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DIFFERENCES IN FINE ROOT FUNCTIONAL TRAITS AMONG FIVE TREE SPECIES IN COASTAL SALINE-ALKALI SOIL AND THE INFLUENCE OF SOIL PHYSICOCHEMICAL FACTORS

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Abstract

Fine roots (φ ≤ 2) play an important role in underground ecological processes in plants; however, their adaptation strategy to the soil environment is unclear. In this study, differences in fine root morphology, biomass, productivity, and decomposition and turnover rates of 5 different tree species: *Ligustrum lucidum*, *Salix matsudana*, *Sapium sebifera*, *Robinia pseudoacacia*, and *Quercus virginiana*, on newly reclaimed saline-alkali coastal land were investigated via the root drill continuous sampling method. Influencing soil physicochemical factors were also investigated. *R. pseudoacacia* had the greatest specific root length and surface area; root density and productivity were greatest in *L. lucidum* fine root decomposition was highest in *S. sebifera* and *S. matsudana* had the greatest turnover rate. Redundancy analyses of the relationships between fine root traits and soil physicochemical properties revealed that soil electrical conductivity, moisture, temperature, total N, and organic matter were the main factors influencing fine root traits. Based on differences in fine root functional traits and adaptation to coastal saline-alkali soils, the species recommended for restoration planting were ranked as LI, SA, SM, RP, and QV, in descending order. These findings provide a scientific basis and technical support for greening tree species screening and ecological restoration in coastal saline-alkali soils.

Key words: Fine root functional traits; Soil characteristics; Adaptability; Greening tree species; Coastal saline-alkali land

Introduction

Soil salinization has become an increasingly serious ecological, environmental, and social issue worldwide (Rengasamy, 2006; Chi *et al*., 2012; Bui, 2013; Jiang *et al*., 2016). There are approximately 950 million ha of saline-alkali land globally, of which around 35 million ha are in China, including in the newly reclaimed coastal area in eastern China. The soil in such areas is primarily formed by the deposition of seabed sediments via suction dredging. It is characterized by high salinity, elevated pH levels, nutrient deficiency, and high bulk density, which severely impacts plant growth. These conditions contribute to low vegetation coverage and poor landscape quality. Therefore, studies on the adaptative mechanisms of plants to the saline-alkali soil environment of newly reclaimed coastal land are required to facilitate the selection and cultivation of suitable greening tree species for its ecological restoration.

Fine roots are among the most active and sensitive plant organs. Their functional traits, including morphology, biomass, productivity, and decomposition and turnover rates, are significantly influenced by environmental factors such as soil water content (SWC), temperature, salinity, and nutrient availability (Persson, 1980; Steele *et al*., 1997; Burton *et al*., 2000; Cronan, 2003; Huang *et al*., 2008; Han *et al*., 2017; Xu *et al*., 2020; Feng *et al*., 2024). Fine roots exhibit considerable plasticity (Fitter *et al*., 1994; Hodge, 2006), allowing them to adapt to changing soil environments. They can enhance their adaptability by adjusting their morphological characteristics, biomass allocation patterns, and production and turnover rates in response to environmental changes (Burton *et al*., 2000; Zou *et al*., 2022; Sun *et al*., 2023). Therefore, investigating the relationship between the functional traits of fine roots and soil physiochemical parameters can help reveal the ecological adaptability of fine roots to specific soil environments.

Previous studies have shown that different tree species exhibit varying root characteristics (deep vs. shallow roots) and distribution patterns (vertical vs. horizontal) in soil environments. Due to the differing soil resource utilization strategies of fine roots—whether acquisitive or conservative—changes in soil conditions often lead to alterations in fine root distribution patterns. For instance, in drought-stressed environments, plants adapt by increasing root growth depth and adjusting their morphological traits such as root diameter, surface area,

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specific root length (SRL), and root length density (RLD) to better cope with the changing conditions (Cai *et al*., 2015; Proctor & He, 2017; Bo *et al*., 2018). In a high-salt stress environment, the water use efficiency of plants decreases. Due to the "salt island" effect in the root crown area, indicators such as the distribution, biomass, and morphological characteristics of fine roots are affected to varying degrees (Ashraf and Harris, 2004). Plants can adapt to salt-stressed environments by reducing the total biomass of fine roots and increasing that of dead fine roots (Hasegawa *et al*., 2000). Furthermore, fine roots can adapt to infertile soil by reducing their total length and SRL (Comas & Eissenstat, 2004).

The phenological characteristics (production, decomposition, and turnover) of fine roots also change with soil conditions (Jourdan *et al*., 2008; Finzi *et al*., 2015). However, there are very few studies on this aspect in high salinity environments; further research is therefore clearly warranted. Additionally, the majority of studies on the relationship between plant roots and soil environments have focused on arid areas (Mackie-Dawson *et al*., 1995), temperate forests (Schmid and Kazda, 2002), tropical and subtropical evergreen broad-leaved forests, and other natural ecosystems (Hendrick & Pregitzer, 1993; Xiao *et al*., 2008; Finér *et al*., 2011). Furthermore, most studies have only investigated above-ground parts of the forest ecosystem, without considering the role of the subsurface root system. Fine roots are the link between the above-ground plant parts and the soil. Due to the difficulty of sampling fine roots in the field, there is a lack of research on the ecological adaptability of roots from the perspective of underground roots. Moreover, in previous studies of forest ecosystems under more suitable growth environments, it is impossible to rule out the influence of biological and abiotic soil factors on plant functional traits. Therefore, the key factors affecting fine root functional traits are not fully understood.

The soil in newly reclaimed coastal areas serves as a blank control compared to that of natural forest ecosystems, allowing for a clearer understanding of how environmental factors influence root systems without the complexities found in established ecosystems. Additionally, there are relatively few studies on the relationship between plant roots and soil in saline-alkali land plantations in newly reclaimed coastal areas under humid climate conditions. Therefore, differences in biomass morphology (length ratio, length density, and surface area, etc.) and phenology (production [PRO], mortality, decomposition rate [DEC], and turnover rate [TUR]) among different tree species in this specific soil environment (high soil salinity, high pH, and low nutrients) are unclear. Reports on the relationship between the differences in morphological and phenological characteristics of fine root biomass (FRB) in different tree species and their adaptations to coastal saline-alkali soil are also lacking. Therefore, investigating the relationship between the fine root characteristics of different tree species and soil physicochemical properties in the saline-alkali soil of newly reclaimed coastal areas can help to reveal the adaptative strategies of different species. Furthermore, it can facilitate the screening of suitable greening tree species and guide the ecological restoration of saline-alkali land.

Therefore, this study aimed to investigate: (1) differences in fine root FRB, morphological characteristics, PRO, DEC, and TUR patterns among 5 tree species (*Ligustrum lucidum*, *Salix matsudana*, *Sapium sebifera*, *Robinia pseudoacacia*, and *Quercus virginiana*) in the saline-alkali soils of newly reclaimed coastal areas in China; (2) differences in the adaptation strategies among these species to the soil environment; and (3) key environmental factors affecting differences in fine root functional traits.

Materials and Methods

Study area: The experimental region is located in Shanghai Lingang New City, China (120° 53′–121° 17′ E, 30° 59′–31° 16′ N), as shown in Fig. 1. The area has a warm and humid subtropical oceanic climate, with abundant rainfall. The average annual temperature is 15.2–15.8°C, with an average annual precipitation of 900–1,050 mm, and an average monthly evaporation of 91.9 mm. The annual average relative humidity is 77–83% and the annual average wind speed is 2.9 m/s. This region has saline-alkali soil, with soil conductivity, pH, and bulk density in the ranges of 214–1,200 $\mu s \cdot cm^{-1}$, 8.42–9.08, and 1.24–1.46 $g \cdot cm^{-3}$, respectively. It has a low organic matter content (< 20 $g \cdot kg^{-1}$), total soil N contents of 0.84 ± 0.14 $g \cdot kg^{-1}$, and total soil P contents of 1.27 ± 0.08 $g \cdot kg^{-1}$. The underground water level is shallow (0.5–2.5 m) and the groundwater is highly mineralized. The total area of the experimental site is approximately 9,000 m^2; 900 m in length and 10 m in width. The experimental area mainly contains the following arbor trees: *Salix matsudana*, *Ligustrum lucidum*, *Robinia pseudoacacia*, *Quercus virginiana*, *Sapium sebiferum*, *Cinnamomum camphora* and *Melia azedarach*, and the shrubs *Eurya emarginata*, *Hibiscus hamabo*, *Amorpha fruticose*, *Photinia fraseri* and *Pittosporum brevicalyx* plants: *Humulus scandens*, *Astragalus sinicus*, *Solidago canadensis*, and *Suaeda salsa*.

