

RESPONSE OF FINE ROOT MORPHOLOGY, BIOMASS, PRODUCTIVITY, AND TURNOVER RATE OF FIVE TREE SPECIES ON SOIL SALINITY GRADIENT IN NEWLY RECLAIMED SALINE SOIL

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Abstract

Fine roots ($\phi \leq 2$ mm) are important participants in plant underground ecological processes and take major role in the energy flow and material cycling of forest ecosystems. The ecological function of fine roots is often influenced by soil saline-alkali characteristics. Therefore, five tree species including *Ligustrum lucidum*, *Salix matsudana*, *Sapium sebifera*, *Robinia pseudoacacia* and *Quercus virginiana* whose tree height, diameter at breast height, crown width, and tree age are basically the same in the newly reclaimed salt land on the coast are used as the research object to analyze the response characteristics of fine root morphology, biomass, production, and turnover rates of these five tree species to soil salinity gradients. Results showed that soil salinity gradient greatly affect functional traits of plant fine root. As soil salinity increases, both fine root biomass and productivity of the five tree species decrease with a slower turnover rate in low-salt, medium-salt and high-salt areas. Meanwhile, the growth depth of fine roots becomes shallower, causing niche differentiation of fine roots and changing the allocation strategy of fine root biomass. Fine roots adapt to salt stress environments by changing structural characteristics such as increasing diameter, volume, surface area and reducing total length. The results of this study can provide scientific basis for the selection of saline-alkali land greening tree species and the formulation of saline-alkali land greening strategies.

Key words: Fine root functional traits; Salt gradient; Response characteristics; Newly reclaimed salt land; Shanghai.

Introduction

At present, global soil salinization is becoming increasingly serious, which has been a global ecological environment and social problem (Rengasamy, 2006; Chi *et al.*, 2012; Bui, 2013). There are approximately 950 million hectares of saline-alkali land in earth, and China has approximately 35 million hectares, mainly distributed in arid, semi-arid, semi-humid and coastal areas. As saline-alkali soil has the characteristics of poor aeration, bulk density, small porosity and permeability coefficient, poor nutrients, high salt content, and extremely poor natural desalination, it seriously affects the growth of plants (Wu *et al.*, 2009; Hassani *et al.*, 2021; Haj-amor *et al.*, 2022). Therefore, studying the effects of salt-alkali stress on plants and the adaptation mechanisms of plants to salt-alkali stress environments, and screening and cultivating salt-alkali resistant species have important guiding significance for the ecological restoration of saline-alkali lands. With the acceleration of urbanization, urban development space is obviously insufficient. Coastal areas usually use reclamation to expand urban development space. This newly formed blow fill soil is a typical saline-alkali soil containing large salt content (≥ 4.0 g·kg⁻¹), large pH value (≥ 8.5), and low organic matter amount (< 20 g·kg⁻¹) (Jiang *et al.*, 2016a). Due to the short formation time of the filled soil, high soil salinity and pH, poor nutrients, and heavy bulk, it is difficult for plants to grow normally on the filled soil, resulting in low green coverage and poor

landscape effects. In addition, there are very few studies on the ecological adaptability of plant roots on filled soil. Therefore, studying the stress of filling soil on green plants and the adaptation mechanism of plants to filling soil has important theoretical and practical significance for selecting and cultivating excellent greening tree species and improving the urban greening environment.

Fine roots ($\phi \leq 2$ mm) are considered as the most active and sensitive organs in the plant root system. Due to the direct contact with the soil, fine roots are most susceptible to adverse environmental effects (Steele *et al.*, 1997; Huang *et al.*, 2008; Han *et al.*, 2018; Xu *et al.*, 2019). Fine root morphological features, biomass, productivity and turnover rate are important trait indicators for quantifying the response of fine roots to environmental changes and establishing connections with ecosystems (Violle *et al.*, 2007; Bardgett *et al.*, 2014). The above functional traits of root systems are often affected by factors such as tree species type, soil moisture, salinity, and nutrients (Leena *et al.*, 2011; Ma *et al.*, 2013; Hulugalle *et al.*, 2015; Xu *et al.*, 2019; Ning *et al.*, 2024). In addition, roots have strong plasticity (Fitter, 1994; Yang *et al.*, 2002; Hodge, 2005). In changing soil environments, fine root biomass distribution patterns can be adjusted and fine root functional traits (such as configuration) to enhance its adaptability to the environment (Burton & Hendrick, 2000). Therefore, studying the growth status of fine root functional traits on saline-alkali soil will help reveal the ecological adaptability of fine roots to the saline-alkali soil environment.

At present, domestic and foreign scholars have accumulated rich knowledge and experience in research on fine root ecology (Noguchi *et al.*, 2014; Zhu *et al.*, 2016). However, research on the fine root ecology of greening tree species on fill soil has rarely been reported yet. This work takes fine roots of five species on different saline soils in Shanghai Lingang New Area as the research object, analyzing the differences between the morphological features, biomass, productivity and turnover rate of fine roots, and subsequently revealing adaptation mechanism of different trees to the saline soil environment. The research results can provide theoretical basis and technical support for formulating greening strategies for soil filling and saline-alkali land.

Material and Methods

Overview of the studying area: Shanghai Lingang New City (30°59'22" N, 121°17'31" E) locates at the intersection of the Yangtze River and Hangzhou Bay, belong to a subtropical maritime climate with warm and abundant rainfall, distinct seasons. The annual average temperature ranges from 15.2°C to 15.8°C with corresponding average precipitation of 900 ~ 1050 mm/year and total sunshine hours of 2000 ~ 2200 h/year. The trends in monthly average temperature and rainfall in the past three years are basically consistent, and the differences in average temperature and rainfall between months are not significant (Fig. 1).

The experimental forest locating in Shanghai Lingang New City was planted in February 2011 with the completion in April 2011. The planting method adopts regular planting with the planting spacing of 15 × 15 m². The entire experimental site is 900 m in long with an average width of 10 m and a total area of ~ 9000 m². Most of the plants in the experimental site are native tree species of Shanghai, with a small number of exotic tree species (Table 1).

