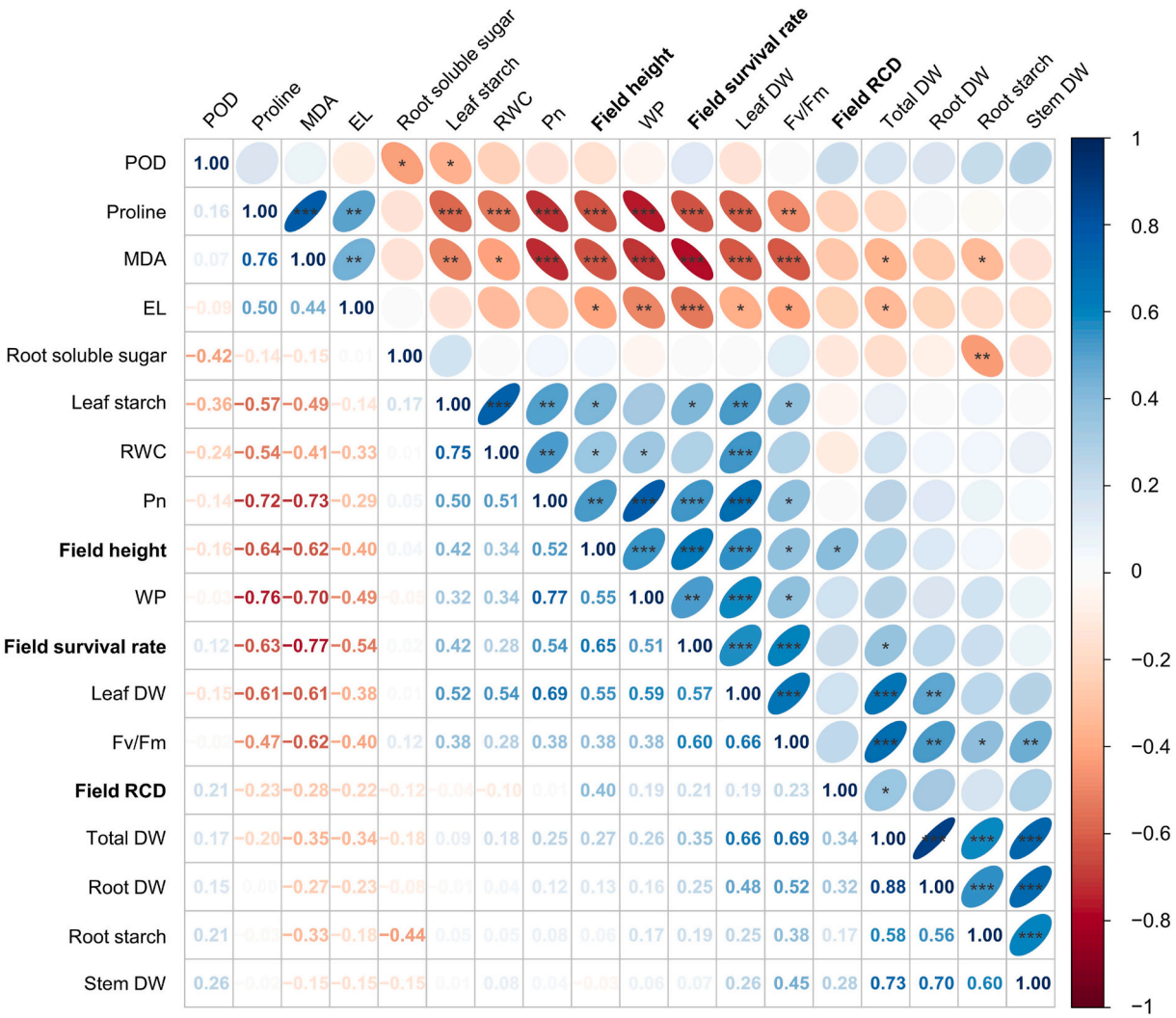

Fig. 5. Spearman correlation coefficients (ρ) between parameters from pot and field experiments; the high and low intensity of color represent strong and weak relationships (blue for positive and red for negative) between a pair of parameters, respectively; $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, $n = 36$. Abbreviations: *RCD* (root collar diameter), *DW* (dry weight), *Pn* (net photosynthetic rate), *Fv/Fm* (Maximum quantum efficiency of PSII), *WP* (midday leaf water potential), *EL* (electrolyte leakage), *RWC* (relative water content), *MDA* (malondialdehyde), *POD* (leaf peroxidase). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

tree species is crucial for enhancing the success of these efforts. Natural selection has driven the evolution of salt-tolerant species and ecotypes within species. Typically, better results in salt tolerance tests are obtained from species that naturally grow in saline environments and from their progeny selected under high-salt conditions. However, the screening for salt tolerance of many species is conducted in greenhouses with seedlings, and field trial results for validation are lacking (Niknam and McComb, 2000). A meta-analysis indicates that the correlation between lab and field phenotypic data is modest ($R^2 = 0.26$), likely because lab conditions do not mimic field environments (Poorter et al., 2016). In our pot experiments, the short-term salt treatment has not yet significantly impacted seedling height, RCD, or root length for most species. Because the salt treatment was applied at the end of the growing season to align with field conditions, these aspects of morphological growth are generally not suitable for reflecting the field results. Regarding the field RGR of RCD, it showed a low correlation with most indicators from pot experiments, primarily attributed to an overall increase in RCD during the second growth season post-planting. Except for *M. azedarach*, other species exhibited significant RCD growth under prolonged salt stress in high-salinity areas, thereby reducing interspecies differences. The individuals enduring long-term salt stress developed adaptations, with increased secondary growth observed as a critical response to combat salt stress (Shafi and Zahoor, 2019). In contrast, the RGR of height more clearly differed among species, correlating with several pot-experiment parameters. Plant height growth involves cell elongation, but increased cell wall rigidity to withstand salt stress reduces wall extensibility. Elongation is facilitated by the oxidation of cell wall polysaccharides through ROS and the loosening of cell walls by expansin, which breaks hydrogen bonds (Julkowska and Testerink, 2015). Thus, except for the differences in tree growth habits, interspecies variations in salt tolerance, particularly regarding cell wall traits and ROS regulation, impact long-term seedling height growth. Correlation analysis identified a significant negative relationship between proline levels and the growth and survival of seedlings in the field. This trend is primarily attributed to the substantial accumulation of proline observed in most species, including those sensitive to salt, under salt stress conditions. Although the highly salt-tolerant species *H. littoralis* demonstrated considerable proline levels in saline environments, this phenomenon is likely a manifestation of its inherent stress resistance mechanisms. This suggests that proline accumulation may not be a suitable indicator of salt tolerance across different species. As a recognized compatible solute, proline is crucial for plant salt tolerance.

