Fine root and leaf functional traits of coastal herbaceous plants and their relationships with soil factors: Postprint

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Date: 2023-08-24T00:00:00+00:00

Abstract

As the organs with highest environmental sensitivity, investigating the interrelationships between root and leaf functional traits and their responses to environmental factors helps reveal plant resource utilization patterns and adaptive strategies to environmental conditions. This study focused on herbaceous plants on the sandy coast of Pingtan Island, establishing three distance gradients from sea to land, selecting six leaf functional traits and five fine root functional trait indicators, to analyze leaf and fine root functional traits of coastal plants and their responses to soil factors. The results showed: (1) The coefficient of variation for root and leaf functional traits was smallest in the intertidal zone and largest at the 30-60 m gradient from the high tide line. Average single leaf area, leaf phosphorus content, fine root average diameter, root tissue density, and root phosphorus content showed increasing trends with increasing distance from sea to land; leaf dry matter content, leaf tissue density, specific root length, and specific root area showed decreasing trends. (2) Through trait combinations, plants make resource allocation trade-offs between growth and defense, manifested as varying degrees of correlation among leaf traits, root traits, and between root and leaf traits. Among the aboveground-belowground corresponding traits, leaf thickness and fine root average diameter, as well as leaf phosphorus content and root phosphorus content, showed extremely significant positive correlations; while specific leaf area with specific root area and specific root length, and leaf tissue density with root tissue density, showed no significant correlations. (3) Soil factors explained 52.05% of variation in coastal plant functional traits, with soil salinity having the greatest influence, followed by soil water content, electrical conductivity, and pH value. Overall, in the harsh coastal environment, soil salinity, electrical conductivity, water content, and pH value gradually decreased from sea to land, with generally low phosphorus and high salinity-alkalinity conditions, and plants exhibited different survival strategies: plants closer to the sea adopted a 'leaf resource-conservative, root resource-acquisitive' strategy; those farther from the sea adopted a 'leaf resource-acquisitive, root resource-conservative' strategy. These results provide a valuable reference for understanding the response mechanisms and adaptability of coastal herbaceous plants to environmental gradient changes, while also facilitating the selection of suitable species for planting according to gradients by analyzing soil and other environmental characteristics, promoting coastal plant restoration and protection.

Full Text

Preamble

DOI:10.11931/guihaia.gxzw202211007

Fine root and leaf functional traits of coastal herbs and their relationship with soil factors

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Abstract

As the most environmentally sensitive organs, plant roots and leaves exhibit functional traits that reflect long-term adaptive strategies to environmental changes. This study investigated sandy coastal herbaceous plants on Pingtan Island, establishing three distance gradients from sea to land. Six leaf functional traits and five fine root functional traits were selected to analyze the characteristics of coastal plant leaves and fine roots and their responses to soil factors. The results showed: (1) The coefficient of variation for root and leaf functional traits was smallest in the intertidal zone and largest at the gradient 30–60 m from the high tide line. Individual leaf area, leaf phosphorus content, fine root average diameter, root tissue density, and root phosphorus content increased with distance from sea to land, while leaf dry matter content, leaf tissue density, specific root length, and specific root area showed decreasing trends. (2) Plants balanced resource allocation between growth and defense through trait combinations, manifested as varying degrees of correlation among leaf traits, root traits, and root-leaf traits. Among the aboveground-belowground corresponding traits, leaf thickness and fine root average diameter, as well as leaf phosphorus content and root phosphorus content, showed extremely significant positive correlations; however, specific leaf area with specific root area and specific root length, and leaf tissue density with root tissue density showed no significant correlations. (3) Soil factors explained 52.05% of the variation in coastal plant functional traits, with soil salt content having the greatest influence, followed by soil water content, electrical conductivity, and pH value. Overall, in the harsh coastal environment, soil salt content, electrical conductivity, water content, and pH value gradually decreased from sea to land, presenting a generally low-phosphorus, high-salinity-alkalinity condition. Plants exhibited different survival strategies: those closer to the sea adopted a "leaf resource-conservative, root resource-acquisitive" strategy, while those farther from the sea adopted a "leaf resource-acquisitive, root resource-conservative" strategy. These findings provide valuable insights into the response mechanisms and adaptability of coastal herbaceous plants to environmental gradient changes, and facilitate the selection of suitable species for planting along gradients based on soil and other environmental characteristics, thereby promoting coastal vegetation restoration and protection.