Plot setting and sample collection: In July 2018, 5 different tree species were selected from primary, planted forests, including the deciduous species *R. pseudoacacia* (RP), *S. sebifera* (SA), and *S. matsudana* (SM), and the evergreen species *Q. virginiana* (QV) and *L. lucidum* (LI), ensuring that the average age, height, diameter at breast height, and crown width were consistent (Table 1). For each species, five individuals were chosen to form parallel samples, totaling 25 samples. The distance between each species was maintained at over 15 m to avoid interference between root systems.

Samples were collected via sequential coring. Soil drills (diameter [φ] = 5.0 cm, length = 10 cm) were sampled at equal intervals of five points along the center of the trunk to the crown boundary in three directions and at a sampling depth of 50 cm. The soil was divided into 0–10, 10–20, 20–30, 30–40, and 40–50 cm layers (Fig. 2) (Jian *et al*., 2015; Jiang *et al*., 2016). The electrical conductivity and temperature of each soil layer were then measured with the corrected EC Tester 11+ (Spectrum Technologies Inc., USA). After mixing three soil cores from the same soil layer at the same distance from the center of the tree trunk, the roots were selected. Subsequently, the root and soil samples were collected and placed in separate resealable bags, then transported back to the laboratory for storage at 4°C in a refrigerator (Li *et al*., 2021). Sampling was conducted every 2 months.

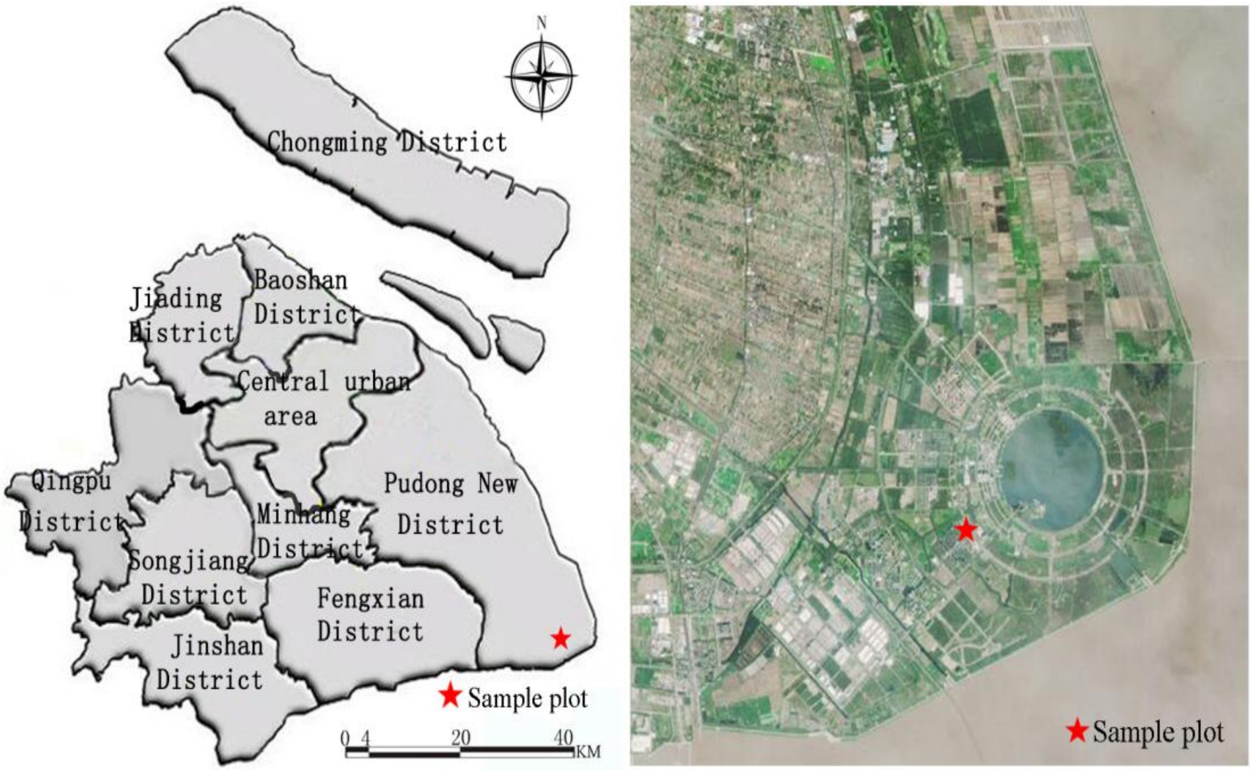

Fig. 1. Study area. The figures were created using an aeronautical reconnaissance coverage geographic information system (Arc GIS10.7) and Adobe Photoshop CS6.

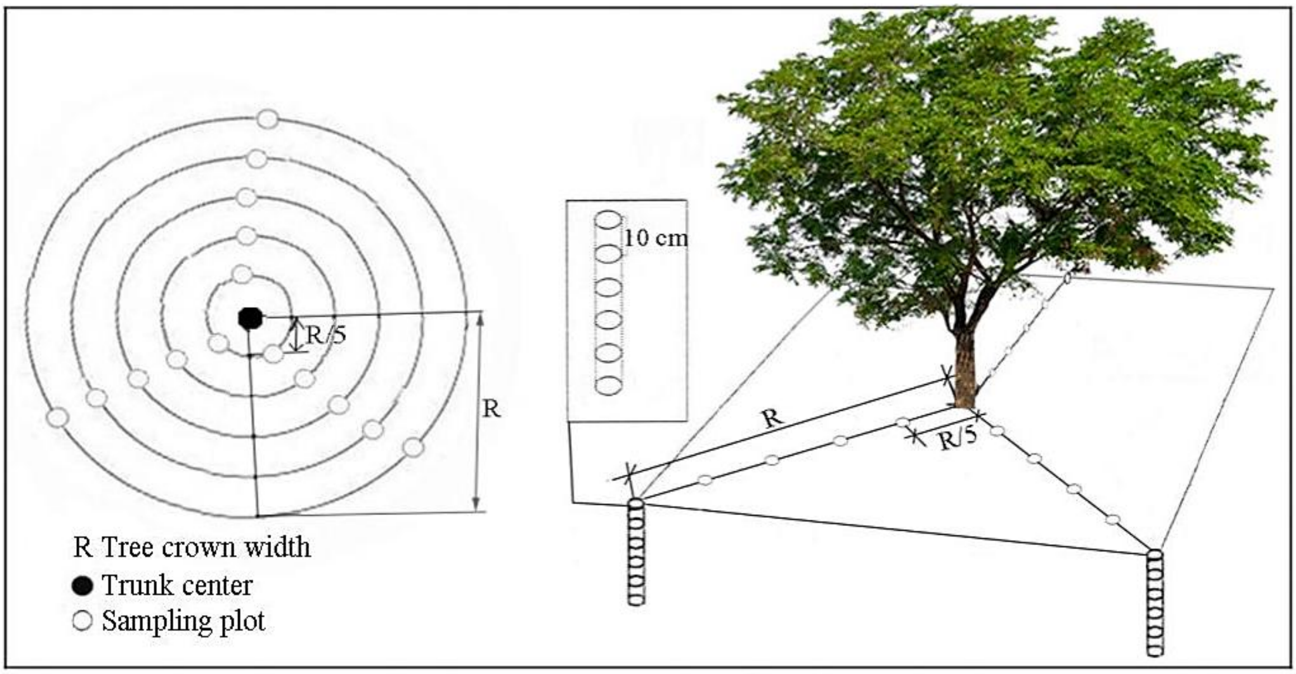

Fig. 2. Fine-root sampling diagram.

Table 1. General characteristics of the five different tree species.

Tree species	Abbreviation	Year (y)	Height (m)	DBH (cm)	Crown width (m)
Robinia pseudoacacia	RP	8	5.45 ± 0.25	10.38 ± 0.21	3.10 ± 0.30
Sapium sebiferum	SA	8	5.50 ± 0.30	11.11 ± 0.10	3.10 ± 0.50
Salix matsudana	SM	8	5.80 ± 0.50	11.43 ± 0.17	3.10 ± 0.20
Quercus virginiana	QV	8	5.10 ± 0.45	10.56 ± 0.15	3.30 ± 0.30
Ligustrum lucidum	LI	8	5.37 ± 0.31	10.01 ± 0.27	3.31 ± 0.25

N.B. RP: *Robinia pseudoacacia*, LI: *Ligustrum lucidum*, SA: *Sapium sebiferum*, SM: *Salix matsudana*, QV: *Quercus virginiana*

Root ingrowth cores: Fine root growth was measured using ingrowth cores (Persson, 1980; Majdi *et al*., 2008). The rootless soil was placed into a nylon net bag (length = 50 cm, φ = 5 cm), with a 2-mm mesh size. The nylon bag was then placed in the hole generated by the original soil core, and the soil in the core was firmly stepped on by foot. A PVC pipe (φ = 5 cm, length = 2 cm) was finally used to mark the position of the soil core. After 12 months, all ingrown bags that were established for the five tree species were removed. The full excavation method was adopted to collect the soil core. An iron shovel was used to excavate around the nylon bag of the inner soil core, and the root system connecting the nylon net and soil was cut using a sharp soil knife. After the soil core was removed, roots were collected according to the five layers of 0–10, 10–20, 20–30, 30–40, and 40–50 cm, and quickly packed into plastic bags and returned to the laboratory for preservation.