However, the precise mechanisms connecting proline with salt tolerance are still unclear (El Moukhtari et al., 2020). Additionally, multiple effectors regulate free proline biosynthesis, leading to diverse responses to salt stress in different studies and among various plant species (Mansour and Ali, 2017).

As the final product of the peroxidation of unsaturated fatty acids in cell membranes, MDA is widely used to assess oxidative stress or cell damage. Numerous studies have shown that genotypes with higher salt tolerance within species often have lower leaf MDA content, suggesting MDA as a suitable indicator for assessing salt tolerance (Ashrafi et al., 2015; Kumar et al., 2018; Singh & Kumar, 2021). In this study, MDA levels from pot experiments effectively reflected the field growth patterns of various tree species, exhibiting a strong negative correlation with field survival rates. This finding underscores the potential of MDA measurements from controlled experiments to serve as a reliable tool for assessing salt tolerance among different species under real-world conditions. Similarly, an elevation in EL indicates increased cell membrane damage, which often correlates highly with MDA content (Yan et al., 2022). In addition, owing to its straightforward measurement process, EL is a practical indicator for predicting the field survival rates of various tree species. Furthermore, the correlation between leaf biomass from pot experiments and in-field height growth and survival rates indicates that a short-term decline in photosynthetic efficiency can significantly impact long-term growth. However, leaf shedding in response to salt stress is a crucial salt exclusion mechanism that reduces salt accumulation within the plant (Abdellaoui et al., 2023). Therefore, accurately controlling the simulation of salt stress in experimental settings is essential for obtaining reliable results. In this study, we replicated field-like soil salinization periods and continuously applied saline water, mimicking the gradual increase in salt levels typically observed in the field. This approach was instrumental in preventing certain species from employing leaf shedding as a short-term salt avoidance mechanism, a factor that could potentially obscure the correlation between leaf biomass and species' salt tolerance. Finally, physiological parameters from pot experiments, such as Pn, WP, and Fv/Fm, showed a moderate positive correlation with field survival rates. This suggests that the efficiency of seedlings' photosystem and water status under short-term salt stress can moderately indicate their long-term growth performance in the field. The rapid measurability of these parameters using portable devices offers significant advantages for extensive salt tolerance testing across a broader range of tree species, thereby expediting the identification of species suitable for extremely salt-affected environments.

4.4. Implications and limitations

The most common cause of afforestation failure is poor site/species matching, coupled with a lack of understanding of hydrological, topographical, and soil conditions, which significantly affects planting outcomes (Wodehouse and Rayment, 2019). In Taiwan, the Forestry Agency has established specific regulations for prioritizing native tree species in ecological forestry, adhering to the principle of "right tree, right place." However, the soil in coastal areas often undergoes human-induced degradation, which is exacerbated by disturbances such as waste from road development and terrain features that prevent salt expulsion, conditions observed in our afforestation projects. In such scenarios, selecting tree species for afforestation can be challenging when relying solely on the ecological distribution of plants or by referencing the composition of nearby forests. Consequently, it is crucial to develop methods and indicators for assessing the salt tolerance of native plants. This approach, combined with environmental assessments, helps identify the best species for sites affected by salinity. Notably, the selection process should prioritize native species to support long-term adaptation and minimize ecological impacts. For example, the early and extensive plantings of the exotic species *Casuarina* spp. along Taiwan's coasts not only grew rapidly but also effectively stabilized wind-blown sand. However, these species struggle with natural regeneration, are susceptible to pests and diseases, and have shorter lifespans, all of which contribute to the decline of these coastal forests. Recent efforts by Taiwan's Forestry Agency to rejuvenate these areas with native coastal species and create mixed-species forests have shown promising results (Cheng and Ho, 2012). Beyond indigenous species, tree selection can also focus on those already widely cultivated and demonstrating potential salt tolerance. Although *P. costalis*, featured in our study, is originally from the coastal cliffs of Taiwan's offshore island, its significant ornamental value has led to its widespread cultivation across mainland Taiwan, making it a viable choice. Planting a diversity of species in areas affected by salinity not only enhances biodiversity but also prevents the dominance and exclusion effects associated with monocultures.