Keywords: coastal plants, leaf, fine root, functional traits, soil factors, ecological strategy

Introduction

For fragile island ecosystems, coastal zones serve as ecological barriers. Coastal vegetation in the land-sea transition zone provides buffering effects against tidal scouring and wind-sand invasion (Wang et al., 2005), holding significant ecological value. However, coastal front sandlands are chronically affected by sea winds, waves, intense light, high temperatures, and human disturbances, resulting in few suitable plants and tending toward simplified plant community species composition (Wu et al., 2021). These systems are extremely vulnerable, and once damaged or degraded through succession, they are difficult to restore naturally.

During growth, plants respond to various environmental factor changes by adopting appropriate survival strategies, which are manifested through changes in functional traits (Zhao et al., 2020). However, current research on plant functional traits and their relationships with the environment has focused primarily on inland forests and grasslands (Zhang et al., 2021; Wu et al., 2021; Sun et al., 2022), with relatively limited studies on coastal plants. Among coastal plant studies, most have concentrated on leaf functional traits (Liu et al., 2020; Zhang et al., 2020; Wang et al., 2022; He et al., 2022). For example, coastal bamboo species increase specific leaf area and leaf area to enhance light resource capture and utilization efficiency (Li et al., 2022), while trees such as *Casuarina equisetifolia* and *Pinus elliottii* reduce specific leaf area and leaf area and increase leaf thickness and leaf dry matter content to maintain high nutrient resorption efficiency (Zhou et al., 2019). Some studies have also examined root structure, morphology, and distribution characteristics, but these have mostly focused on single-organ functional traits, such as Sun et al. (2021) investigating the effects of different population densities on root morphology and growth characteristics in coastal beaches, and Li et al. (2020) analyzing the interactive effects between root distribution and soil in coastal saline-alkali lands of different forest ages.

Leaves are the most sensitive and plastic aboveground organs of plants, and their trait characteristics directly influence physiological processes such as photosynthesis, respiration, and transpiration (Zhang and Luo, 2004; Mao et al., 2012). Roots serve as important belowground organs that interact with soil factors (Xu et al., 2010). Fine roots (generally diameter < 2 mm) are considered particularly sensitive to soil environmental changes (McCormack et al., 2015) and are the primary sites for water and nutrient absorption. Environmental factors such as climate (Fan et al., 2022; Wu et al., 2022), latitude (Wang et al., 2022), topography (Shang et al., 2022), soil (Zhang et al., 2023), and grazing (Zhang et al., 2022) all represent important influences shaping plant functional traits. Plant functional traits change with environmental variations (Shui et al., 2022). For example, with increasing altitude, leaf dry matter content, leaf thickness, leaf tissue density, and leaf relative water content increase significantly (Wang et al., 2021), while fine root average diameter, specific root length, and specific root area values gradually increase (Huang et al., 2023). In karst regions, branch-leaf traits of woody plants are mostly correlated (Zhong et al., 2018). Research indicates that under suitable environmental conditions, different organ traits tend toward co-evolution (Zhao, 2016; Chen et al., 2020; Wang et al., 2021), whereas under severe stress or extreme environments, plants adopt stronger trade-off strategies (Gao et al., 2017). For instance, under water stress, leaf area of *Alhagi sparsifolia* seedlings shows extremely significant negative correlations with specific root length, specific leaf area with root length, and root tissue density (Xu et al., 2021). Evidently, the response mechanisms of plant functional traits to environmental factor changes do not operate independently; correlations exist both among traits within the same organ and among functional traits across different organs. Along coastal distance gradients (environmental gradients extending from sea to inland), the impacts of strong winds and water-salt intrusion gradually weaken, and various environmental factors (soil texture, water-salt content, nutrient content, etc.) may differ. Under such conditions, whether correlations exist among root and leaf traits within and between organs, and what response mechanisms they exhibit toward the environment, remain unclear. This study selected the sandy coast of Dafu Bay on Pingtan Island, Fujian Province as the research area, establishing three gradients from sea to land, selecting six leaf functional traits and five fine root functional trait indicators, and employing one-way ANOVA and correlation analysis methods to address the following questions: (1) What differences exist in plant functional traits among the three coastal gradients? (2) Are correlations present between root and leaf functional traits, and what response mechanisms do they exhibit toward the soil environment? This study aims to reveal the survival strategies of coastal plants and provide theoretical support for coastal vegetation protection and restoration.