Fine root processing: Root systems were rinsed clean in clear water using a 40-mesh sieve (with an aperture of 0.42 mm). After the surface moisture of the roots was blotted dry with absorbent paper, they were placed in self-sealing bags and stored in a refrigerator at 4°C. Once all samples were cleaned, all fine roots with a φ of ≤ 2 mm in the root systems were selected using tweezers and vernier calipers (Wang *et al*., 2022). Live and dead fine roots were distinguished according to their characteristics such as appearance, color, odor, and elasticity (Noguchi *et al*., 2007; Imada *et al*., 2015; Ma & Chen, 2017).

Fine root index calculation: The root scan analyzer Win-RHIZO 2005C (Regent Instruments Inc., Quebec, Canada) was used to measure the average diameter, surface area), volume, and length of the fine roots. The scanned fine roots were placed in an oven at 80°C and dried to a constant weight. The following indices were then calculated for each soil layer: FRB, root tissue density (RTD), RLD, SRL, specific root surface area (SRSA), and root surface area density (RSAD) (Brédoire *et al*., 2016; Li *et al*., 2021) (Table 2). The formulae were as follows:

Table 2. Abbreviations of fine root traits.

Fine root traits/Unit	Abbreviation
Length (cm)	L
Surface area (cm^2)	S
Volume (cm^3)	V
Diameter (mm)	D
Fine root biomass (g·m^{-2})	FRB
Root tissue density (g·cm^{-3})	RTD
Fine root length density (m·m^{-3})	RLD
Specific root length (m·g^{-1})	SRL
Specific root surface area (cm^2·g^{-1})	SRSA
Root surface-area density (m^2·m^{-3})	RSAD
Productivity (g·m^{-2}·y^{-1})	PRO
Decomposition rate (g·m^{-2}·y^{-1})	DEC
Turnover rate (times·y^{-1})	TUR

$$FRB\ (\mathrm{g\cdot m^{-2)}} = m\ (g)\times 10^4/[\pi(d/2)^2] \quad (1)$$

$$RTD\ (\mathrm{g\cdot cm^{-3}}) = m\ (g)/v\ (cm^3) \quad (2)$$

$$RLD\ (\mathrm{m\cdot m^{-3}}) = l\ (m)\times 10^6/[\pi(d/2)^2\times h] \quad (3)$$

$$SRL\ (\mathrm{m\cdot g^{-1}}) = l\ (m)/m\ (g) \quad (4)$$

$$SRSA\ (\mathrm{cm^2\cdot g^{-1}}) = s\ (cm^2)/m\ (g) \quad (5)$$

$$RSAD\ (\mathrm{m^2\cdot m^{-3}}) = s\ (m^2)\times 10^6/[\pi(d/2)^2\times h] \quad (6)$$

where *m* is fine root mass, *v* is fine root volume, *l* is fine root length, *s* is fine root surface area, *d* is the diameter of soil core, and *h* is the length of soil core.

Fine PRO: The fine roots growing in root-free soil cores over a specific period are considered the fine root PRO of that time frame (Wang *et al*., 2022). In this study, fine root PRO was calculated by measuring the biomass of fine roots that grew within the soil cores over a 12-mo period, as follows:

$$\mathrm{PRO} = \mathrm{FR}_L + \mathrm{FR}_D \quad (7)$$

where PRO represents the annual net productivity of fine roots (g·m^{-2}·y^{-1}), and FR_L and FR_D denote the biomass of live and dead fine roots, respectively, within the root-free soil columns over the 12 months.

DEC and TUR: Fine root DEC was assessed using the nylon mesh bag method (Fahey *et al*., 1988). In the laboratory, the soil on the surface of the root was washed off with water, and fine roots with a φ ≤ 2 mm were selected. The fine root samples were then dried in an oven at 80°C until a constant weight was achieved. The dried samples were cut into segments of ≤ 1 cm in length and thoroughly mixed. For each species, 5 g of fine root samples were placed in decomposition bags (10 cm × 15 cm, with a pore size of 0.12 mm), which were then randomly buried in the soil at a depth of 10–20 cm in each plot. A total of 60 decomposition bags were placed in each species plot and labeled. Every 2 months, five decomposition bags from each species were collected to calculate the fine root DEC.

The DEC of fine roots is characterized by the mass residue rate: the proportion of root dry mass residue in each stage to the initial dry weight. The root DEC constant (*k*) was calculated using the negative exponential decay model (Olson, 1963), using the following formula:

$$W_t = W_0\, e^{-kt} \quad (8)$$

where *t* is the decomposition time (unit: d), W_0 is the initial fine root mass (g), and *k* is the annual decomposition rate constant (kg^{-1} kg^{-1} d^{-1}). The decomposition time of 50% is $t_{50\%} = \ln(W_0/50)/k$, and the decomposition time of 95% is $t_{95\%} = \ln(W_0/5)k$

The fine root TUR was calculated as follows (Shan *et al*., 1993):

$$M = X_{max} - X_{min} + D \quad (9)$$

$$P = Y_{max} - Y_{min} + M \quad (10)$$

$$TUR = P/Y \quad (11)$$

where *M*, *P*, *D*, and *TUR* are the annual mortality, annual production volume, annual decomposition volume, and turnover rate (times·y^{-1}), respectively. X_{max} and X_{min} were the maximum and minimum values, respectively, of the existing amount of dead fine roots, and Y_{max}, Y_{min}, and *Y* were the maximum, minimum, and average values of the existing amount of live fine roots, respectively.

Vertical root distribution coefficient: Based on the root system distribution characteristics of the different tree species (Gale and Grigal, 1987), the fine root decay coefficient β was calculated using a root vertical distribution model, as follows:

$$Y = 1\text{-}\beta^{d} \quad (11)$$

where Y is the cumulative percentage of root biomass from the surface to a certain depth, d is the depth of the soil layer (cm), and β is the vertical root distribution coefficient. The value of β mainly characterizes the relationship between root vertical distribution and soil depth. The higher the β value, the larger the percentage of the roots in deep soil, and the smaller the β value, the closer the plant roots are to the surface.

Soil physical and chemical properties: During fine root collection at each site, the portable conductivity meter EC Tester 11+ (Spectrum Technologies Inc., USA) and a pH meter (Spectrum Technologies Inc.) were used to measure the electrical conductivity (EC), temperature, and pH of each of the five soil layers. Soil water content (SWC) was determined by the oven-drying method, soil organic matter (SOM) by the potassium dichromate external heating method, total N (TN) by the Kjeldahl method, and total P (TP) by the molybdenum-antimony anti-colorimetric method; following the methods described by Bao (Bao, 2005; Jiang *et al*., 2016; Xu *et al*., 2020).

Data analysis: FRB, RTD, SRL, RLD, SRSA, RSAD, PRO, DEC, and TUR were analyzed in Microsoft Excel (Microsoft Corporation, Redmond, WA, USA) to obtain the mean ± standard deviation. The mean ± standard deviation SWC, temperature, EC, pH, TN, TP, and SOM were also determined. Statistical analyses are conducted using Statistical Product and Service Solutions (SPSS) version 16.0 (SPSS, Chicago, IL, USA). One-way ANOVA and the least significant difference method were employed to analyze the differences in FRB and morphological characteristics among species. Additionally, two-way ANOVA was used to assess the effects of species, soil depth, and their interaction with FRB, morphological characteristics, PRO, and TUR. The normality of the root trait data was tested at the significance level of 0.05 via the Kolmogorov-Smirnov test. Logarithmic transformation was performed on the root trait data that failed the normality test. The least square method was used for linear fitting. The relationships between fine root indices and soil physiochemical parameters were analyzed using SPSS 21.0 (IBM Corp., Armonk, NY, USA) and R software. The analysis diagrams were drawn using Origin Pro 9.0 software (Origin Lab., Northampton, MA, USA).