Sample plot settings: Five greening trees including *Ligustrum lucidum*, *Salix matsudana*, *Sapium sebifera*, *Robinia pseudoacacia* and *Quercus virginiana* with similar height, diameter at breast height and crown width crown width in both the high salinity zone (coastal, EC ≥ 12000 μs·cm⁻¹, 30°56'12.96" N, 121°57'55.39" E) and the medium salinity zone were chosen as researching objects, while the same five green species in the low salinity areas (Minhang Campus, East China Normal University, China; EC < 200 μs·cm⁻¹, 31°01'55.22" N, 121°26'53.61" E) were used as controls (Fig. 2). The physical and chemical properties of soil in different soil salinity areas are shown in Table 2.

In sample plots with different soil salinity, tree species with basically the same diameter at breast height, crown width and tree height were regarded as experimental samples. Three parallel samples were set up for each tree species, and a total of 135 samples were selected from the five tree species. The planting spacing of standard trees in each area is more than 15 m, and there are no root systems of other tree species within the sampling range.

Sequential coring: From January to December 2018, a T-type soil drill (φ=5 cm, H=10 cm) was utilized to choose 3 different positions within 1/4 of the crown width of each standard tree at a distance of R/3 (m), 2/3 R (m), R (m) of the concentric circles under 5 layers (0-10 cm, 10-20 cm, 20-30 cm, 30-40 cm and 40-50 cm) for root sampling every 2 months (Fig. 3). Then the soil samples of same tree species in the same soil layer were mixed, and all roots in the mixed sample of the same soil layer were picked out before being collected and taken back to the lab and kept at 4°C. After the root system is collected, the soil containing no roots was put into a nylon mesh bag with a hole diameter of 2 mm (L=50 cm, φ=5 cm), and then the bag was placed in a hole created by drilling the soil core. After that, the soil in the soil core was patted by hands and marked by a PVC pipe to record its position. Finally, the PVC pipe was covered by with thinner soil.

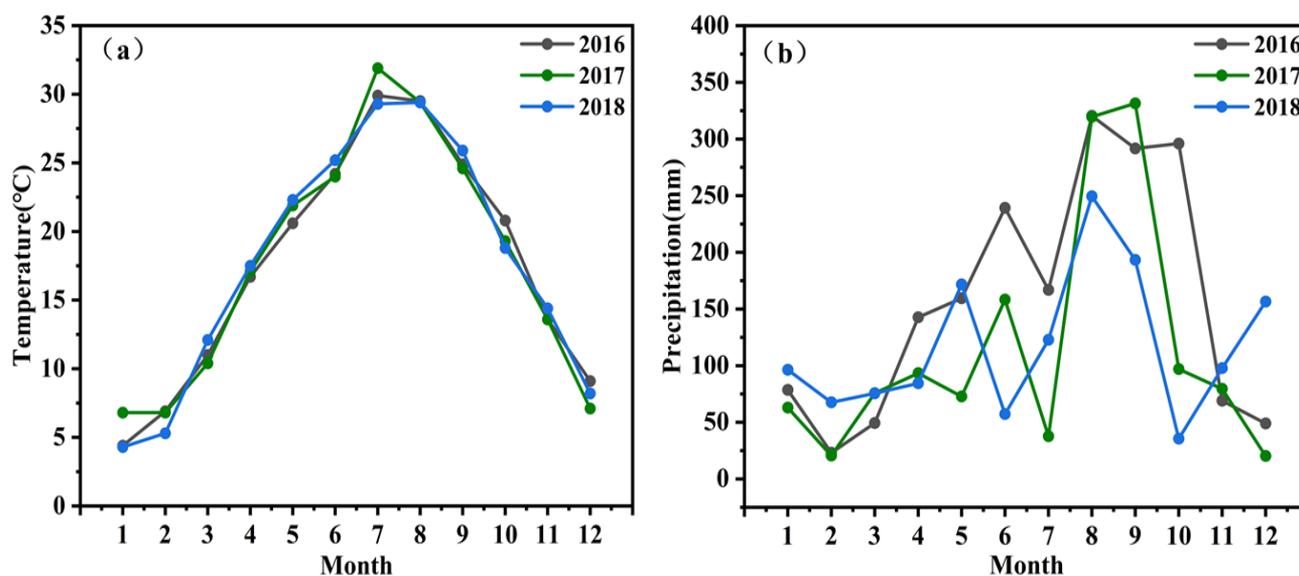


Fig. 1. Monthly temperature and rainfall from 2016 to 2018 in Shanghai.