1.1 Study Area Description

Pingtan Island (119°32 –120°10 E, 25°15 –25°45 N) is located in the eastern sea area of Fujian Province, with its main island, Haitan Island, being the largest island in Fujian. The region features a south subtropical maritime monsoon climate, with annual precipitation ranging from 900 to 2100 mm, concentrated mainly in spring and summer, and high annual evaporation of approximately

1900 mm. The study area, Dafu Bay, is situated in the southeastern part of Pingtan Island, characterized by low-lying sandy coasts dominated by shrubs and herbaceous plants (Chen et al., 2022).

1.2.1 Sample Plot Setup and Community Survey

Field investigations were conducted in June 2022, establishing three gradients from sea to land (detailed in Table 1): T1, T2, and T3, with average elevations of approximately 3 m, 7 m, and 11 m, respectively. Environmental factors within each gradient were basically similar. Three 10 m × 10 m sample plots were established within each gradient, with three 2 m × 2 m quadrats randomly selected within each plot, totaling 27 quadrats. All herbaceous species, individual counts, heights, and coverages were recorded within each quadrat. Based on plant distribution patterns within the sample plots, distances between quadrats ranged from approximately 5 to 15 m.

Table 1 Gradient profile and vegetation characteristics

Gradient	Position	Environmental characteristics	Plant distribution characteristics
T1	Intertidal zone, the area between the high tide line and the low tide line of seawater	Under the influence of tidal dynamics, flooding stress is serious	Vegetation coverage is about 10%, mainly including *Cyperus rotundus*, *Stephania japonica*
T2	30–60 m from high tide line	Semi-mobile sandy land with serious sand burial	Vegetation coverage is about 50%, mainly including *Spinifex littoreus*, *Oenothera drummondii*, *Wedelia prostrata*, *Ipomoea pes-caprae*
T3	90–120 m from high tide line	Near the *Casuarina equisetifolia* trunk forest belt, the soil nutrient conditions are relatively good	Vegetation coverage is about 90%, mainly including *Spinifex littoreus*, *Oenothera drummondii*, *Stephania japonica*, *Cynodon dactylon*

1.2.2 Sample Processing and Measurement

Plant sample collection: Within each quadrat, for each dominant species (importance value > 0.1), 3–5 plants were randomly selected to harvest approximately 20 g of mature, healthy leaves. Root samples were collected from at least three plants and transported to the laboratory.

Plant sample processing: Leaf fresh weight was measured using an electronic balance with 0.001 g precision. Mean individual leaf area (ILA) was calculated by analyzing scanned leaf images using ImageJ (64-bit) software. Leaf thickness (LT) was measured using a vernier caliper with 0.01 mm precision. Leaves were oven-dried at 80°C for 48 h to constant weight, then weighed to calculate specific leaf area (SLA), leaf tissue density (LTD), and leaf dry matter content (LDMC). Roots were washed with deionized water to remove adhering soil and impurities, and intact living roots (diameter < 2 mm) were selected. Root fresh weight was measured using an electronic balance with 0.001 g precision. A root scanner (WinRHIZO Pro 2009b) was used to analyze root length, average diameter (RAD), root surface area, and root volume. Samples were oven-dried at 80°C for 48 h and weighed to calculate specific root length (SRL), specific root area (SRA), and root tissue density (RTD).