Results

Fine root morphological characteristics: The average fine root length, surface area, volume, diameter, RLD, SRL, SRSA, and RSAD exhibit distinct distribution characteristics. RLD was the highest in LI (18,533.45 $m\cdot m^{-3}$), and the lowest in RP (6,413.50 $m\cdot m^{-3}$) (Fig. 3). LI had the highest RSAD (22.08 $m^{2}\cdot m^{-3}$), while QV had the lowest (6.16 $m^{2}\cdot m^{-3}$). The vertical distributions of RLD and RSAD differed among the species. The RLD and RSAD of LI, SA, and SM were the highest in the soil surface layer, and then gradually decreased with increasing soil depth. The RSAD of RP gradually decreased from the 0–10 to 30–40 cm layer, and then gradually increased in 40–50 cm layer. The RSAD of SA and SM decreased with increasing soil depth, while the RSAD of QV gradually increasing from the 0–10 to 30–40 cm layer, and then gradually decreased at the 40–50 cm layer.

The overall SRL and SRSA trends were consistent among species (Fig. 3). The SRL (135.38 $m\cdot g^{-1}$) and SRSA (1,141.07 $cm^{2}\cdot g^{-1}$) of RP were the greatest. The smallest SRL (39.17 m g^{-1}) and SRSA (315.22 cm^{2} g^{-1}) were recorded in QV. The vertical distribution patterns of SRL and SRSA differed among species. The SRL and SRSA of LI, SA, and QV gradually increased from the 0–10 cm to 40–50 cm layer, peaking at the 40–50 cm layer. The SRL and SRSA of RP and SM were the greatest in the 20–30 cm layer.

Fine root biomass distribution characteristics: There were also significant differences in the biomass and total biomass of live fine roots ($p<0.01$), and in the biomass of dead fine roots ($p<0.05$). The interaction between tree species and soil depth had a significant effect on the total FRB and live FRB ($p<0.01$), and on the dead FRB ($p<0.05$). The largest live FRB was recorded in LI (231.68 $g\cdot m^{-2}$), with the smallest in RP (73.78 $g\cdot m^{-2}$). SM and RP had the largest and smallest dead FRB of 102.87 $g\cdot m^{-2}$ and 3.27 $g\cdot m^{-2}$, respectively. The largest and smallest FRB was recorded in LI (273.42 $g\cdot m^{-2}$), and RP (77.05 $g\cdot m^{-2}$), respectively (Fig. 4).

The vertical distribution of FRB differed among species. In the soil layer of 0–10 cm, the FRB of RP was 21.20 $g\cdot m^{-2}$, accounting for 27.51% of the total FRB, while that of SA, SM and, LI was 46.43 $g\cdot m^{-2}$ (29.78%), 78.80 $g\cdot m^{-2}$ (32.23%), and 116.37 $g\cdot m^{-2}$, (42.56%), respectively. The maximum FRB of QV was 53.44 $g\cdot m^{-2}$ in the 10–20 cm layer, accounting for 26.29% of the total FRB. The FRB of the RP, SA, SM, QV, and LI was mainly distributed in the 0–30 cm layer, with percentages of the total FRB at 61.86%, 75.15%, 69.20%, 62.93%, and 78.15%, respectively.

The vertical root distribution coefficients of QV (0.9693) and RP (0.9657) were the highest, indicating that these are deep-rooted species. However, the vertical root distribution coefficients of LI, SM, and SA were lower at 0.9607 0.9599, and 0.9556, respectively, revealing that they were shallow root species with a lower root growth depth (Table 3).

Table 3. Vertical root distribution coefficient of total fine root biomass for the five tree species.

Tree species	Vertical root distribution coefficient (β)
RP	0.9657
SA	0.9556
SM	0.9599
QV	0.9693
LI	0.9607

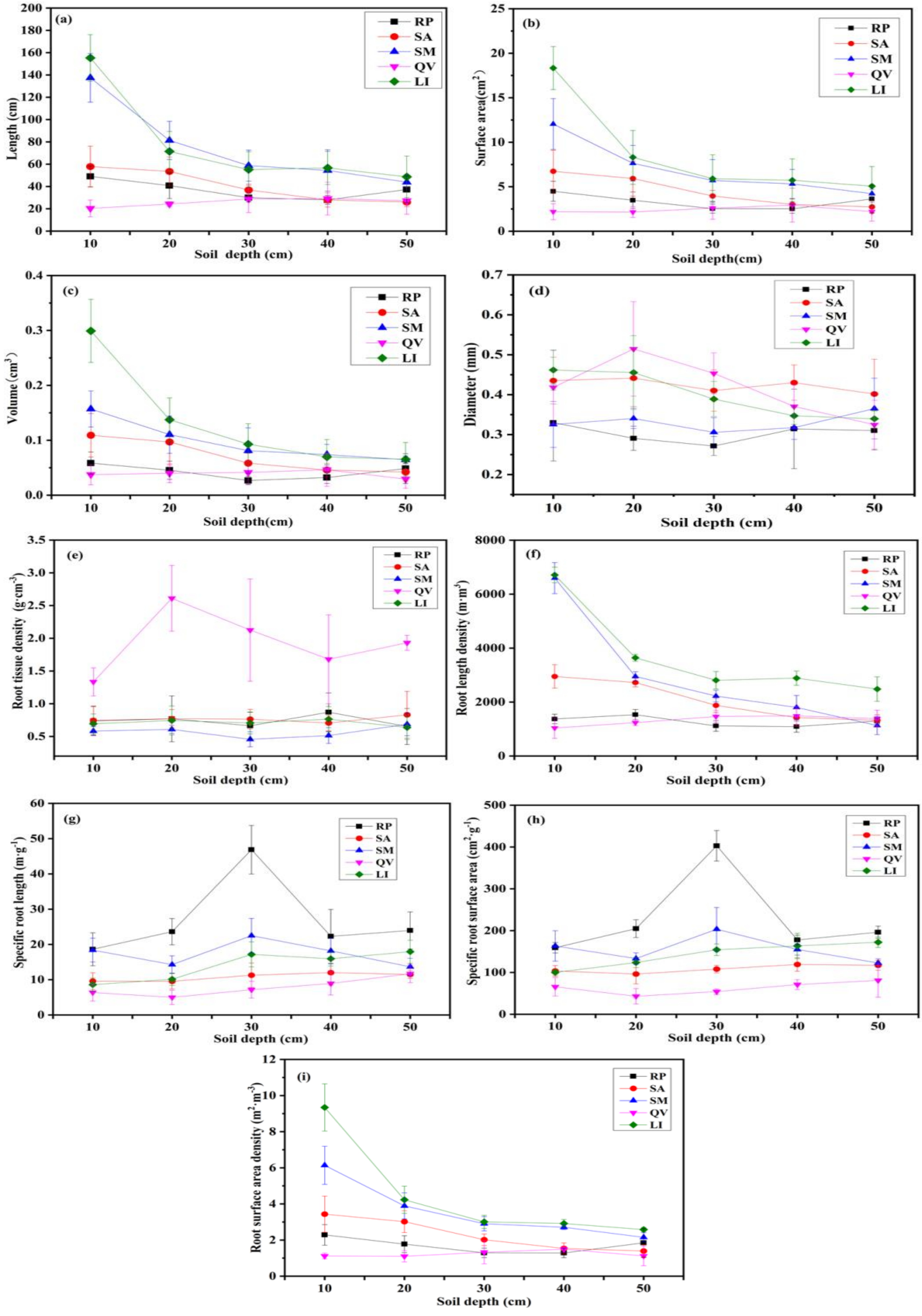

Fig. 3. Changes in the fine root morphological characteristics of the five tree species at different soil depths.
N.B. RP: *Robinia pseudoacacia*, LI: *Ligustrum lucidum*, SA: *Sapium sebiferum*, SM: *Salix matsudana*, QV: *Quercus virginiana.*