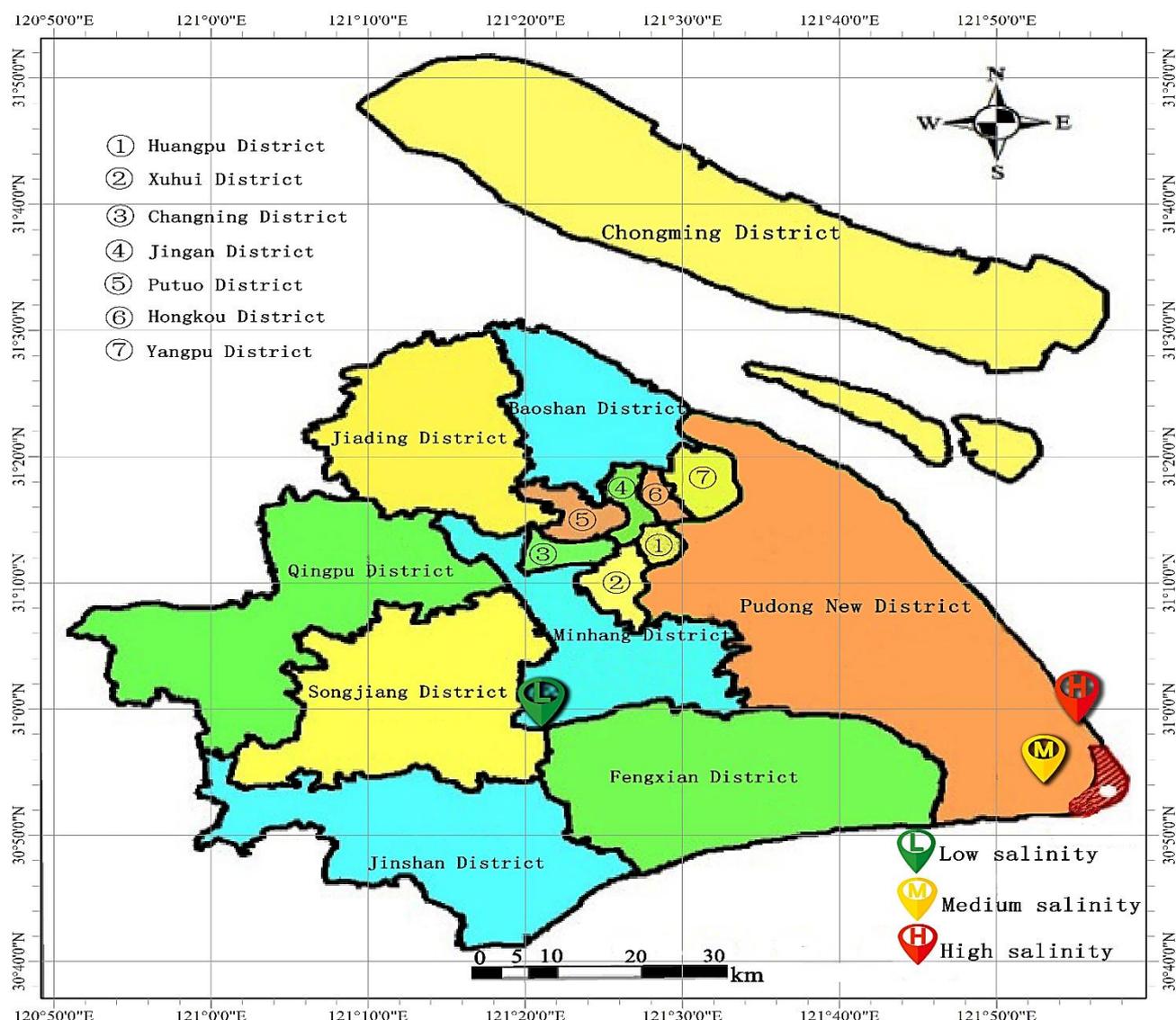


Fig. 2. Study area and plot setting.

Table 1. Basic characteristics of different tree species.

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

Table 2. Physical and chemical properties of soil in low salt, middle salt and high salt areas.

Physical and chemical properties of soil	Low salinity	Middle salinity	High salinity
SM (%)	26.77 ± 2.23 a	29.23 ± 1.78 a	30.01 ± 2.01 a
EC (µs·cm ⁻¹)	137.42 ± 35.31 a	549.57 ± 47.64 b	1321.32 ± 141.20 c
Ph	8.23 ± 0.10 a	8.78 ± 0.17 a	8.81 ± 0.24 a
TN (g·kg ⁻¹)	0.94 ± 0.05 a	0.82 ± 0.03 a	0.79 ± 0.07 a
TP (g·kg ⁻¹)	0.44 ± 0.06 a	0.34 ± 0.12 a	0.26 ± 0.14 a
TK (g·kg ⁻¹)	7.13 ± 0.09 a	6.42 ± 0.31 a	6.51 ± 0.94 a
SOM (g·kg ⁻¹)	14.55 ± 0.11 a	14.21 ± 0.15 a	13.65 ± 0.10 a
SVW (g·cm ⁻³)	1.22 ± 0.07 a	1.35 ± 0.03 a	1.43 ± 0.09 a

Note: SM: Soil moisture; EC: Electrical conductivity; TN: Total nitrogen; TP: Total phosphorus; TK: Total kalium; SOM: Soil organic matter; SVW: Soil volume-weight

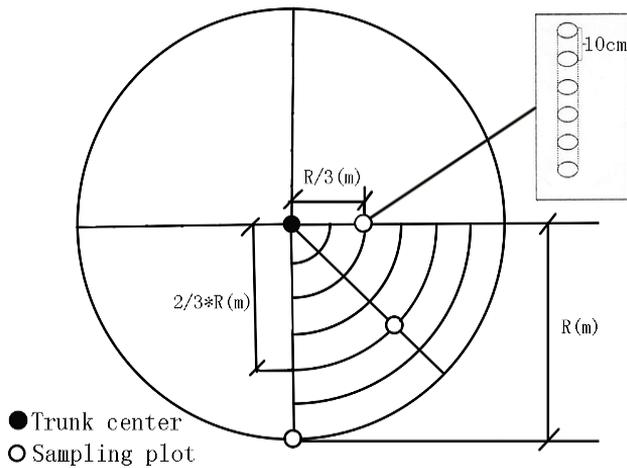


Fig. 3. Root sampling diagram.

Determination of fine root growth: Fine root growth was investigated via ingrowth method. The root system that re-grows into the mesh bag is the root growth amount. In January 2019, the root system in the nylon mesh bag was sampled using the full excavation method. When taking the soil core, a shovel was used to dig around the nylon bag in which the soil core grows. During excavation, a sharp soil knife was used to cut off the root system connecting the nylon mesh to the surrounding soil. The bottom area of the soil core was cut by a soil knife, and the nylon bag with the soil core was then taken out. Subsequently, newly grown roots in five layers: 0-10 cm, 10-20 cm, 20-30 cm, 30-40 cm and 40-50 cm were collected. The collected roots that were collected into plastic bags and taken back to the lab in time were treated within 1 week.

Processing of fine root samples: The roots, rinsed by deionized water to remove all soil on its surface, were put into a plastic bag and stored in the refrigerator (4°C) after that the moisture on its surface was absorbed. After that all samples were cleaned and sorted out, tweezers and vernier calipers were used to pick out all $\phi \leq 2$ mm fine roots in the root system (Wang *et al.*, 2016), and the grass roots were subsequently removed. Finally, live and dead fine roots were distinguished according to some features such as appearance, color, odor as well as elasticity (Noguchi *et al.*, 2007; Ma & Chen, 2017).

Fine root morphological indicators and biomass measurement: The fine roots processed were put in a scanner tray and all the roots were completely stretched. Then, the root system scanning analyzer Win-RHIZO 2005C was utilized to scan samples to obtain the average diameter (D), surface area (S), volume (V) and length (L).

After scanning, the fine root biomass (FRD) specimen were dried in 80 ovens for 24 h, and then the fine root biomass in each soil layer was calculated (Bredoire *et al.*, 2016). The calculation formula is as follows:

$$\text{Fine root biomass (FRD)} \text{ (g} \cdot \text{m}^{-2}\text{)} = \text{fine root mass (g)} \times 10^4 / [\pi(d/2)^2] \quad (1)$$

where d (cm) is the inner diameter of the soil drill and h (cm) is the length of the soil drill.