Oven-dried root and leaf samples were ground into powder and passed through a 0.149 mm sieve. Leaf phosphorus concentration (LPC) and root phosphorus concentration (RPC) were determined using the acid dissolution-molybdenum antimony colorimetric method.

Soil sample collection: Soil salt content (SSC) and electrical conductivity (SEC) were measured on-site using a soil detector. Using a 50 mm × 50.46 mm cutting ring, three replicate samples from the 0–20 cm soil layer were collected in each quadrat to determine soil bulk density (SBD) and soil water content (SWC). Additionally, five replicate samples from the 0–20 cm soil layer were collected (in a quincunx pattern), mixed uniformly, and after removing impurities and air-drying, soil pH was measured using the potentiometric method. A portion of the sample was passed through a 0.149 mm sieve, and total phosphorus content (STP) was determined using the acid dissolution-molybdenum antimony colorimetric method.

1.3 Data Processing

One-way analysis of variance (ANOVA) was used to analyze differences in soil factors and plant leaf and root functional traits among different gradients. Results were expressed as means and standard deviations. For multiple comparisons, LSD tests were used when homogeneity of variance was confirmed, and Dunnett's T3 tests were used when heterogeneity was present (Xu et al., 2021). Pearson correlation analysis was employed to examine correlations among plant functional traits. Redundancy analysis (RDA) was used to analyze relationships between root and leaf functional traits and soil factors.

Microsoft Excel 2013, SPSS 26, and CANOCO 5 software were used for data processing, statistical analysis, and graphical presentation.

2.1.1 Leaf Functional Traits

The results showed that plant individual leaf area and leaf phosphorus content increased from sea to land. Leaf thickness exhibited the pattern T1 < T3 < T2, while specific leaf area showed T2 < T1 < T3. Leaf dry matter content and leaf tissue density gradually decreased from sea to land. The coefficient of variation for leaf functional traits across gradients ranged from 10.98% to 63.08%, 24.32% to 134.52%, and 30.54% to 88.48%, respectively. Leaf phosphorus content (LPC) showed significant differences among the three gradients ($P < 0.05$).

Table 2 Characteristics and correlation of plant leaf functional traits at different coastal distances

Trait	T1	CV (%)	T2	CV (%)	T3	CV (%)
LT (mm)	0.38 ± 0.148b	39.55%	0.86 ± 0.53a	61.77%	0.60 ± 0.42ab	69.92%
ILA (cm^2)	3.85 ± 1.54	40.08%	6.61 ± 8.89	134.52%	8.16 ± 7.22	88.48%
LDMC ($g \cdot kg^{-1}$)	240.48 ± 69.72a	28.99%	192.95 ± 85.99ab	44.56%	167.09 ± 58.91b	35.26%
SLA ($cm^2 \cdot g^{-1}$)	190.22 ± 74.02ab	38.91%	134.89 ± 56.72b	42.05%	230.21 ± 116.92a	50.79%
LTD ($g \cdot cm^{-3}$)	0.19 ± 0.12	63.80%	0.14 ± 0.09	72.27%	0.11 ± 0.06	56.08%
LPC ($g \cdot kg^{-1}$)	2.30 ± 0.25c	10.98%	3.64 ± 0.89b	24.32%	4.80 ± 1.47a	30.54%

Note: T1. Intertidal zone; T2. 30–60 m from the high tide line; T3. 90–120 m from the high tide line. Different lowercase letters indicate significant differences among gradients ($P < 0.05$). CV. Coefficient of variation (mean/standard deviation × 100%). The same below.

2.1.2 Fine Root Functional Traits

The results indicated that fine root average diameter, root tissue density, and root phosphorus content gradually increased from sea to land, while specific root length and specific root area gradually decreased. The coefficient of variation for root functional traits across gradients ranged from 14.72% to 91.85%, 32.41% to 136.24%, and 34.00% to 133.44%, respectively.