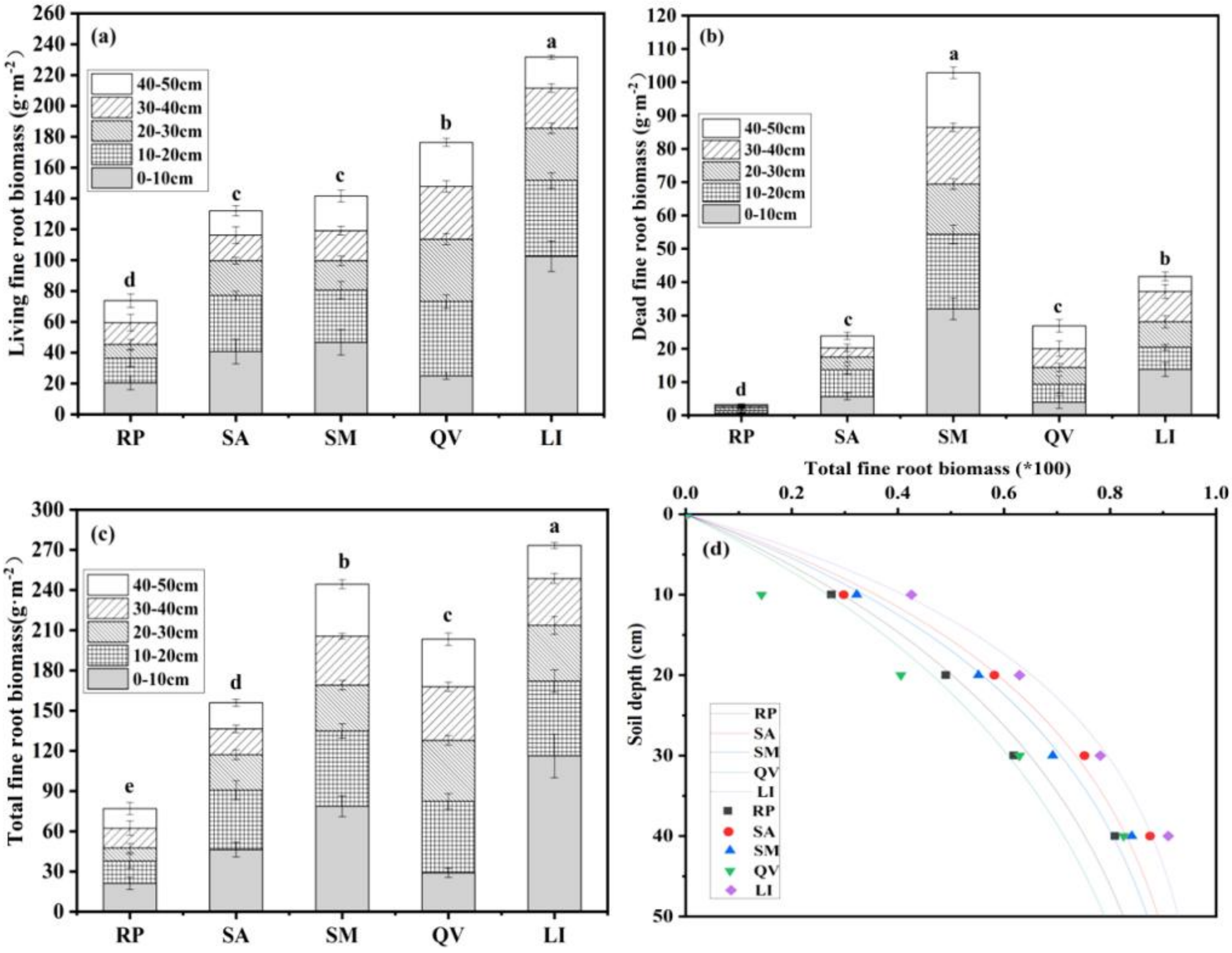

Fig. 4. Fine root biomass comparisons among the five tree species.
N.B. RP: *Robinia pseudoacacia*, LI: *Ligustrum lucidum*, SA: *Sapium sebiferum*, SM: *Salix matsudana*, QV: *Quercus virginiana*. Different lowercase letters indicate $p<0.05$.

Table 4. Results of ANOVA of the effects of tree species and soil depths on fine root productivity.

Parameter	Source of variation					
	Tree species		Soil depth		Tree species × Soil depth	
	F	*P*	*F*	*P*	*F*	*P*
Productivity (g·m^{-2}·y^{-1})	7.56	＜0.01**	1.521	Ns	1.39	Ns

Note: **At 0.01 level (double side) significant difference, * at 0.05 level (double side) significant difference

The FRB horizontal distribution pattern differed among species (Fig. 5). The horizontal distribution ranges of the RP and SA root systems were the largest, followed by those of SM and QV, with the smallest recorded for LI.

Fine root productivity: Fine root PRO significantly differed among species ($p<0.01$). Soil depth did not have a significant effect on fine root PRO ($p>0.05$), neither did the interaction between species and soil depth ($p>0.05$, Table 4). The fine root PRO of the five tree species ranged from 17.80 to 166 g·m^{-2}·y^{-1}, among which, that of LI was the highest (166.00 g·m^{-2}·y^{-1}), and that of RP was the lowest (17.80 g·m^{-2}·y^{-1}) (Fig. 6). The fine root PRO of the five species was the highest in the 0–30 cm layer, consistent with the FRB vertical distribution.

Fine root decomposition and turnover rates: With increasing decomposition time, the fine root residual quality gradually decreased (Fig. 7). At the early stage of decomposition (0–60 d), the fine root decomposition quality was the largest in each species. Among them, RP had the smallest residual value, which was 2.27 g, with a residual rate of 45.47%. The fine root residual mass of SA and LI was 2.99 g and 3.79 g, with residual rates of 59.87% and 75.86%, respectively. The residues of QV and SM were generally the same; 4.14 g and 4.13 g, respectively, with residue rates of 82.89% and 82.72%, respectively. Within 60 d, the decomposition mass of the species was ranked as follows: RP > SA > LI > QV > SM. At the middle stage of fine root decomposition (180 d), there was an obvious gradient pattern, and the fine root residue was ranked as: SM > QV > LI > RP > SA. At the late stage of fine root decomposition (180–360 d), the residual mass decreased significantly, and the residual masses of SM, QV, LI, RP, and SA were 2.22, 1.92, 1.76, 0.57, and 0.39 g, respectively, with residual rates of 44.45, 38.35, 35.18, 11.92, and 7.01%, respectively.

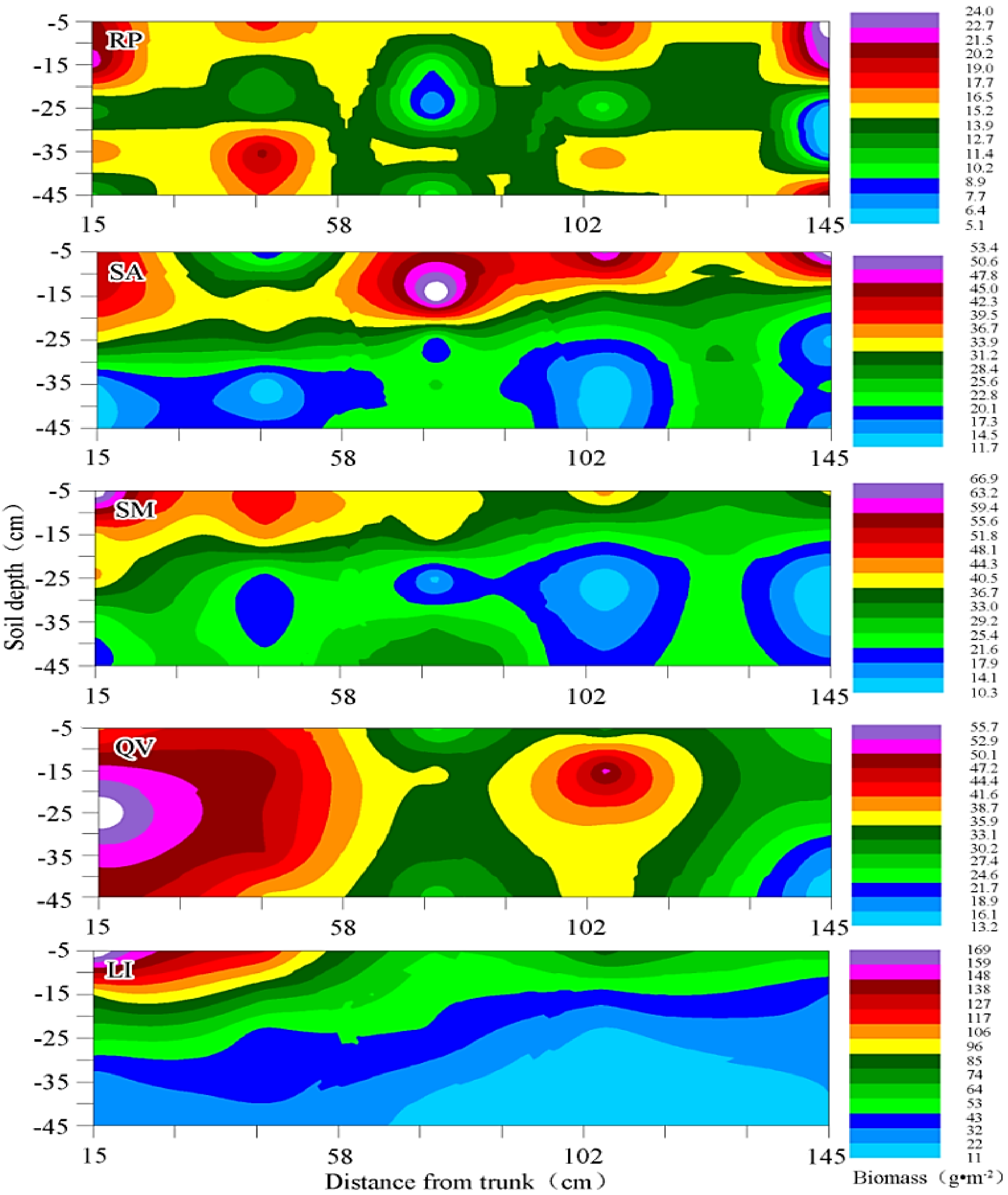

Fig. 5. Horizontal distribution of fine root biomass in the five tree species.
N.B. RP: *Robinia pseudoacacia*, LI: *Ligustrum lucidum*, SA: *Sapium sebiferum*, SM: *Salix matsudana*, QV: *Quercus virginiana.*

A negative exponential decay model was used to linearly fit the fine root decomposition quality of the 5 species. The DEC of SA, RP, QV, LI, and SM was 0.007, 0.005, 0.003, 0.003, and 0.002 $kg\cdot kg^{-1}\cdot d^{-1}$, respectively (Table 5). The highest DEC was recorded for SA and the lowest for SM. SA, RP, LI, QV, and SM needed 68, 92, 195, 201, and 315, respectively, for the decomposition amount to reach 50%, and 421, 528, 963, 969, and 1,466 d, respectively, to reach 95%.