Fine root productivity (PRO) and turnover rate (TUR):

The FRD in the soil core under a certain period is considered as the net fine root production, which is the PRO (Gill, 2000). In this work, the PRO of the root system was obtained by testing the FRD growing in the soil core within 12 months. The equation is as follows:

$$\text{PRO} = \text{FR}_L + \text{FR}_D \quad (2)$$

where the PRO is the net productivity per year ($\text{g} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$). FR_L and FR_D are the live fine root biomass (LFRB) and dead fine root biomass (DFRB) in the rootless soil column, respectively.

The calculation of the turnover of fine roots is as follows (McClagherty *et al.*, 1985; Liu *et al.*, 2014):

$$\text{TUR} = \text{PRO}/Y \quad (3)$$

where the TUR is the fine root turnover rate ($\text{times} \cdot \text{a}^{-1}$); the PRO is the net productivity per year, and Y is the average living fine root biomass (the method of continuous soil drilling is used in this research to measure the living fine root biomass average) (Liu, 2011).

Data processing: The average and standard deviation of all experimental parameters including the diameter (D), surface area (S), volume (V), length (L), fine root biomass (FRD), productivity (PRO), turnover rate (TUR), soil moisture, temperature, conductivity, pH value, total nitrogen, total phosphorus and organic matter were investigated by Microsoft Excel software.

SPSS (Statistical Product and Service Solutions 16.0) software was utilized for statistical analyzing. Before statistical analysis, all data were acquired for homogeneity of variances. If the variances were uneven, logarithmic transformation was performed. One-way ANOVA and the least significant difference (LSD) method were adopted to investigate differences in morphological characteristics, FRD, PRO and TUR of fine roots from different tree species. The significance level of statistical analysis was $\alpha \leq 0.05$, and the analysis graph was obtained by Origin Pro 9.0 software.

Results

Morphological characteristics of fine roots under different soil salinities:

Under different soil salinities, the L, S, V and D of fine roots of the same tree species differ significantly ($p < 0.05$). The V, D and S of fine roots of the five species gradually increase with the increase of soil salinity, while the L of fine roots is gradually decreasing (Fig. 4a-d).

Fine root biomass distribution under different soil salinities:

With the enlargement of soil salinity, LFRB and total biomass (TFRB) of the five tree species show a gradually decreasing trend, while the DFRB gradually increases (Fig. 5).

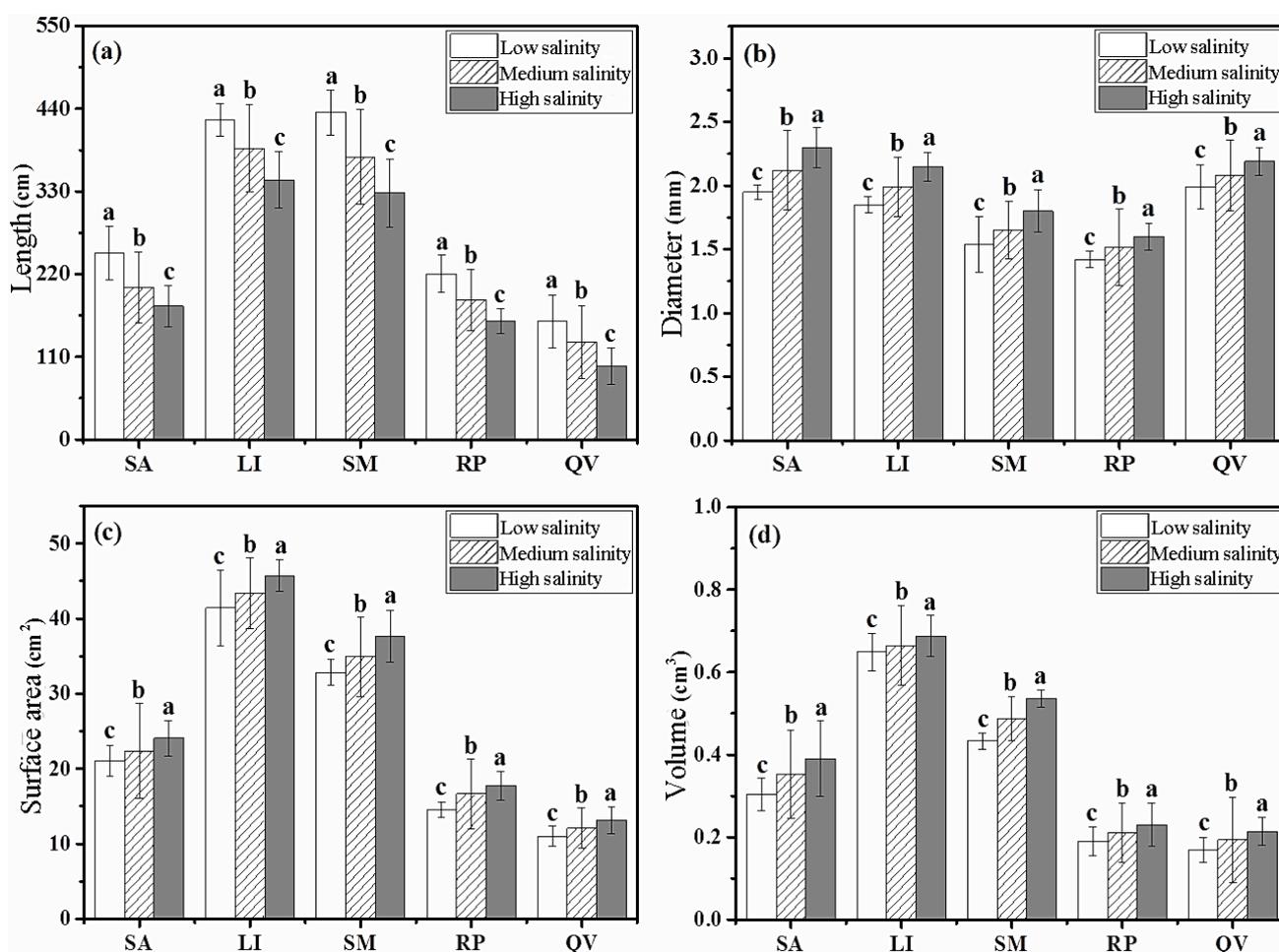


Fig. 4. Fine root morphological features of different tree species in different soil salinity
 Note: RP: *Robinia pseudoacacia*, LI: *Ligustrum lucidum*, SA: *Sapium sebiferum*, SM: *Salix matsudana*, QV: *Quercus virginiana*. Different lowercase letters indicate significant difference at the 0.05 level. The same below.