Table 3 Characteristics and correlation of plant root functional traits at different coastal distances

Trait	T1	CV (%)	T2	CV (%)	T3	CV (%)
RAD (mm)	0.61 ± 0.09b	15.87%	1.23 ± 0.57a	46.30%	1.30 ± 0.47a	35.75%
RTD ($g \cdot cm^{-3}$)	0.23 ± 0.13b	55.35%	0.29 ± 0.09ab	32.41%	0.34 ± 0.14a	41.83%
SRL ($m \cdot g^{-1}$)	119.40 ± 108.18a	90.60%	49.39 ± 67.28b	136.24%	39.21 ± 52.33b	133.44%
SRA ($m^2 \cdot g^{-1}$)	0.10 ± 0.09a	91.85%	0.03 ± 0.03b	76.84%	0.02 ± 0.01b	62.79%
RPC ($g \cdot kg^{-1}$)	1.59 ± 0.24b	14.72%	2.80 ± 1.15a	40.91%	3.66 ± 1.24a	34.00%

2.2 Functional Trait Correlation Analysis

Correlation analysis results showed that various leaf functional traits in the study area were interrelated. Specifically, leaf thickness showed extremely significant negative correlations with leaf dry matter content, specific leaf area, and leaf tissue density; leaf tissue density showed extremely significant negative correlation with leaf phosphorus content; and leaf dry matter content showed significant negative correlation with leaf phosphorus content. Leaf dry matter content showed extremely significant positive correlation with leaf tissue density, and specific leaf area showed extremely significant positive correlation with leaf phosphorus content.

Among fine root functional traits, fine root average diameter and root phosphorus content showed extremely significant negative correlations with specific root length and specific root area; root tissue density showed extremely significant negative correlation with specific root area; and specific root length showed extremely significant positive correlation with specific root area.

Varying degrees of correlation also existed between leaf and fine root functional traits. Specifically, extremely significant positive correlations were observed between leaf thickness and fine root average diameter; leaf dry matter content and specific root length/specific root area; specific root area and root phosphorus content; leaf tissue density and root tissue density/specific root length; and leaf phosphorus content and root tissue density/root phosphorus content. Significant positive correlations were found between specific leaf area and root tissue density, and between individual leaf area and root phosphorus content. Extremely significant negative correlations were observed between leaf thickness and specific root length; leaf dry matter content and fine root average diameter/root phosphorus content; leaf tissue density and specific root area/root phosphorus content; and leaf phosphorus content and specific root area. Significant negative correlations were found between leaf thickness and specific root area/root phosphorus content, and between leaf phosphorus content and specific root length.

Table 4 Correlation analysis of plant root-leaf functional traits

	LT	ILA	LDMC	SLA	LTD	LPC	RAD	RTD	SRL	SRA	R
LT	1										
ILA	-0.47**	1									
LDMC	-0.64**	-0.41**	1								
SLA	0.90**	-0.26*	-0.32**	1							
LTD	-0.46**	0.32**	0.83**	-0.44**	1						
LPC	0.52**	-0.52**	0.26*	0.75**	0.66**	1					
RAD	-0.24*	-0.57**	-0.28*	0.55**	-0.37**	-0.32**	1				
RTD	-0.45**	-0.36**	0.80**	-0.26*	0.27*	-0.34**	-0.46**	1			
SRL	0.49**	-0.46**	0.41**	-0.37**	-0.32**	-0.37**	-0.32**	0.41**	1		
SRA	0.33**	-0.44**	0.75**	-0.24*	0.83**	0.66**	-0.45**	0.80**	0.33**	1	
RPC	-0.37**	0.55**	-0.32**	0.49**	-0.36**	0.90**	-0.64**	-0.26*	-0.45**	-0.36**	1

*Note: ** indicates significant correlation at P < 0.01 level (two-tailed); * indicates significant correlation at P < 0.05 level (two-tailed). LT: Leaf thickness; ILA: Individual leaf area; LDMC: Leaf dry matter content; SLA: Specific leaf area; LTD: Leaf tissue density; LPC: Leaf phosphorus content; RAD: Root average diameter; RTD: Root tissue density; SRL: Specific root length; SRA: Specific root area; RPC: Root phosphorus content.*