The effect of species on fine root TUR was significant ($p<0.01$), but the effect of soil depth was not significant ($p>0.05$), neither was the interaction between species and soil depth ($p>0.05$) (Table 6). The fine root TUR of SM was the highest (1.05 $times\cdot y^{-1}$), while that of RP (0.24 $times\cdot y^{-1}$) was the lowest (Fig. 8).

Relationship between fine root characteristics and soil physiochemical factors: The redundancy analysis (RDA) method was used to rank the fine root characteristics and soil physiochemical factors, resulting in a two-dimensional ordination diagram (Fig. 9). The statistical parameter of the first and second principal component axis was 0.588 and 0.112, respectively, accounting for 58.8% and 70.0% of the total parameters respectively, potentially reflecting over half of the relevant information of the variables. Moreover, the first two axes could accurately express the relationship between fine root characteristics and soil physiochemical factors. The RDA analysis showed that RLD and RASD were significantly negatively correlated with soil EC and SWC ($p<0.05$), and significantly positively correlated with soil T and TN ($p<0.05$) (Fig. 9). Soil EC, SWC, T, and TN were the main soil physiochemical factors affecting the morphological characteristics of fine roots.

There was a significant negative correlation between fine root PRO and soil EC ($p<0.05$), and significant positive correlation between soil T and TN ($p<0.05$). This indicated that soil EC, SWC, and TN were the main environmental factors associated with fine root PRO. The DEC was only significantly positively correlated with SWC ($p<0.05$), while the TUR was only significantly positively correlated with SOM, TN, and T ($p<0.05$).

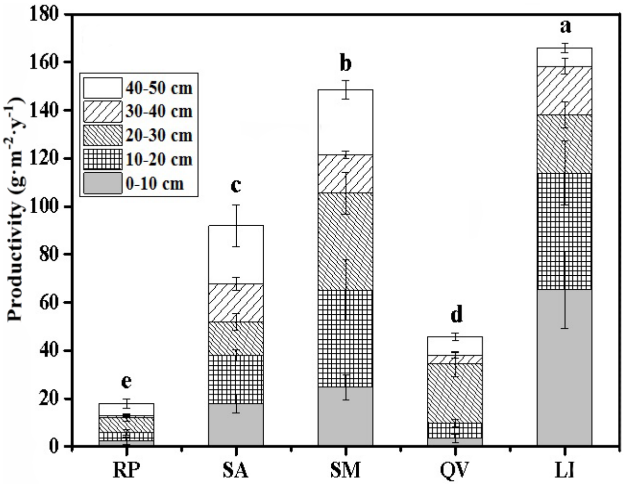

Fig. 6. Fine root PRO in the five tree species.
N.B. RP: *Robinia pseudoacacia*, LI: *Ligustrum lucidum*, SA: *Sapium sebiferum*, SM: *Salix matsudana*, QV: *Quercus virginiana*. Different lowercase letters indicate $p<0.05$.

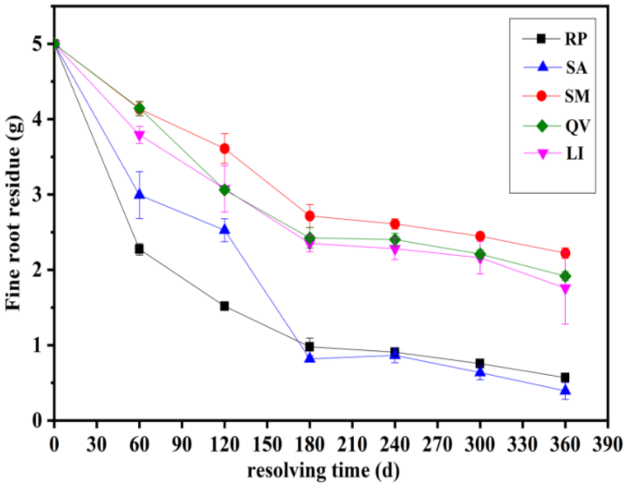

Fig. 7. Variations in the remaining mass during fine root decomposition in the five species.
N.B. RP: *Robinia pseudoacacia*, LI: *Ligustrum lucidum*, SA: *Sapium sebiferum*, SM: *Salix matsudana*, QV: *Quercus virginiana*.

Table 5. Regression equations, and time and residual rate parameters, of fine root decomposition in the five tree species.

Tree species	Equation	Decision coefficient (R^2)	Decomposition coefficient ($kg\cdot kg^{-1}\cdot d^{-1}$)	Measured value (%)	Theoretical value (%)	50% Time (d)	95% Time (d)
RP	$y=69.990e^{-0.005x}$	0.91	0.005	11.92	11.57	68	528
SA	$y=95.155e^{-0.007x}$	0.95	0.007	7.01	7.66	92	421
SM	$y=93.776e^{-0.002x}$	0.94	0.002	44.45	45.65	315	1466
QV	$y=91.27e^{-0.003x}$	0.92	0.003	38.35	31.00	201	969
LI	$y=89.627e^{-0.003x}$	0.94	0.003	35.18	30.44	195	963

Table 6. Results of ANOVA of the effects of tree species and soil depths on fine root turnover rate.

Parameter	Source of variation					
	Tree species		Soil depth		Tree species × Soil depth	
	F	*P*	*F*	*P*	*F*	*P*
Turnover rates ($times\cdot y^{-1}$)	6.95	<0.01**	1.755	Ns	1.33	Ns

Note: **At 0.01 level (double side) significant difference, * at 0.05 level (double side) significant difference

Discussion

Fine root morphological characteristics: Tree species have specific root characteristics, which differ considerably among species regarding morphology and function. Root morphological characteristics are directly related to the function of fine roots (Pregitzer *et al*., 2002). The diameter, surface area, SRL, and RLD can be used to characterize the main morphological characteristics of fine roots, determine the SWC and nutrient uptake ability, and indicate the root adaptation strategies to the soil environment. In this study, surface area, RLD, and RSAD were the largest in LI, and gradually decreased with increasing soil depth (Fig. 3). This indicated that LI fully utilized the SWC and nutrients in each soil layer and expanded its root foraging range in the vertical soil space. The surface area, RLD, and RSAD of QV were the smallest in the different soil layers, revealing that this species had the weakest blow-fill resource utilization capacity.

Fine root diameter and length were the main indicators reflecting the resource utilization strategy. Roots with a small diameter and large length are thought to have a higher spatial development and nutrient absorption capacity, conducive to expanding the root growth space (Eissenstat, 1992, 1991). However, a larger diameter, smaller SRL, and weak root expansion ability indicates a resource-conserving species (Ryan *et al*., 1996; Weemstra *et al*., 2016). Among the 5 tree species of the present study, RP had the smallest diameter and largest SRL, indicating that it was a resource-harvesting tree species; therefore, its root system had a higher soil water and nutrient utilization efficiency (Zou *et al*., 2022; Feng *et al*., 2024). In contrast, QV, had the largest fine root diameter and smallest SRL, indicating that it was a resource-conserving species. In addition to the influence of the soil environment, the varying strategies of the root systems of different tree species on soil resource utilization may be determined by their biological characteristics.