Our experimental results confirmed that MDA serves as a reliable indicator of salt tolerance. However, this study analyzed only five tree species, while the local coastal region hosts dozens of native species that vary in their proximity to the sea. Thus, further verification through additional research is required to establish the applicability of this indicator to other species. Moreover, there are numerous limitations to the broader application of salt tolerance indicators. On one hand, salt tolerance indicators developed from studies on individual species, such as leaf SOD activity and soluble sugar content in Siberian elm (Mu and Ding, 2022), may not be applicable across multiple species. These two indicators did not show significant differences across our analyzed tree species. On the other hand, cross-species salt tolerance research has developed various indicators, such as leaf count and height growth in 19 woody species (Sun and Dickinson, 1993), Fv/Fm in 30 woody species (Percival, 2005), biomass and Na^+/K^+ ratios in 15 *Acacia* species (Joseph et al., 2015), and measurements of photosynthesis, stomatal conductance, and antioxidant enzymes (SOD, POD, and CAT) in 5 woody species (Hussain et al., 2021). However, due to budgetary and resource constraints, such research often tests only a few physiological parameters and may not fully reflect true salt tolerance characteristics. Moreover, using varying NaCl concentrations in experiments may not accurately reflect natural salt compositions, which could potentially cause disparities between experimental and real environmental conditions. Additionally, confining experiments solely to pots may limit root development and overlook the adaptive strategies of deep-rooted species in their natural habitats. Therefore, establishing salt tolerance indicators requires further verification from field planting outcomes, especially in coastal areas where plants often face multiple stressors such as high temperatures, strong winds, intense sunlight, and drought. These conditions necessitate a diverse range of adaptive mechanisms for plants to survive. As for our field planting sites, Site M, located upwind, may experience greater effects from salt spray carried by strong winds, while Site L might face biotic stress due to the rapid growth of weeds and vines. Despite these complexities, the strong correlation between the pot experiment results and field growth confirms that salt stress is the primary limitation to plant growth in this area. This finding establishes plant salt tolerance as a key factor in selecting appropriate species for afforestation on salt-affected lands. Furthermore, a precise understanding of the environmental conditions at the planting area helps maximize planting outcomes. Although *M. azedarach* has a lower salt tolerance, its rapid growth makes it suitable for planting in low-salinity areas to enhance carbon sequestration.

5. Conclusions

This study establishes the importance of tree species selection in afforestation projects on saline-degraded coastal lands. Short-term salt stress simulated in controlled pot experiments effectively reflects the growth performance of plants in salt-affected field conditions. The content of MDA in leaves shows a strong negative correlation with relative height growth and survival rates of various tree species in field results, demonstrating its effectiveness in cross-species assessment of

salt tolerance. Additionally, parameters such as EL and leaf DW exhibit moderate correlation to field performance and can be integrated for a more detailed evaluation of salt tolerance. Portable measurements of Pn, WP, and Fv/Fm effectively determine the photosynthetic activity and water status of seedlings, moderately correlating with their long-term survival post-transplantation. These metrics are instrumental in identifying tree species potentially suitable for afforestation. The *H. littoralis* exhibits the highest salt tolerance, likely due to the considerable proline accumulation under salt stress. In contrast, the *M. azedarach* shows the lowest salt tolerance, with complete defoliation under short-term salt stress and a marked decline in growth performance with increasing salt levels in field observations. In summary, practical simulation experiments and salt tolerance assessment parameters can identify potential tree species suitable for planting in degraded salt-affected areas. By conducting small-scale, short-term saline experiments at the nursery stage to select species suited for transplantation, we can enhance afforestation success in saline environments affected by extreme climate or anthropogenic disturbances. This approach not only contributes to the environmental restoration of degraded lands and the conservation of resources, but also supports the objectives of sustainable development.

Funding

This work was supported by the Yunlin-Chiayi-Tainan Region Branch Office, Highway Bureau, MOTC, Taiwan (Grant number 20212307, 20242377).

CRediT authorship contribution statement

Tzu-Hao Su: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis. **Yang Shen:** Methodology, Investigation. **Yao-Yu Chiang:** Writing – review & editing, Investigation, Data curation. **Yu-Ting Liu:** Investigation. **Han-Ming You:** Writing – review & editing, Resources, Conceptualization. **Hung-Chih Lin:** Writing – review & editing, Resources. **Kuan-Ning Kung:** Writing – review & editing, Resources. **Yao-Moan Huang:** Writing – review & editing, Resources. **Chih-Ming Lai:** Writing – review & editing, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

The authors thank Chih-Yung Yeh, Shin-Der Lin, Yuan-Shiang Lin, Jei-Chen Wu, Jung Chen, Jiun-Tze Chang, Yen-Hsin Tsai, Yi-Han Lin, and Fang-Tsen Lo for their assistance in field investigations and data organization. Special thanks are also extended to the Yunlin-Chiayi-Tainan Region Branch Office, Highway Bureau, MOTC, for their professional advice and assistance in site preparation.

References

Abdellaoui, R., Elkelish, A., El-Keblawy, A., Mighri, H., Boughalleb, F., Bakhshandeh, E., 2023. Editorial: halophytes: salt stress tolerance mechanisms and potential use. Front. Plant Sci. 14, 1218184 https://doi.org/10.3389/fpls.2023.1218184.

Abogadallah, G.M., 2010. Antioxidative defense under salt stress. Plant Signal. Behav. 5 (4), 369–374. https://doi.org/10.4161/psb.5.4.10873.

Abogadallah, G.M., Serag, M.M., Quick, W.P., 2010. Fine and coarse regulation of reactive oxygen species in the salt tolerant mutants of barnyard grass and their wild-type parents under salt stress. Physiol. Plantarum 138 (1), 60–73. https://doi.org/10.1111/j.1399-3054.2009.01297.x.

Aebi, H., 1984. [13] Catalase in vitro. In: Methods in Enzymology, vol. 105. Academic press, pp. 121–126. https://doi.org/10.1016/S0076-6879(84)05016-3.

Al Kharusi, L., Al Yahyai, R., Yaish, M.W., 2019. Antioxidant response to salinity in salt-tolerant and salt-susceptible cultivars of date palm. Agriculture 9 (1), 8. https://doi.org/10.3390/agriculture9010008.