2.3.2 Relationship Between Plant Root/Leaf Functional Traits and Soil Factors

RDA ordination was used to analyze plant functional trait responses to soil factors. The results showed that soil factors explained 52.05% of the variation. Soil salt content had the greatest influence, followed by soil water content > electrical conductivity > pH value > soil bulk density > soil total phosphorus content. Soil electrical conductivity, salt content, water content, and pH were positively correlated with leaf dry matter content, leaf tissue density, specific root length, and specific root area, but negatively correlated with root tissue density, leaf thickness, individual leaf area, specific leaf area, leaf phosphorus content, root phosphorus content, and fine root average diameter. Soil bulk density was negatively correlated with specific leaf area. Soil total phosphorus content was positively correlated with both fine root and leaf phosphorus content, but the correlations were weak.

Figure 1 [Figure 1: see original paper] Redundancy analysis (RDA) between plant root and leaf functional properties and soil factors

3.1 Plant Leaf/Root Functional Traits and Relationships Among Traits

The degree of variation in plant functional traits is often jointly influenced by habitat and species (Campetella et al., 2020). The results showed that the coefficient of variation for root and leaf functional traits was smallest in the intertidal zone and largest at the gradient 30–60 m from the high tide line. The intertidal zone suffers severe water-salt stress with extremely few surviving species, mainly *Cyperus rotundus* and *Stephania japonica*. Environmental filtering causes plant traits coexisting in local habitats to converge (He et al., 2021), meaning that in harsh, extreme environments, plants typically adopt similar traits to maintain mutually beneficial coexistence relationships (Laure et al., 2018; Cheng et al., 2022), resulting in low variation. At the gradient 30–60 m from the high tide line, the number of dominant species increased, and interspecific morphological characteristics with “respective strengths” formed survival advantages. For example, *Ipomoea pes-caprae* in this gradient possessed larger leaf area, conferring obvious aboveground competitive advantages, while *Cynodon dactylon* had greater specific root length, demonstrating strong belowground resource acquisition capacity, thereby causing large functional trait variation.

Differential changes in leaf functional traits across gradients showed leaf thickness following T1 < T3 < T2 and specific leaf area following T2 < T1 < T3. Individual leaf area and leaf phosphorus content increased from sea to land, while leaf dry matter content and leaf tissue density gradually decreased. Specific leaf area reflects plant light resource utilization capacity, while leaf thickness is closely related to resource acquisition and water retention capacity. T2, located 30–60 m from the high tide line, consists mostly of semi-mobile sandy land severely affected by sea winds, with serious sand burial and poor soil fertility. Plants in this zone had thicker leaves and lower specific leaf area, enabling more photosynthates to be allocated toward increasing mesophyll density and constructing protective tissues, thereby enhancing water and nutrient storage capacity (Kleiman & Aarssen, 2007). At T3, 90–120 m from the high tide line, environmental stress relatively decreased due to proximity to the coastal backbone forest belt dominated by *Casuarina equisetifolia*, and litter from *C. equisetifolia* improved soil properties and increased nutrient availability. Plants in this zone had reduced demand for nutrient and water storage in aboveground parts, decreased investment in defensive tissues, and increased leaf area to fully capture and utilize light resources (Yuan et al., 2020).