The biomass of live fine roots of the same species under different soil salinities is significantly different ($p < 0.05$, Fig. 5a). *Ligustrum lucidum* has the largest live fine root biomass in soils in low, medium and high salinity areas, which are 255.44 g·m⁻², 231.68 g·m⁻² and 217.12 g·m⁻², respectively. Compared with the low-salt area, the LFRB of *Ligustrum lucidum* in medium and high salinity regions decreases by 9.30% and 15.00 %, respectively. The LFRB of *Ligustrum lucidum* was the least affected by salt. The values of LFRB of *Quercus virginiana* are 162.37 g·m⁻², 136.39 g·m⁻² and 112.04 g·m⁻² respectively. Compared to the low-salt area, the LFRB of medium and high salt areas is respectively decreases by 16.00% and 31.00%. The live fine root biomass of *Quercus virginiana* is reduced the most by salt. *Robinia pseudoacacia* has the smallest live fine root biomass. The live fine root biomass in low-salt, medium-salt and high-salt areas are 84.52 g·m⁻², 73.78 g·m⁻² and 61.70 g·m⁻² respectively. Compared with the low-salt area, the living fine-root biomass in the high-salt area decreases by 12.70% and 27.00% respectively. The LFRB of *Sapium sebiferum* in low, medium and high salinity areas are 153.34 g·m⁻², 132.04 g·m⁻² and 118.22 g·m⁻², respectively. Its LFRB in medium and high salinity areas reduces by 14.00 % and 23.00 %

respectively compared with that in the low-salt area. As for *Salix matsudana*, its live fine root biomass is 159.10 g·m⁻², 141.60 g·m⁻² and 128.87 g·m⁻², respectively in low, medium and high salinity areas. It shows a decrease by 11.00% and 19.00% in the medium and high-salt areas respectively, compared to that in the low-salt region. Therefore, with the increase of soil salinity, the live fine root biomass of the five tree species shows a gradually decreasing trend. *Ligustrum lucidum* presents the smallest reduction proportion while Virginia oak shows the largest one.

The DFRB of same tree species under different soil salinities is significantly different ($p < 0.05$, Fig. 5b). In the soils of low, medium and high salinity areas, the DFRB of *Salix matsudana* is the largest, which are 90.84 g·m⁻², 102.87 g·m⁻² and 105.87 g·m⁻² respectively. In compare with the low-salt zone, the DFRB increases by 13.24% and 16.54% respectively in the medium and high-salt areas. The biomass of dead fine roots of *Sapium sebiferum*, *Ligustrum lucidum* and *Quercus virginiana* comes second. The DFRB of *Sapium sebiferum* is 22.65 g·m⁻², 23.90 g·m⁻² and 25.68 g·m⁻² in the low, medium and high salt areas respectively. Compared with the low salt area, the medium and high salt areas have higher DFRB, increasing by 5.51% and 13.39% respectively.

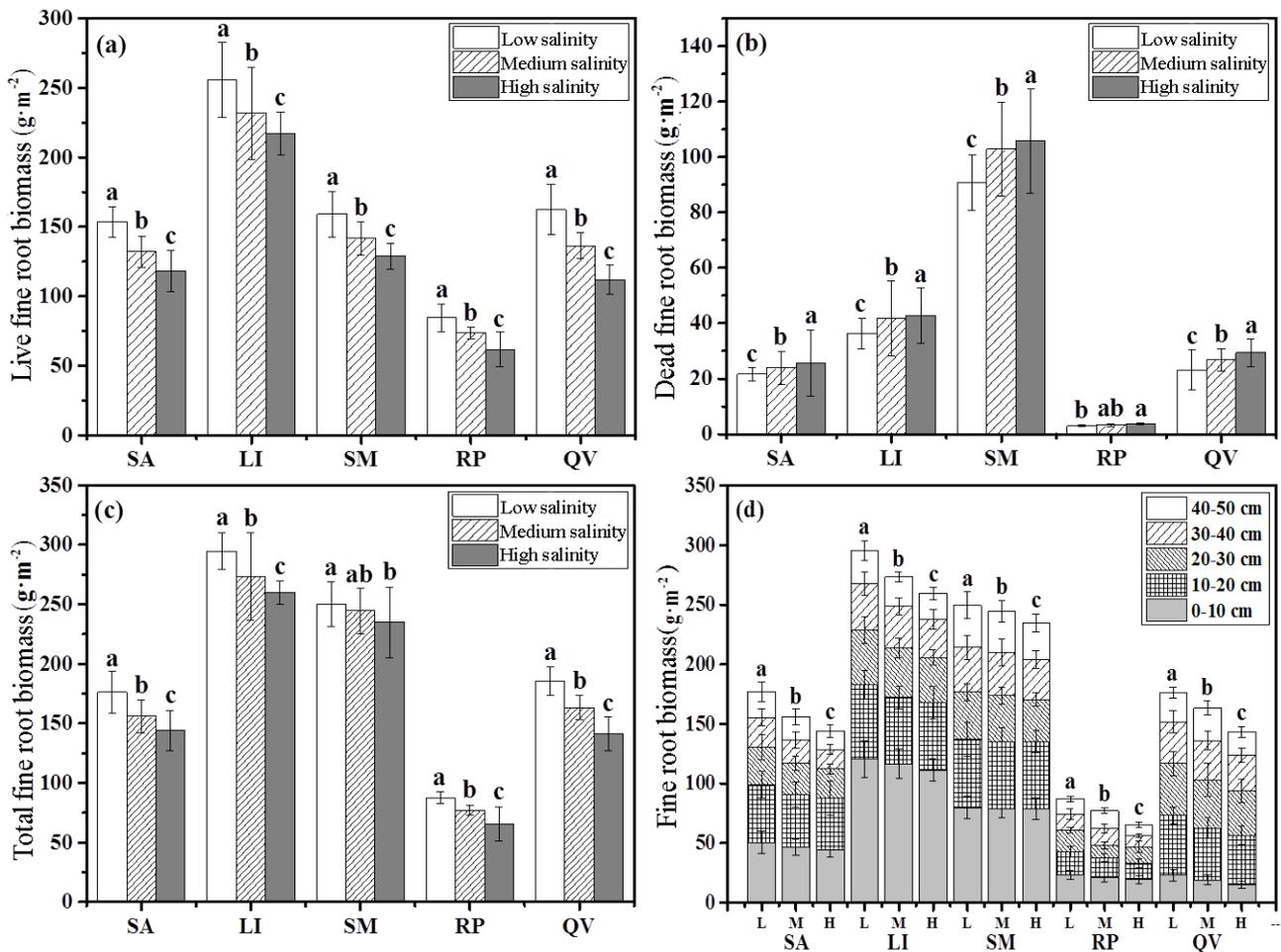


Fig. 5. Fine root biomass distribution of different tree species in different soil salinity.
Note: L: Low salt area, M: Mid salt area, H: High salt area.