Alexieva, V., Sergiev, I., Mapelli, S., Karanov, E., 2001. The effect of drought and ultraviolet radiation on growth and stress markers in pea and wheat. Plant Cell Environ. 24 (12), 1337–1344. https://doi.org/10.1046/j.1365-3040.2001.00778.x.

Arkema, K.K., Griffin, R., Maldonado, S., Silver, J., Suckale, J., Guerry, A.D., 2017. Linking social, ecological, and physical science to advance natural and nature-based protection for coastal communities. Ann. N. Y. Acad. Sci. 1399 (1), 5–26. https://doi.org/10.1111/nyas.13322.

Ashrafi, E., Razmjoo, J., Zahedi, M., Pessarakli, M., 2015. Screening Alfalfa for salt tolerance based on lipid peroxidation and antioxidant enzymes. Agron. J. 107 (1), 167–173. https://doi.org/10.2134/agronj14.0248.

Balali, A., Gholami, S., Javanmardi, M., Valipour, A., Yunusa-Kaltungo, A., 2023. Assessment of heavy metal pollution in the soil of a construction and demolition waste landfill. Environ. Nanotechnol. Monit. Manag. 20 https://doi.org/10.1016/j.enmm.2023.100856.

Bastam, N., Baninasab, B., Ghobadi, C., 2012. Improving salt tolerance by exogenous application of salicylic acid in seedlings of pistachio. Plant Growth Regul. 69 (3), 275–284. https://doi.org/10.1007/s10725-012-9770-7.

Bates, L.S., Waldren, R.P., Teare, I.D., 1973. Rapid determination of free proline for water-stress studies. Plant Soil 39, 205–207. https://doi.org/10.1007/BF00018060.

Bradford, M.M., 1976. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. Anal. Biochem. 72 (1–2), 248–254. https://doi.org/10.1016/0003-2697(76)90527-3.

Bordenave, C.D., Rocco, R., Maiale, S.J., Campestre, M.P., Ruiz, O.A., Rodríguez, A.A., Menéndez, A.B., 2019. Chlorophyll a fluorescence analysis reveals divergent photosystem II responses to saline, alkaline and saline–alkaline stresses in the two Lotus japonicus model ecotypes MG20 and Gifu-129. Acta Physiol. Plant. 41, 1–13. https://doi.org/10.1007/s11738-019-2956-0.

Chakraborty, K., Bishi, S.K., Goswami, N., Singh, A.L., Zala, P.V., 2016. Differential fine-regulation of enzyme driven ROS detoxification network imparts salt tolerance in contrasting peanut genotypes. Environ. Exp. Bot. 128, 79–90. https://doi.org/10.1016/j.envexpbot.2016.05.001.

Chance, B., Maehly, A.C., 1955. Assay of catalase and peroxidase. Methods Enzymol. 2, 764–775. https://doi.org/10.1016/S0076-6879(55)02300-8.

Chen, Y.-C., Shih, C.-H., 2019. Sustainable management of coastal wetlands in Taiwan: a review for invasion, conservation, and removal of mangroves. Sustainability 11 (16). https://doi.org/10.3390/su11164305.

Cheng, C.Y., Ho, K.Y., 2012. Stand adaptabilities in an ecological afforestion study on the west coast of Taiwan. Taiwan J. For. Sci. 27 (1), 41–57. https://doi.org/10.7075/TJFS.201203.0041.

Cheng, R., Zhu, H., Cheng, X., Shutes, B., Yan, B., 2020. Saline and Alkaline tolerance of wetland plants—what are the most representative evaluation indicators? Sustainability 12 (5), 1913. https://doi.org/10.3390/su12051913.

Du, J., Hesp, P.A., 2020. Salt spray distribution and its impact on vegetation zonation on coastal dunes: a review. Estuar. Coast 43 (8), 1885–1907. https://doi.org/10.1007/s12237-020-00820-2.

Duarte, B., Santos, D., Marques, J.C., Cacador, I., 2013. Ecophysiological adaptations of two halophytes to salt stress: photosynthesis, PS II photochemistry and anti-oxidant feedback—implications for resilience in climate change. Plant Physiol. Biochem. 67, 178–188. https://doi.org/10.1016/j.plaphy.2013.03.004.

DuBois, M., Gilles, K.A., Hamilton, J.K., Rebers, P.t., Smith, F., 1956. Colorimetric method for determination of sugars and related substances. Anal. Chem. 28 (3), 350–356. https://doi.org/10.1021/ac60111a017.

El Moukhtari, A., Cabassa-Hourton, C., Farissi, M., Savouré, A., 2020. How does proline treatment promote salt stress tolerance during crop plant development? Front. Plant Sci. 11, 1127. https://doi.org/10.3389/fpls.2020.01127.

El Shinawi, A., Kuriqi, A., Zelenakova, M., Vranayova, Z., Abd-Elaty, I., 2022. Land subsidence and environmental threats in coastal aquifers under sea level rise and over-pumping stress. J. Hydrol. 608 https://doi.org/10.1016/j.jhydrol.2022.127607.

Esterbauer, H., Cheeseman, K.H., 1990. Determination of aldehydic lipid peroxidation products: malonaldehyde and 4-hydroxynonenal. In: Methods in Enzymology, vol. 186. Elsevier, pp. 407–421. https://doi.org/10.1016/0076-6879(90)86134-H.

FAO, 2021. Global map of salt affected soils version 1.0. https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/global-map-of-salt-affected-soils/en/. January 2024.

Feagin, R.A., Figlus, J., Zinnert, J.C., Sigren, J., Martínez, M.L., Silva, R., Smith, W.K., Cox, D., Young, D.R., Carter, G., 2015. Going with the flow or against the grain? The promise of vegetation for protecting beaches, dunes, and barrier islands from erosion. Front. Ecol. Environ. 13 (4), 203–210. https://doi.org/10.1890/140218.