Differential changes in fine root functional traits across gradients showed that fine root average diameter, tissue density, and phosphorus content gradually increased from sea to land, while specific root length and specific root area gradually decreased. Generally, plants in arid, infertile environments are considered to have greater specific root length (Kramer-Walter et al., 2016) and smaller tissue density, promoting root elongation growth and accelerating turnover rates to enhance soil water and nutrient acquisition capacity (Melissa et al., 2015). In this study, plants in the intertidal zone had the greatest specific root length and specific root area, and the lowest fine root diameter and tissue density. On one hand, this may be because the soil in this gradient is beach-deposited sandy tidal soil with poor permeability; smaller root tissue density facilitates improved transport efficiency. On the other hand, the dominant species *Cyperus rotundus* and *Stephania japonica* belong to shallow-root systems that, to acquire as many resources as possible in the short term, allocate limited resources toward increasing specific root length and specific root area. Additionally, leaf phosphorus content was higher than root phosphorus content, possibly because coastal plants suffer severe salt stress, and plants allocate more nutrients to leaves to enhance synthesis of additional photosynthetic storage products, which benefits osmotic regulation and self-protection capacity (Castellanos et al., 2018; Liu et al., 2020).

In different growth environments, plants balance resource acquisition and allocation through trade-offs among functional traits, ultimately forming optimal trait combinations adapted to the environment (Wright et al., 2007). In this study, varying degrees of correlation existed among leaf traits, root traits, and root-leaf traits. Leaf dry matter content showed extremely significant positive correlation with leaf tissue density, while leaf thickness showed extremely significant negative correlations with specific leaf area, leaf dry matter content, and leaf tissue density, indicating that plants reduced leaf area while increasing mesophyll density, simultaneously using leaf photosynthates to accumulate dry matter and enhance risk avoidance capacity (Zhong et al., 2018). Leaf phosphorus content was negatively correlated with leaf dry matter content and leaf tissue density. High phosphorus content benefits plant photosynthesis and promotes growth, while plants with high dry matter content and tissue density have slower turnover growth rates and promote carbon accumulation to resist environmental stress (Dijkstra & Lambers, 1989), demonstrating trade-offs in resource allocation between growth and defense and strong adaptability. Fine root functional traits were similar to previous research results (Chen, 2022). Specific root length and specific root area reflect plant soil resource utilization efficiency, and the two showed extremely significant positive correlation. As specific root length increased, specific root area also continuously expanded, effectively extending the resource-available space of roots in soil. Generally, greater root tissue density indicates stronger resistance to physical damage and mechanical strength, and in natural environments, specific root area often shows negative correlation with it, reflecting plant resource allocation strategies in different environments to some extent (Zhang, 2014). Fine root phosphorus content and average diameter showed extremely significant negative correlations with specific root length and specific root area. Typically, smaller root diameter corresponds to higher root respiration rate, stronger metabolic activity, and shorter lifespan, meaning that specific root length and specific root area are not only related to nutrient absorption but also closely linked to root lifespan (Qiu et al., 2010; Eissenstat et al., 2000).

Habitat condition differences cause variation in trade-offs between paired traits (May et al., 2009). Traits representing stress resistance—leaf dry matter content and leaf tissue density—showed positive correlations with resource acquisition traits—specific root length and specific root area—indicating that water and nutrients acquired through belowground roots were used to enhance aboveground leaf defense construction. The study found that among aboveground-belowground corresponding traits, leaf thickness–fine root diameter and leaf–root phosphorus content showed positive correlations; however, specific leaf area with specific root area/specific root length, and leaf and root tissue densities showed no significant correlations, similar to findings in temperate grassland plants (Zhou et al., 2010). This may be because root structures are complex, with multi-level branching roots serving different functions and exhibiting uncertainty (Guo et al., 2004), and also due to influences from fine root sampling and processing methods (Qi et al., 2015).