The DFRB of *Ligustrum lucidum* are 39.24 g·m⁻², 41.74 g·m⁻² and 42.70 g·m⁻² respectively. Compared with the low-salt area, the DFRB increases by 6.37% and 8.81% in the medium and high salt areas, respectively. The DFRB of *Ligustrum lucidum* is least affected by salt. The DFRB of *Quercus virginiana* accounts for 23.20 g·m⁻², 26.92 g·m⁻² and 29.40 g·m⁻² respectively, increasing by 16.00% and 26.69% in the medium and high salt areas than that in the low-salt region. The biomass of dead fine roots of *Robinia pseudoacacia* is the smallest, which are 2.97 g·m⁻², 3.27 g·m⁻² and 3.71 g·m⁻² respectively, and it rises by 10.00% and 25.00% in medium and high salt zones compared with that in the low-salt area. In short, as the soil salinity increases, the DFRB of the five species shows a gradually increasing trend.

The TFRB of the same tree species under different salinities varies significantly ($p < 0.05$, Fig. 5c). The TFRB of the *Salix matsudana* is 249.94 g·m⁻², 244.47 g·m⁻² and 234.74 g·m⁻² in low, medium and high salinity areas, respectively. In the high-salt area, the TFRB of *Salix matsudana* is least affected by soil salinity. Compared with the low-salt area, the TFRB of the medium and high-salt areas deduces by 2.19% and 6.08% respectively. The *Robinia pseudoacacia* has the smallest TFRB of fine roots, accounting for 87.49 g·m⁻², 77.05 g·m⁻² and 65.41 g·m⁻² respectively, and there are 11.93% and 25.23% reduce of TFRB in the medium and high-salt areas compared to that

in the low-salt part, illustrating that total root biomass of the *Robinia pseudoacacia* is most affected by soil salinity. Among the five tree species, *Ligustrum lucidum* exhibits the largest TFRB, which are 294.68 g·m⁻², 273.42 g·m⁻² and 259.82 g·m⁻² respectively, decreasing by 7.21% and 11.83% of TFRB in medium and high-salt areas than that in the low-salt region. For the Chinese tallow tree, its TFRB is 176.19 g·m⁻², 155.94 g·m⁻² and 143.91 g·m⁻², respectively, and it reduces by 11.94% and 18.32% in the medium- and high-salt areas compared with the low-salt location. It can be seen that the TFRB of the five tree species illustrates a gradually decreasing trend with the increase of soil salinity.

In addition, through the analysis of the vertical distribution pattern of fine root biomass of five species, it is found that as soil salinity increases, the distribution of fine root biomass in deep soil becomes less, while increases in shallow soil. The more there are, which means that the growth depth of fine roots becomes shallower due to the influence of soil salinity, and the ecological niche of fine roots moves upward (Fig. 5d).

Fine root productivity and turnover rate under different soil salinities: With the increase of soil salinity, the PRO of the five tree species decreases significantly ($p < 0.05$, Fig. 6a). In low, medium and high salinity areas, the PRO of *Sapium sebiferum* is 99.45

$\text{g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$, $91.99 \text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ and $85.12 \text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ respectively. Compared with low-salt areas, PRO in medium- and high-salt areas decreases by 7.50% and 14.40% respectively. The PRO of *Ligustrum lucidum* are $187.10 \text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$, $166.00 \text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ and $143.01 \text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ respectively. Compared with low-salt areas, PRO decreases by 11.28% and 23.56% respectively in medium- and high-salt areas. Besides, the PRO of willow is considered as $157.23 \text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$, $148.50 \text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ and $124.87 \text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ respectively in the medium, high salinity areas, reducing by 5.56% and 20.58% respectively in comparison with that in the low-salt region. In the low, medium and high salinity areas, the PRO of *Quercus virginiana* is $49.89 \text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$, $45.73 \text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ and $40.21 \text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ respectively, and the PRO decreases by 8.34% and 19.40% respectively in medium and high salinity areas compared with that in the low-salt region. For the block locust, the values of the fine root production from low salinity area to high salinity area are $20.01 \text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$, $17.80 \text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ and $14.81 \text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ respectively and there are 11.04 % and 25.99 % reduction of the fine root production in the medium and high salinity areas, respectively compared to that in the low one. In summary, it means that although the PRO of *Ligustrum lucidum* is reduced by a higher proportion due to the influence of salt, the PRO is still the largest in all

three salinity areas. In addition, the PRO of *Robinia pseudoacacia* is the smallest in all salinity areas but is greatly affected by soil salinity.

As soil salinity increases, the fine root TUR of the five species significantly decreases ($p < 0.05$, Fig. 6b), that is, the fine root TUR gradually slows down. Compared with the low-salt area, the fine root TUR of *Quercus virginiana* decreases the most, reducing by 10.34% and 20.69% respectively in medium and high salinity areas. For the *Robinia pseudoacacia*, its fine root TUR decreases by 11.11% and 18.52% respectively in medium and high salinity areas compared to that in the low area. Meanwhile, the fine root TUR of Chinese tallow tree under medium and high salinity areas decreases by 9.09% and 15.58% respectively and the *Ligustrum lucidum* exhibits a decrease by 8.86% and 13.92% respectively in medium and high salinity areas. Besides, the fine root TUR of *Salix matsudana* decreases the least, reducing by 4.45% and 11.82% respectively in medium and high salinity areas compared to that in the low region. It can be seen that in low, medium and high salinity areas, the fine root TUR of *Salix matsudana* is the fastest, followed by the Chinese tallow tree and *Ligustrum lucidum*, while the TUR of *Quercus Virginiana* and *Robinia pseudoacacia* is the slowest (Fig. 6b).