Francoz, E., Ranocha, P., Nguyen-Kim, H., Jamet, E., Burlat, V., Dunand, C., 2015. Roles of cell wall peroxidases in plant development. Phytochemistry 112, 15–21. https://doi.org/10.1016/j.phytochem.2014.07.020.

Ghosh, U.K., Islam, M.N., Siddiqui, M.N., Cao, X., Khan, M.A.R., 2022. Proline, a multifaceted signalling molecule in plant responses to abiotic stress: understanding the physiological mechanisms. Plant Biol (Stuttg) 24 (2), 227–239. https://doi.org/10.1111/plb.13363.

Giannopolitis, C.N., Ries, S.K., 1977. Superoxide dismutases: I. Occurrence in higher plants. Plant Physiol. 59 (2), 309–314. https://doi.org/10.1104/pp.59.2.309.

Gil-Muñoz, F., Pérez-Pérez, J.G., Quiñones, A., Primo-Capella, A., Cebolla, J., Forner-Giner, M.A., Badenes, M.L., Del Mar Naval, M., 2020. A cross population between D. kaki and D. virginiana shows high variability for saline tolerance and improved salt stress tolerance. PLoS One 15 (2), e0229023. https://doi.org/10.1371/journal.pone.0229023.

Gupta, S.R., Dagar, J.C., Mukesh-Kumar, 2016. Tree plantations in saline environments: ecosystem services, carbon sequestration and climate change mitigation. In: Dagar, J., Minhas, P. (Eds.), A, Groforestry for the Management of Waterlogged Saline Soils and Poor-Quality Waters. Advances in Agroforestry, vol. 13. Springer, New Delhi. https://doi.org/10.1007/978-81-322-2659-8_11.

Hansen, J., Møller, I., 1975. Percolation of starch and soluble carbohydrates from plant tissue for quantitative determination with anthrone. Anal. Biochem. 68 (1), 87–94. https://doi.org/10.1016/0003-2697(75)90682-X.

Hayat, S., Hayat, Q., Alyemeni, M.N., Wani, A.S., Pichtel, J., Ahmad, A., 2012. Role of proline under changing environments: a review. Plant Signal. Behav. 7 (11), 1456–1466. https://doi.org/10.4161/psb.21949.

Hossain, M.A., Hoque, M.A., Burritt, D.J., Fujita, M., 2014. Proline protects plants against abiotic oxidative stress: biochemical and molecular mechanisms. In: Oxidative Damage to Plants. Elsevier, pp. 477–522. https://doi.org/10.1016/B978-0-12-799963-0.00016-2.

Hou, Z., Liu, Y., Wei, C., 2018. Influence of construction and demolition waste on fitness and community structure of cicada nymphs: new bioindicators of soil pollution. PLoS One 13 (9), e0203744. https://doi.org/10.1371/journal.pone.0203744.

Hsieh, C.F., 2002. Composition, endemism and phytogeographical affinities of the Taiwan flora. Taiwania 47 (4), 298–310. https://doi.org/10.6165/tai.2002.47(4).298.

Huang, X., Soolanayakanahally, R.Y., Guy, R.D., Shunmugam, A.S., Mansfield, S.D., 2020. Differences in growth and physiological and metabolic responses among Canadian native and hybrid willows (*Salix* spp.) under salinity stress. Tree Physiol. 40 (5), 652–666. https://doi.org/10.1093/treephys/tpaa017.

Hunt, R., 1982. Plant Growth Curves. The Functional Approach to Plant Growth Analysis. Edward Arnold Ltd. https://doi.org/10.2307/2531040.

Hussain, S., Luro, F., Costantino, G., Ollitrault, P., Morillon, R., 2012. Physiological analysis of salt stress behaviour of citrus species and genera: low chloride accumulation as an indicator of salt tolerance. South Afr. J. Bot. 81, 103–112. https://doi.org/10.1016/j.sajb.2012.06.004.

Hussain, M.S., Naeem, M.S., Tanvir, M.A., Nawaz, M.F., Abd-Elrahman, A., 2021. Eco-physiological evaluation of multipurpose tree species to ameliorate saline soils. Int. J. Phytoremediation 23 (9), 969–981. https://doi.org/10.1080/15226514.2020.1871321.

Javed, M., Ashraf, M., Iqbal, M., Farooq, M.A., Zafar, Z.U., Athar, H.U.R., 2022. Chlorophyll fluorescence, ion uptake, and osmoregulation are potential indicators for detecting ecotypic variation in salt tolerance of Panicum antidotale Retz. Arid Land Res. Manag. 36 (1), 84–108. https://doi.org/10.1080/15324982.2021.1957038.

Joseph, S., Murphy, D.J., Bhave, M., 2015. Identification of salt tolerant Acacia species for saline land utilisation. Biologia 70 (2), 174–182. https://doi.org/10.1515/biolog-2015-0032.

Julkowska, M.M., Testerink, C., 2015. Tuning plant signaling and growth to survive salt. Trends Plant Sci. 20 (9), 586–594. https://doi.org/10.1016/j.tplants.2015.06.008.

Kanai, M., Higuchi, K., Hagihara, T., Konishi, T., Ishii, T., Fujita, N., Nakamura, Y., Maeda, Y., Yoshiba, M., Tadano, T., 2007. Common reed produces starch granules at the shoot base in response to salt stress. New Phytol. 176 (3), 572–580. https://doi.org/10.1111/j.1469-8137.2007.02188.x.

Kuang, Y., Xu, Y., Zhang, L., Hou, E., Shen, W., 2017. Dominant trees in a subtropical forest respond to drought mainly via adjusting tissue soluble sugar and proline content. Front. Plant Sci. 8, 802. https://doi.org/10.3389/fpls.2017.00802.