Fine root biomass: FRB not only represents the utilization efficiency of soil water and nutrients by plants, but also directly reflects the distribution of photosynthetic products from the above-ground part of plants to the below-ground parts, and is often used as an index to evaluate plant adaption to stressful environments (Eissenstat and Yanai, 1997). In this study, the FRB significantly differed among species; LI had the largest (273.42 g·m^{-2}), and RP the smallest (77.05 g·m^{-2}), indicating that LI had the strongest adaptability to the saline-alkali soil environment. The vertical root distribution coefficient indicates the root distribution in soil; the greater the value, the deeper the root distribution[43]. The vertical root distribution coefficients of QV and RP were the highest, indicating that they are deep-rooted species, which is conducive to absorbing water and nutrients from deep soil. However, the vertical root distribution coefficients of LI, SM, and SA were lower, revealing that their root growth depth was shallower, and classifying them as shallow-rooted species. Additionally, there was also a difference in the FRB horizontal distribution pattern among species (Fig. 5). The horizontal foraging range of RP and SA was the largest, indicating that they possess the ability to quickly absorb SWC and nutrients laterally, reflecting the pioneering characteristics of their root systems. The horizontal FRB distribution range was the smallest in LI, SM, and QV. These conservative characteristics indicate these species have adapted to the poor quality saline-alkali soil environment by preserving nutrients and resources. Collectively, these findings reveal the adaptation strategies of the five tree species to a saline-alkali soil environment.

The FRB vertical distribution differed among species; however, it generally decreased with increasing soil depth, consistent with previous findings (Ruess *et al*., 2003). The FRB of was mainly concentrated in the 0–30 cm soil layer; accounting for 49.05, 57.18, 55.18, 40.57, and 62.93% of the total FRB of RP, SA, SM, QV, and LI, respectively, consistent with previous research. For example, Jackson *et al*., (1997) found that the FRB distribution in the northern cold zone was the shallowest in the 0–30 cm soil layer, accounting for 80–90% of the total biomass (Jackson *et al*., 1997). The root distribution was the deepest in the temperate zone, where the FRB in the 0–30 cm soil layer accounted for 50% of the total biomass.

In this study, the vertical distribution of FRB gradually decreased with increasing soil depth for all species (except for QV). There are several potential reasons for this. First, there was a gradual decrease in soil nutrients with increasing soil depth (Weemstra *et al*., 2017). Second, the surface texture of the soil was loose, with good permeability, which is conducive to the growth of fine roots and soil nutrient absorption. Third, soil temperature gradually decreased with soil depth, which was one of the reasons for the reduced FRB (Steele *et al*., 1997). Fourth, to reduce energy expenditure, plants distribute carbohydrates obtained from photosynthesis to the fine roots at the soil surface (Lai *et al*., 2016). Fifth, the root system had a greater distribution in the surface layer of the soil, potentially to avoid the influence of high salinity on roots in deeper soil, an adaption strategy to high salinity soil environments. Finally, the FRB distribution pattern may also be related to the species biological characteristics, explaining why the five tree species showed different adaptation strategies to the saline-alkali soil environment.

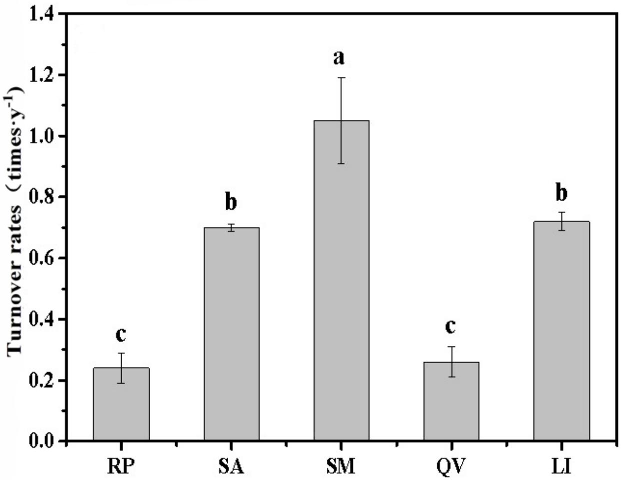

Fig. 8. Fine root turnover rate of the five tree species.
N.B. RP: *Robinia pseudoacacia*, LI: *Ligustrum lucidum*, SA: *Sapium sebiferum*, SM: *Salix matsudana*, QV: *Quercus virginiana*. Different lowercase letters indicate p<0.05.

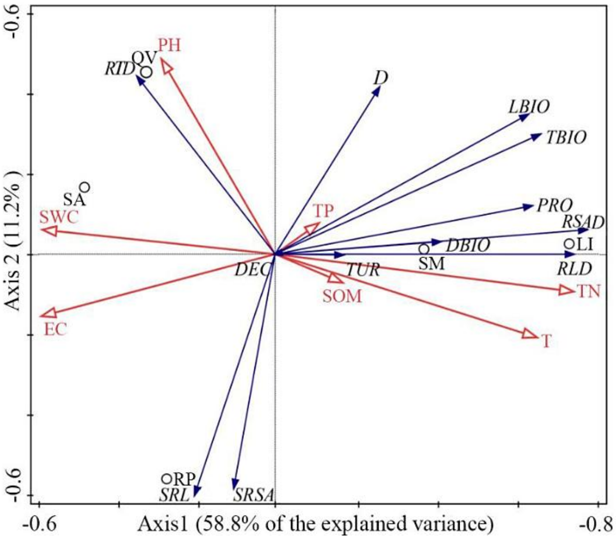

Fig. 9. Redundancy analysis ordination plot.
N.B. RP: *Robinia pseudoacacia*, LI: *Ligustrum lucidum*, SA: *Sapium sebiferum*, SM: *Salix matsudana*, QV: *Quercus virginiana*. EC: electrical conductivity; SWC: soil water content; T: temperature: SOM: soil organic matter: TN: total N; TP: total P. LBIO: living biomass; DBIO: dead biomass; PRO: productivity; DEC: decomposition rate; TUR: turnover rate; D: fine root

diameter; RTD: root tissue density; RLD: root length density; SRL: specific root length; SRSA: specific root surface area; RSAD: root surface area density.

Fine root productivity: Fine root PRO is related to soil nutrients, climatic conditions, and fine root biological characteristics (Ma & Chen, 2017; Tan *et al.*, 2017; Xiong *et al.*, 2017). It is also closely related to soil depth (Burton *et al.*, 2000; Usman *et al.*, 2000; Tan *et al.*, 2017). In this study, the fine root PRO of the five species ranged from 17.80 to 166.00 $g \cdot m^{-2} \cdot y^{-1}$, among which that of LI was the highest, while that of RP was the lowest. The fine root PRO of five tree species differed from that of forest ecosystems in other study areas such as the Mexican desert (0.031 $mg \cdot ha^{-1} \cdot y^{-1}$ in the dry season and 0.315 $mg \cdot ha^{-1} \cdot y^{-1}$ in the rainy season) and European pine forests (159–183 $g \cdot m^{-2} \cdot y^{-1}$) (Pavón & Briones, 2000; Hertel & Leuschner, 2002). The main potential reasons for these differences are: (1) tree species and age differed among studies, implying differences in fine root growth; (2) variations in site conditions, resulting in large differences in temperature, precipitation, and soil nutrients. The present study area was located in the subtropical zone and on coastal blow-fill soil, with high salinity and low nutrients, resulting in a lower root PRO; and (3) differences in experimental design such as root sampling methods, sampling intervals, and live and dead fine root identification methods, which could have led to differences in fine root growth. Fine roots were affected by SWC, temperature, and nutrients, and their PRO also varied vertically. Previous studies in coastal sandy plantations and forests found that the fine root PRO was mainly distributed in 0–30 cm soil layers (Jiang, 2016; Sun *et al.*, 2023). In the present study, it was mainly concentrated in the 0–30 cm layer, consistent with these previous findings.

Fine root decomposition and turnover rates: In addition to the biological characteristics of the trees, other factors affecting fine root decomposition are soil physicochemical properties (Guo *et al.*, 2023), topography soil microorganisms, and other environmental factors. Fine root decomposition occurs in two stages: fast and slow decomposition (McClaugherty *et al.*, 1985; Arunachalam *et al.*, 1996; Yang *et al.*, 2004). In this study, the fine root decomposition of the 5 tree species also presented fast and slow stages. The DEC was higher in the early stage (1–180 d), which may be due to the following reasons: (1) this stage occurred in spring and summer; with higher temperatures and sufficient rainfall, SWC enabled fine root leaching and significantly promoted decomposition; and (2) there was a large proportion of soluble substances such as carbohydrates in the fine roots, which led to a faster DEC. Furthermore, high temperature and abundant rainfall in the early decomposition stage can create a suitable environment for soil organisms, promote soil biological respiration, and improve soil biological vitality, which is conducive to fine root decomposition. Moreover, abundant precipitation can promote root rot and thus accelerate decomposition (Jilling *et al.*, 2018; Yuan *et al.*, 2018).