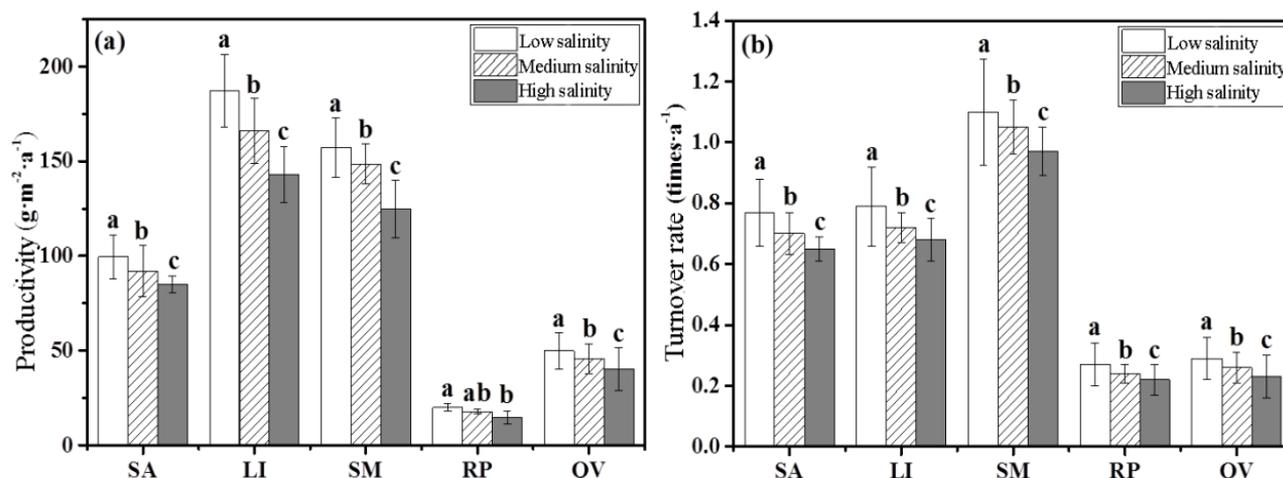


Fig. 6. Fine root productivity and turnover rates of different tree species in different soil salinity.

Discussions

Effect of soil salinity on morphological characteristics of fine roots: Morphological characteristics such as L, D, S and V of fine roots are important parameters that reflect root growth status. Plant root growth is easily affected by environmental factors. When the soil environment changes, plants often adapt to different soil environments by changing root morphology (Rich *et al.*, 2011; Pan *et al.*, 2014; Sasse *et al.*, 2018). For example, in arid areas, soil moisture is the main environmental factor that limits plant root growth. Plants often obtain soil moisture to adapt to arid growth environments by increasing the depth of root growth and reducing the number of lateral roots (Lyr & Hoffmann, 1967; Ponti *et al.*, 2004; Tissink *et al.*, 2024). In this work, soil salinity is the major environmental factor limiting plant root

growth. Since the soil salinity gradually increases with the increase of soil depth (He *et al.*, 2014; Lu *et al.*, 2019), and the root system has the characteristics of tending to a favorable environment, plant roots often adjust the fine root morphology under adversity to adapt to surrounding environment. In this work, as soil salinity increases, the S, V and D of fine roots gradually increase. These changes in the morphological structure of the root system expand the contact area between the root system and the external environment and improve the ability of plant roots to absorb and transport water and nutrients, thereby improving the plant's ability to adapt to changes in the external environment, which is important to the survival of plants (Gedroc *et al.*, 1996). In summary, fine roots have strong plasticity, and plants can adapt to salt-stressed soil environments by changing the shape of fine roots.

Effect of soil salinity on fine root biomass: As the most sensitive organ in plant roots, fine roots are sensitive to soil environments. In high-salinity soils, plants can respond to the environment by adjusting the distribution pattern of root biomass (Bardgett *et al.*, 2014; Jin *et al.*, 2017). Studies have shown that the increase in soil salinity will affect the distribution characteristics of root biomass (Zandt *et al.*, 2003). This result shows that the TFRB of *Ligustrum lucidum* and *Salix matsudana* is larger in both high-salt and low-salinity areas. Compared with the other three species, the proportion of TFRB reduction of these two species in high-salinity area is smaller than that in the low-salt region, indicating that *Ligustrum lucidum* and *Salix matsudana* may be less affected by soil salinity and are more suitable for soil filling environments. Moreover, the TFRB of fine roots of *Robinia pseudoacacia* is the smallest in the high-salt and low-salt regions, and the proportion of the TFRB decreases in the high-salt regions was larger, indicating that *Robinia pseudoacacia* is greatly affected by soil salinity and is not suitable for growing in the high-salinity soil environment. Other scholars' research on the adaptability of *Robinia pseudoacacia* to saline-alkali soil presents that *Robinia pseudoacacia* displays obvious degradation after growing on the saline-alkali soil in the Yellow River Delta for many years (Mao *et al.*, 2016), which also verifies that *Robinia pseudoacacia* is not suitable for planting in saline-alkali soil. In this study, the TFRB of *Robinia pseudoacacia* is the smallest among the five tree species. The size of its biomass may be related to its own biological characteristics. It is not convincing to evaluate whether *Robinia pseudoacacia* is suitable for soil filling environment just from the perspective of fine root biomass. Therefore, multiple physiological indicators of fine roots should be combined to evaluate the adaptability of *Robinia pseudoacacia* to the soil-drifting environment in future research. In addition, according to the summary of previous scholars, the variation range of fine root biomass in different ecosystems is often between 46–2805 $\text{g}\cdot\text{m}^{-2}$ (Aber *et al.*, 1985). Except for *Robinia pseudoacacia*, the fine root biomass of the other four species is within the range of change. This phenomenon can be inferred from the following two aspects: First, the soil type in this study area is coastal blow fill, and the high content of soil salt leads to the decrease of the fine root biomass of *Robinia pseudoacacia*. Besides, the fine root decomposition and turnover rate of *Robinia pseudoacacia* is extremely fast. The dead fine roots can be quickly decomposed these fine roots cannot be obtained, thus affecting the TFRB of *Robinia pseudoacacia*.