Kumar, M., Kumar, R., Jain, V., Jain, S., 2018. Differential behavior of the antioxidant system in response to salinity induced oxidative stress in salt-tolerant and salt-sensitive cultivars of Brassica juncea L. Biocatal. Agric. Biotechnol. 13, 12–19. https://doi.org/10.1016/j.bcab.2017.11.003.

Le Gall, H., Philippe, F., Domon, J.M., Gillet, F., Pelloux, J., Rayon, C., 2015. Cell wall metabolism in response to abiotic stress. Plants 4 (1), 112–166. https://doi.org/10.3390/plants4010112.

Lee, T.M., 2005. Monitoring the dynamics of coastal vegetation in southwestern Taiwan. Environ. Monit. Assess. 111 (1–3), 307–323. https://doi.org/10.1007/s10661-005-0209-8.

Li, K.C., Liu, H.C., Lin, H.C., 2021. Multiple environmental factors increase the niche complexity and species diversity of Brachyuran crabs in an intertidal algal reef ecosystem in northwestern Taiwan. Zool. Stud. 60, e73. https://doi.org/10.6620/ZS.2021.60-73.

Li, S., Lu, S., Wang, J., Chen, Z., Zhang, Y., Duan, J., Liu, P., Wang, X., Guo, J., 2023. Responses of physiological, morphological and anatomical traits to abiotic stress in woody plants. Forests 14 (9). https://doi.org/10.3390/f14091784.

Li, S., Luo, W., Jia, Z., Tang, S., Chen, C., 2018. The effect of natural rainfall on salt leaching under watertable management. Land Degrad. Dev. 29 (6), 1953–1961. https://doi.org/10.1002/ldr.2956.

Li, X., Zhang, C., 2021. Effect of natural and artificial afforestation reclamation on soil properties and vegetation in coastal saline silt soils. Catena 198. https://doi.org/10.1016/j.catena.2020.105066.

Liang, W., Ma, X., Wan, P., Liu, L., 2018. Plant salt-tolerance mechanism: a review. Biochem. Biophys. Res. Commun. 495 (1), 286–291. https://doi.org/10.1016/j.bbrc.2017.11.043.

Lichtenthaler, H.K., 1987. [34] Chlorophylls and carotenoids: pigments of photosynthetic biomembranes. In: Methods in Enzymology, vol. 148. Elsevier, pp. 350–382. https://doi.org/10.1016/0076-6879(87)48036-1.

Llanes, A., Palchetti, M.V., Vilo, C., Ibañez, C., 2021. Molecular control to salt tolerance mechanisms of woody plants: recent achievements and perspectives. Ann. For. Sci. 78 (4) https://doi.org/10.1007/s13595-021-01107-7.

Lu, Y., Zeng, F.J., Li, X.Y., Zhang, B., 2021. Physiological changes of three woody plants exposed to progressive salt stress. Photosynthetica 59 (1), 171–184. https://doi.org/10.32615/ps.2021.007.

Mansour, M.M.F., 2013. Plasma membrane permeability as an indicator of salt tolerance in plants. Biol. Plantarum 57, 1–10. https://doi.org/10.1007/s10535-012-0144-9.

Mansour, M.M.F., Ali, E.F., 2017. Evaluation of proline functions in saline conditions. Phytochemistry 140, 52–68. https://doi.org/10.1016/j.phytochem.2017.04.016.

Mihailova, G., Kocheva, K., Goltsev, V., Kalaji, H.M., Georgieva, K., 2018. Application of a diffusion model to measure ion leakage of resurrection plant leaves undergoing desiccation. Plant Physiol. Biochem. 125, 185–192. https://doi.org/10.1016/j.plaphy.2018.02.008.

Moore, S., Stein, W.H., 1954. A modified ninhydrin reagent for the photometric determination of amino acids and related compounds. J. Biol. Chem. 211 (2), 907–913. https://doi.org/10.1016/s0021-9258(18)71178-2.

Moura, J.C., Bonine, C.A., de Oliveira Fernandes Viana, J., Dornelas, M.C., Mazzafera, P., 2010. Abiotic and biotic stresses and changes in the lignin content and composition in plants. J. Integr. Plant Biol. 52 (4), 360–376. https://doi.org/10.1111/j.1744-7909.2010.00892.x.

Mu, D., Ding, C., 2022. Developing a salinity tolerance indicator for tree varieties at challenging sites and urban forests based on inferences of physiological responses: an example of Ulmus pumila. Trees (Berl.) 36 (2), 593–607. https://doi.org/10.1007/s00468-022-02331-y.

Munns, R., Tester, M., 2008. Mechanisms of salinity tolerance. Annu. Rev. Plant Biol. 59, 651–681. https://doi.org/10.1146/annurev.arplant.59.032607.092911.

Muszyńska, A., Jarocka, K., Kurczynska, E.U., 2014. Plasma membrane and cell wall properties of an aspen hybrid (Populus tremula × tremuloides) parenchyma cells under the influence of salt stress. Acta Physiol. Plant. 36 (5), 1155–1165. https://doi.org/10.1007/s11738-014-1490-3.

Niknam, S., McComb, J., 2000. Salt tolerance screening of selected Australian woody species—a review. For. Ecol. Manag. 139 (1–3), 1–19. https://doi.org/10.1016/S0378-1127(99)00334-5.

Osman, K.T., 2018. Management of Soil Problems. Springer. https://doi.org/10.1007/978-3-319-75527-4.

Percival, G.C., 2005. Identification of foliar salt tolerance of woody perennials using chlorophyll fluorescence. Hortscience 40 (6), 1892–1897. https://doi.org/10.21273/HORTSCI.40.6.1892.