In the late stage of decomposition (180–360 d), fine root DEC was decreased, potentially due to: (1) increased proportion of organic components that were difficult to decompose (lignin, cellulose, tannin, polyphenols, and acid-insoluble substances) (Hendricks *et al.*, 2000) and (2) relatively low temperatures and precipitation in autumn and winter. Because the soil in this study area was considerably salinized, the DEC will be lower than that in areas with a greater abundance of soil microorganisms, to a certain extent. Additionally, the DEC of fine roots is also related to C and N contents, and C/N ratio. For example, Usman *et al.* (2000) found that the initial N concentration of fine roots was strongly related to DEC. In fine roots, DEC is significantly positively correlated with the contents of N, P, and Ca^{2+}, and negatively correlated with the C/N ratio (Hobbie, 2000; Chen *et al.*, 2002, 2004). It can be concluded that fine root DEC differed among the species in the present study, which may be due to the soil environment, and the fine root structure and other characteristics.

The time required for 95% decomposition of fine roots per species was as follows: SA, 421 d; RP, 528 d; LI, 963 d; QV, 969 d; and SM, 1,466 d (Table 5). However, these values were significantly different compared to other tree species in the same climatic zone. For the 7 tree species in the subtropical forests of Fujian (*Tsoongiodendron odorum*, *Schima superba*, *Castanopsis fabri*, *Cinnamomum chekiangense*, *Altingia gracilipes*, *Pinus massoniana*, and *Cunninghamia lanceolata*), the time required for 95% decomposition of fine roots ranged from 3.44 to 11.10 y (Lin *et al.*, 2011). In the present study, the time needed for 95% decomposition of fine roots among the 5 tree species also significantly differed to that observed in plants from arid and semi-arid regions, such as 8.52 y and 18.80 a for 95% root decomposition of *Caragana caragana* and *Salix psammophila* in the Mu Us Desert area (Lai, 2015). The potential reason for higher DEC in the present study is that it was located in a coastal area with high SWC, which is conducive to fine root leaching.

According to the size of the fine root decomposition coefficient k ($kg \cdot kg^{-1} \cdot d^{-1}$), DEC was divided into three groups: fast ($k>0.01$), medium ($0.005<k<0.01$), and slow ($k<0.005$) (Lin *et al.*, 2011). The fine root decomposition coefficients of the 5 tree species in this study ranged from 0.002 to 0.007 $kg \cdot kg^{-1} \cdot d^{-1}$, among which, the coefficients of QV and LI were 0.003 $kg \cdot kg^{-1} \cdot d^{-1}$, and that of SM was 0.002 $kg \cdot kg^{-1} \cdot d^{-1}$, classified as the slow decomposition group. SA and RP were 0.007 $kg \cdot kg^{-1} \cdot d^{-1}$ and 0.005 $kg \cdot kg^{-1} \cdot d^{-1}$, respectively, and therefore assigned to the medium decomposition group (Table 5). The fine root DEC of the 5 species was significantly higher than that of other tropical and subtropical plants such as coniferous and broad-leaved tree species in a Fujian subtropical forest (0.0008–0.0024 $kg\ kg^{-1}\ d^{-1}$) (Petersen and Cummins, 1974), and two common plants, *Arundinaria pusilla* (0.002 $kg \cdot kg^{-1} \cdot d^{-1}$) and *Hopea ferrea* (0.003 $kg \cdot kg^{-1} \cdot d^{-1}$), in a tropical forest in Thailand (Fujimaki *et al.*, 2008). Previous studies have shown that atmospheric temperature and SWC can significantly affect DEC (Parton *et al.*, 2007), consistent with the findings of the present study.

Fine roots are in the process of growth, aging, death, and decomposition, with new roots constantly replacing original roots (TUR). The TUR refers to the ratio of annual fine root production to the biomass of living fine roots. In this study, the fine root TUR of the five species ranged from 0.24 to 1.05 $times \cdot y^{-1}$, among which RP had the highest (0.24 $times \cdot y^{-1}$) and SM the lowest (1.05 $times \cdot y^{-1}$). The higher the TUR, the easier it is for fine roots to return soil nutrients and promote their growth, to a certain extent. Therefore, under similar soil salinity and nutrient conditions, the TUR of fine roots significantly differed among the five species (p<0.05). Shan *et al.*, (1993) systematically summarized the fine root TUR of 11 tree species in a forest ecosystem and reported a TUR range of 0.29–1.20 times·y^{-1}, with most in the range of 0.5–1.20 times·y^{-1}. Eissenstat and Yanai (1997) reported a global fine root TUR range of 0.02 to 0.64 times·y^{-1}, with an average of 0.56 times·y^{-1}. The fine root TUR of the 5 tree species in this study was somewhat different from the results of these two studies, which may be due to the subtropical coastal saline soil environment of the present study area, and the associated high soil salinity and poor nutrients, which affected the TUR.

The fine root TUR range of the five species in this study also differed from the those reported by Jiang (0.79–0.91 times·y^{-1}) (Jiang, 2016), mainly because of the sampling differences between studies (individual tree species sampling vs. plant communities). The FRB of individual trees and whole communities differed considerably. Additionally, the TUR of the five tree species in the present study also differed from that of different tree species in a desert ecosystem. The TURs of *Salix cheilophila* and *Artemisia desertorum* were 1.39 and 1.03 times·y^{-}1, respectively (Chen *et al.*, 2004). In summary, fine root TUR was affected by several factors such as climatic conditions, geographical location, and soil physicochemical properties. In the coastal saline-alkali soil environment, plants adjust their TUR to adapt to the changing soil environment under soil salinity and nutrient stress.

Environmental adaptability: The distribution of plant roots in the soil can reflect the adaptability of plants to the soil environment. According to the fine root distribution pattern of the 5 tree species, RP, SA, and SM had a horizontal distribution type, consistent with the findings of Cai *et al.* (Cai *et al.*, 2015). RP and QV had a vertical distribution type, indicating a strong penetration ability. A vertical fine root distribution allows the extension into deeper soil to occupy ecological niches at different soil depths, and obtain soil water and nutrients to meet their growth demands. Furthermore, the deeper the fine roots are distributed in the soil, the better they can hold soil and the stronger their adaptability. This was the adaptative strategy of the five species to the saline-alkali soil environment in the newly reclaimed coastal area of the present study.

Distribution characteristics of tree roots are determined by the genetic characteristics of the species (Cai *et al.*, 2015). Understanding the root morphological characteristics of different tree species, their growth and development characteristics under environmental stress, and the growth strategies of their root systems, can reveal the ecological adaptability of fine root morphological characteristics (FRB, PRO, DEC, and TUR) to stress. This can facilitate the screening of suitable tree species for restoration purposes. In this study, based on their adaptation to coastal saline-alkali land, the five tree species were ranked in the order of LI, SA, SM, RP, and QV. High salinity and poor nutrients were the main characteristics of the soil in this newly reclaimed coastal area, and also affected the fine root distribution. Soil conditions, and root characteristics of different tree species and their adaptability to specific habitats should be fully considered for future landscaping construction and ecological vegetation restoration on coastal saline-alkali soil. Furthermore, the principle of "adapting measures to local conditions and planting suitable trees in the right place" should be followed to improve the greening coverage rate and maximize the ecological effects of each species.

Conclusions

Fine root morphological characteristics (diameter, SRL, and SRSA), and FRB, PRO, DEC, and TUR significantly differed among the five tree species. RP and SA were identified as resource-seeking species that expanded the foraging range of their root system. However, the FRB distribution range of LI, SM, and QV was smaller, and they were classified as resource-conserving species. FRB and PRO significantly differed among the five species, with FRB ranging from 77.05 to 273.42 g·m^{-2} and PRO ranging from 17.80 to 166.00 g·m^{-2}·y^{-1}. Among species, LI had the highest FRB and PRO, while RP had the lowest. The vertical root distribution coefficient data revealed that species had different fine root biomass allocation strategies, and could fully utilize deep and shallow soil resources to adapt to the saline-alkali soil environment. Influenced by environmental factors and their biological characteristics, fine root DEC and TUR significantly differed among species; SA had the highest DEC (0.007 kg·kg^{-1}·d^{-1}) and SM the lowest (0.24 times·y^{-1}). Therefore, based on their suitability for growth in saline-alkali soil, the species were ranked as follows: LI > SA > SM > RP > QV.

The RDA of fine root characteristics and soil physicochemical properties revealed that soil EC, SWC, temperature, TN, and SOM were the main environmental factors affecting the morphology, FRB, PRO, DEC, and TUR of fine roots. These findings can provide a theoretical basis and technical support for the selection of greening tree species suitable for growth in saline-alkali soil and for ecological restoration efforts.

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Data Availability: The entire datasets used and/or analyzed in the study are available from the corresponding author.

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