Different soil salinities affect the vertical distribution of fine roots of five species: *Ligustrum lucidum*, *Salix matsudana*, *Sapium sebifera*, *Robinia pseudoacacia* and *Quercus virginiana*. Compared with non-saline-alkali land, as soil salinity increases, the growth depth of fine roots becomes shallower, and root niche differentiation occurs. Its distribution characteristics are to achieve optimal allocation of resources (Fig. 4d, Lloret *et al.*, 1999). Numerous studies have reported that when plant roots encounter deep soil salt stress, plants will reduce the distribution of above-ground photosynthetic products to the deep soil in order to reduce transportation costs, so that more roots are distributed in the shallow soil (Nadelhoffer *et al.*, 2000). When the soil salinity is less than the root salt

tolerance threshold, the roots grow vertically to the ground. However, the roots stop growing vertically to the ground and instead stretch horizontally in the soil layer if the soil salinity is greater than the root salt tolerance threshold (Jackson *et al.*, 1996; Zhun *et al.*, 2024). For coastal fill soil, as the soil depth increases, the soil salinity continues to increase, resulting in a change in root growth characteristics: gravitropism (Eapen *et al.*, 2005; Li *et al.*, 2024). Meanwhile, the increase in soil salinity causes changes in deep soil pH, which promotes the lateral transport of root auxins from the root base, that is, the growth rate of the root tips of lateral roots is faster than the growth rate of the main root tips, resulting in an enhanced trend of horizontal root growth (Gedroc *et al.*, 1996). Based on the above analysis, it can be seen that the root system adapts to the soil environment of salt stress by adjusting the vertical and horizontal distribution pattern of biomass.

Effect of soil salinity on fine root productivity: In our work, the PRO of the five tree species ranged from 17.80–166.00 $\text{g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$. Among them, *Robinia pseudoacacia* has the smallest PRO (17.80 $\text{g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$), which is not suitable for saline-alkali soil environment, while fine roots of the *Ligustrum lucidum* have the highest productivity (166.00 $\text{g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$) and are most suitable for saline-alkali soil environment. The size of PRO may be related to the biological features of species and corresponding environment (Usman *et al.*, 2000; Ma & Chen, 2017; Xiong *et al.*, 2017; Tan *et al.*, 2017; Yang *et al.*, 2024), and it is unconvincing to evaluate the adaptability of different tree species using only PRO as an indicator. Therefore, multiple indicators of fine roots (such as physiological indicators) should be combined for a comprehensive evaluation. The PRO of the five tree species in this study is quite different from that in forest ecosystems in other study areas, such as European spruce forests (Ostonen *et al.*, 2005) and temperate forests (Zhang *et al.*, 2019). The main reasons for the difference are: (1) The selected tree species or tree species are different in age, resulting in differences in fine root growth; (2) The site conditions are different. In temperate forest areas, the temperature is lower with relatively sufficient soil nutrients, resulting in high productivity of root system. This study area is located in the subtropical zone and on the coastal blow fill soil, with high soil salinity and poor soil nutrients, leading to a decrease in root productivity. (3) During the experimental sampling, the phenological stages of plants are different (Zhao *et al.*, 2017). Due to that plants have different phenological characteristics such as bud bursting and leaf emergence in spring, rapid growth in summer, and leaf fall in autumn, root growth shows seasonal dynamic changes. (4) There will be certain differences in different experimental designs, such as root sampling methods, sampling intervals, and methods of identifying live and dead fine roots, which will all lead to differences in fine root growth (Ostonen *et al.*, 2005; Yuan & Chen, 2018). In addition, fine roots are also affected by soil water temperature and nutrients, and their productivity varies in the vertical distribution (Tissink *et al.*, 2024). Previous results on fine root production in this region found that fine root production was also mainly distributed in 0–30 cm soil layer, consistent with the findings in the study (Jiang *et al.*, 2016c).

Effect of soil salinity on fine root turnover rate: Fine roots are in the process of continuous growth, aging, death and decomposition, and the process of new roots constantly replacing the original roots is called fine root turnover. In our work, the TUR of fine roots of the five species ranged from 0.24 times·a⁻¹ to 1.05 times·a⁻¹. Among them, the TUR of *Robinia pseudoacacia* is the slowest (0.24 times·a⁻¹), while that of *Salix matsudana* is the fastest (1.05 times·a⁻¹). The faster the TUR of fine roots, the easier it is for fine roots to return soil nutrients and promote plant growth to a certain extent. It can be seen that there are significant differences in the TUR of fine roots of major tree species under similar soil salinity conditions. Besides, Shan (1993) systematically summarized the TUR of fine roots of 11 species in the forest system and found that their TUR ranged from 0.29-1.20 times·a⁻¹, and most of them ranged from 0.5-1.20 times·a⁻¹. Jackson (1997) analyzed global plant fine root data and found that the TUR of plant fine roots ranged from 0.02 to 0.64 times·a⁻¹, and the average TUR was 0.56 times·a⁻¹. The fine root TUR of the five species in this research is different from that of different tree species summarized by previous scholars, which may be due to the fact that the study area is located in a subtropical coastal soil environment with high salinity and pH value and poor nutrients, which affects the fine root TUR. The change range of fine root turnover in present study is quite different from that of Jiang (2016b) (0.79-0.91 times·a⁻¹), mainly because the study is based on individual tree species sampling. However, Jiang is sampled within the community, and the growth number of fine roots is different between individual tree species and the community, which results in a great difference in the TUR of fine roots. In addition, climate differences also lead to differences in the TUR of fine roots of different species (Xiong *et al.*, 2018). The fine root TUR of the five tree species in this study are certainly different compared with that of European forest ecosystems (Brunner *et al.*, 2013), North American forest ecosystems (Steele *et al.*, 1997) and tropical rainforest forest ecosystems (Katayama *et al.*, 2019). It can be seen that the TUR of fine roots is influenced by many factors containing climatic conditions, geographical location and physical/chemical features of soil. In the coastal saline-alkali soil environment, plants adapt to the changing soil environment by adjusting the TUR of fine roots due to the stress of soil salt.

Conclusions

With the increase of soil salinity, both biomass and productivity of fine roots decrease gradually, while volume, diameter and surface area show a gradually increasing trend. Meanwhile, a reduce in the length with slow turnover rate of fine roots can be discovered. Besides, as the increase of soil salinity, the growth depth of fine roots of the five species become shallow, and the phenomenon of fine root niche differentiation appear. Plants adapt to the salt stressed soil environment by changing the configuration of fine roots, adjusting the biomass allocation strategy of fine roots and slowing down the turnover rate of fine roots. According to the effect of high salinity on the PRO and TUR of fine roots of different tree species, the most desirable tree for planting is *Ligustrum lucidum*, followed by *Salix matsudana*, *Sapium sebifera*, *Robinia pseudoacacia* and *Quercus virginiana*.

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