Pirasteh-Anosheh, H., Ranjbar, G., Pakniyat, H., Emam, Y., 2016. Physiological mechanisms of salt stress tolerance in plants: an overview. Plant-Environment Interaction: Responses and Approaches to Mitigate Stress 141–160. https://doi.org/10.1002/9781119081005.ch8.

Pompelli, M.F., Ferreira, P.P., Chaves, A.R., Figueiredo, R.C., Martins, A.O., Jarma-Orozco, A., et al., 2021. Physiological, metabolic, and stomatal adjustments in response to salt stress in Jatropha curcas. Plant Physiol. Biochem. 168, 116–127. https://doi.org/10.1016/j.plaphy.2021.09.039.

Poorter, H., Fiorani, F., Pieruschka, R., Wojciechowski, T., van der Putten, W.H., Kleyer, M., Schurr, U., Postma, J., 2016. Pampered inside, pestered outside? Differences and similarities between plants growing in controlled conditions and in the field. New Phytol. 212 (4), 838–855. https://doi.org/10.1111/nph.14243.

Quan, X., Liang, X., Li, H., Xie, C., He, W., Qin, Y., 2021. Identification and characterization of wheat germplasm for salt tolerance. Plants 10 (2), 268. https://doi.org/10.3390/plants10020268.

Rasel, M., Tahjib-Ul-Arif, M., Hossain, M.A., Hassan, L., Farzana, S., Brestic, M., 2021. Screening of salt-tolerant rice landraces by seedling stage phenotyping and dissecting biochemical determinants of tolerance mechanism. J. Plant Growth Regul. 40, 1853–1868. https://doi.org/10.1007/s00344-020-10235-9.

Reddy, P.S., Jogeswar, G., Rasineni, G.K., Maheswari, M., Reddy, A.R., Varshney, R.K., Kishor, P.K., 2015. Proline over-accumulation alleviates salt stress and protects photosynthetic and antioxidant enzyme activities in transgenic sorghum [Sorghum bicolor (L.) Moench]. Plant Physiol. Biochem. 94, 104–113. https://doi.org/10.1016/j.plaphy.2015.05.014.

Richards, L.A., 1954. Diagnosis and Improvement of Saline and Alkali Soils. US Government Printing Office. https://doi.org/10.1093/aibsbulletin/4.3.14-a.

Rudianto, E., et al., 2016. Ecosystem-based tsunami disaster risk reduction in Indonesian coastal areas. In: Santiago-Fandiño, V., Tanaka, H., Spiske, M. (Eds.), Tsunamis and Earthquakes in Coastal Environments. Coastal Research Library, vol. 14. Springer, Cham. https://doi.org/10.1007/978-3-319-28528-3_3.

Schachtsiek, T., Lamers, J.P.A., Khamzina, A., 2014. Early survival and growth of six afforestation species on abandoned cropping sites in irrigated drylands of the aral sea basin. Arid Land Res. Manag. 28 (4), 410–427. https://doi.org/10.1080/15324982.2013.855958.

Shafi, A., Zahoor, I., 2019. Plant survival and tolerance under high salinity: primary and secondary cell wall-sensing mechanism. In: Akhtar, M.S. (Ed.), Salt Stress, Microbes, and Plant Interactions: Causes and Solution, vol. 1. Springer, Singapore, pp. 129–146. https://doi.org/10.1007/978-981-13-8801-9_6.

Shaheenuzzamn, M., Shi, S., Sohail, K., Wu, H., Liu, T., An, P., Wang, Z., Hasanuzzaman, M., 2021. Regulation of cuticular wax biosynthesis in plants under abiotic stress. Plant Biotechnology Reports 15 (1), 1–12. https://doi.org/10.1007/s11816-020-00656-z.

Shahid, M.A., Balal, R.M., Khan, N., Simón-Grao, S., Alfosea-Simón, M., Cámara-Zapata, J.M., et al., 2019. Rootstocks influence the salt tolerance of Kinnow Mandarin trees by altering the antioxidant defense system, osmolyte concentration, and toxic ion accumulation. Sci. Hortic. 250, 1–11. https://doi.org/10.1016/j.scienta.2019.02.028.

Shams, M., Khadivi, A., 2023. Mechanisms of salinity tolerance and their possible application in the breeding of vegetables. BMC Plant Biol. 23 (1), 139. https://doi.org/10.1186/s12870-023-04152-8.

Shan, Q., Zhang, J., Sun, S., Chen, G., Zhang, H., Shen, L., 2018. Construction of coastline shelterbelts and assessment of their environmental effects in Yuyao, China. Land Degrad. Dev. 29 (8), 2428–2437. https://doi.org/10.1002/ldr.3062.

Shepherd, T., Wynne Griffiths, D., 2006. The effects of stress on plant cuticular waxes. New Phytol. 171 (3), 469–499. https://doi.org/10.1111/j.1469-8137.2006.01826.x.

Singh, D., Kumar, A., 2021. In vitro screening and characterization of selected elite clones of Eucalyptus tereticornis Sm. for salt stress. J. Plant Growth Regul. 40, 694–706. https://doi.org/10.1007/s00344-020-10138-9.

Sun, D., Dickinson, G., 1993. Responses to salt stress of 16 Eucalyptus species, Grevillea robusta, Lophostemon confertus and Pinus caribea var. hondurensis. For. Ecol. Manag. 60 (1–2), 1–14. https://doi.org/10.1016/0378-1127(93)90019-J.

Tavakkoli, E., Rengasamy, P., McDonald, G.K., 2010. High concentrations of Na+ and Cl–ions in soil solution have simultaneous detrimental effects on growth of faba bean under salinity stress. J. Exp. Bot. 61 (15), 4449–4459. https://doi.org/10.1093/jxb/erq251.

Telfer, A., 2014. Singlet oxygen production by PSII under light stress: mechanism, detection and the protective role of beta-carotene. Plant Cell Physiol. 55 (7), 1216–1223. https://doi.org/10.1093/pcp/pcu040.

Tenhaken, R., 2014. Cell wall remodeling under abiotic stress. Front. Plant Sci. 5, 771. https://doi.org/10.3389/fpls.2014.00771.

Thalmann, M., Santelia, D., 2017. Starch as a determinant of plant fitness under abiotic stress. New Phytol. 214 (3), 943–951. https://doi.org/10.1111/nph.14491.

Thitisaksakul, M., Dong, S., Beckles, D.M., 2017. How rice Glycogen Synthase Kinase-like 5 (OsGSK5) integrates salinity stress response to source-sink adaptation: a proposed model. Plant Signal. Behav. 12 (12), e1403708 https://doi.org/10.1080/15592324.2017.1403708.

Tomar, O.S., Minhas, P.S., Sharma, V.K., Singh, Y.P., Gupta, R.K., 2003. Performance of 31 tree species and soil conditions in a plantation established with saline irrigation. For. Ecol. Manag. 177 (1–3), 333–346. https://doi.org/10.1016/s0378-1127(02)00437-1.

Tyler, R.H., Boyer, T.P., Minami, T., Zweng, M.M., Reagan, J.R., 2017. Electrical conductivity of the global ocean. Earth Planets Space 69 (1), 156. https://doi.org/10.1186/s40623-017-0739-7.

van Zelm, E., Zhang, Y., Testerink, C., 2020. Salt tolerance mechanisms of plants. Annu. Rev. Plant Biol. 71, 403–433. https://doi.org/10.1146/annurev-arplant-050718-100005.

Vita, F., Sabbatini, L., Sillo, F., Ghignone, S., Vergine, M., Guidi Nissim, W., Fortunato, S., Salzano, A.M., Scaloni, A., Luvisi, A., Balestrini, R., De Bellis, L., Mancuso, S., 2022. Salt stress in olive tree shapes resident endophytic microbiota. Front. Plant Sci. 13, 992395 https://doi.org/10.3389/fpls.2022.992395.

Weil, R.R., Brady, N.C., 2016. The Nature and Properties of Soils, fifteenth ed. Pearson Education, Harlow, pp. 456–458.

Wodehouse, D.C., Rayment, M.B., 2019. Mangrove area and propagule number planting targets produce sub-optimal rehabilitation and afforestation outcomes. Estuar. Coast Shelf Sci. 222, 91–102. https://doi.org/10.1016/j.ecss.2019.04.003.

Wu, M., He, Z., Fung, S., Cao, Y., Guan, D., Peng, Y., Lee, S.Y., 2020. Species choice in mangrove reforestation may influence the quantity and quality of long-term carbon sequestration and storage. Sci. Total Environ. 714, 136742 https://doi.org/10.1016/j.scitotenv.2020.136742.

Wu, W., Kuang, L., Li, Y., He, L., Mou, Z., Wang, F., Zhang, J., Wang, J., Li, Z., Lambers, H., Sardans, J., Penuelas, J., Geisen, S., Liu, Z., 2021. Faster recovery of soil biodiversity in native species mixture than in Eucalyptus monoculture after 60 years afforestation in tropical degraded coastal terraces. Global Change Biol. 27 (20), 5329–5340. https://doi.org/10.1111/gcb.15774.

Yan, S., Chong, P., Zhao, M., 2022. Effect of salt stress on the photosynthetic characteristics and endogenous hormones, and: a comprehensive evaluation of salt tolerance in Reaumuria soongorica seedlings. Plant Signal. Behav. 17 (1), 2031782 https://doi.org/10.1080/15592324.2022.2031782.

Ye, C., Li, M., Hu, J., Cheng, Q., Jiang, L., Song, Y., 2011. Highly reflective superhydrophobic white coating inspired by poplar leaf hairs toward an effective "cool roof". Energy Environ. Sci. 4 (9) https://doi.org/10.1039/c0ee00686f.

Yeh, H.-F., Lin, H.-I., Lee, C.-H., 2013. Assessment of spatial and temporal distribution of reference evapotranspiration and pan evaporation in Taiwan. Journal of Taiwan Agricultural Engineering 59 (3), 13–21. https://doi.org/10.29974/JTAE.201309_59(3).0002.

Yun, S., Ryu, D., Khim, J., 2019. Evaluation of the recyclability of construction and demolition waste fines as a garden substrate and soil amendment agent: a case study from the Republic of Korea. J. Mater. Cycles Waste Manag. 22 (2), 479–487. https://doi.org/10.1007/s10163-019-00941-2.

Zhang, J., 2020. Soil environmental deterioration and ecological rehabilitation. In: Study of Ecological Engineering of Human Settlements. Springer, Singapore. https://doi.org/10.1007/978-981-15-1373-2_2.

Zhang, M., Liu, Y., Han, G., Zhang, Y., Wang, B., Chen, M., 2020. Salt tolerance mechanisms in trees: research progress. Trees (Berl.) 35 (3), 717–730. https://doi.org/10.1007/s00468-020-02060-0.

Zhang, X., Ye, P., Wu, Y., Zhai, E., 2022. Experimental study on simultaneous heat-water-salt migration of bare soil subjected to evaporation. J. Hydrol. 609 https://doi.org/10.1016/j.jhydrol.2022.127710.

Zheng, L., Meng, Y., Ma, J., Zhao, X., Cheng, T., Ji, J., Chang, E., Meng, C., Deng, N., Chen, L., Shi, S., Jiang, Z., 2015. Transcriptomic analysis reveals importance of ROS and phytohormones in response to short-term salinity stress in Populus tomentosa. Front. Plant Sci. 6, 678. https://doi.org/10.3389/fpls.2015.00678.