3.2 Effects of Soil on Plant Root and Leaf Functional Traits

Soil plays a crucial role in shaping and forming plant functional traits. Redundancy analysis results of soil factors with plant leaf and root functional traits indicated that soil salt content, water content, electrical conductivity, and pH value were the main factors influencing coastal herb functional traits, demonstrating that plants are sensitive to soil water-salt changes. Analysis of soil factors at different coastal distances showed that soil salt content, water content, electrical conductivity, and pH value gradually decreased from coast to inland, while soil total phosphorus content was generally low. Correlation studies between plant functional traits and soil factors revealed that soil salt content, water content, electrical conductivity, and pH were positively correlated with leaf dry matter content, leaf tissue density, specific root length, and specific root area, but negatively correlated with leaf thickness, individual leaf area, specific leaf area, leaf phosphorus content, fine root average diameter, and fine root tissue density. Soil bulk density was negatively correlated with specific leaf area. In summary, plants closer to the sea had greater leaf dry matter content, leaf tissue density, specific root length, and specific root area, exhibiting a leaf “high-input, low-return” conservative strategy and a root “low-input, high-return” resource-acquisitive strategy. Conversely, plants farther from the sea had greater leaf area, specific leaf area, fine root diameter, and fine root tissue density, showing a leaf resource-acquisitive and root resource-conservative strategy.

Generally, higher soil salt content corresponds to higher soil electrical conductivity and pH value, all reflecting soil salinization-alkalization degree (Chu et al., 2020). Higher salt content, electrical conductivity, and pH value indicate high soil salinization and potential salt stress. As this coast is a sandy coast with low vegetation coverage, rapid surface heating, strong evaporation, and poor water-fertilizer retention capacity of sandy land, water becomes one of the important limiting factors for plant growth in desertified areas (Chang et al., 2017). Soil salt content, electrical conductivity, pH value, and water content decreased from sea to land. Plants closer to the sea had smaller leaf area and specific leaf area, which helps reduce water evaporation, maintain ionic balance, and prevent physiological drought. Simultaneously, these plants increased investment in structural construction costs, exhibiting high leaf dry matter content and tissue density to enhance leaf stress resistance and defense capacity. Roots adopted rapid resource acquisition strategies, increasing specific root length and specific root area to actively absorb soil nutrients and water to meet rapid growth demands, extending adventitious roots to expand living space and effectively utilize resources, and reducing root diameter to accelerate turnover rates. Additionally, high-salt environments affect plant nutrient absorption and utilization efficiency (Hou et al., 2001), as reflected in the negative correlations between soil salt content, electrical conductivity, pH value and leaf/root phosphorus content. This demonstrates that plants can adopt appropriate growth strategies to maximize compensation for habitat deficiencies and maintain their own growth and population reproduction. Soil bulk density is an important indicator of soil compactness and porosity (Zheng et al., 2018). Generally, greater soil bulk density indicates higher soil hardness and compactness, increasing difficulty in resource acquisition and transport. Insufficient resource supply may hinder aboveground development, manifested as smaller specific leaf area. The weak correlation between soil total phosphorus content and leaf/root phosphorus content suggests that leaf and root phosphorus content may not be directly determined by soil total phosphorus. Besides the high soil salt content in the study area affecting phosphorus absorption, plants may also adopt unique adaptation mechanisms. Studies have shown that when phosphorus is deficient, plants alter root external morphology or change root exudate types and concentrations to enhance rhizosphere soil phosphorus availability (Yu et al., 2022), thereby meeting their own demands.

This study analyzed coastal plant root-leaf functional trait characteristics and their relationships with soil factors. Influenced by differences in species numbers and environments, the degree of functional trait variation differed across gradients. Redundancy analysis results of functional traits and soil factors showed that soil salt content, water content, electrical conductivity, and pH value were the main factors affecting coastal herb functional traits, indicating plant sensitivity to soil water-salt changes. Due to soil heterogeneity and differences in plant species and numbers along the coastal gradient, functional traits exhibited varied expressions, representing different survival strategies: from sea to land, soil salt content, electrical conductivity, water content, and pH value gradually decreased, presenting an overall low-phosphorus, high-salinity-alkalinity environment. Plants closer to the sea adopted a “leaf resource-conservative, root resource-acquisitive” strategy, while those farther from the sea adopted a “leaf resource-acquisitive, root resource-conservative” strategy. These findings provide valuable references for understanding response mechanisms and adaptability of coastal herbaceous plants to environmental gradient changes, and facilitate selecting suitable species for gradient-based planting according to soil and other environmental characteristics, thereby promoting coastal vegetation restoration and protection. For example, the intertidal zone has extremely thin soil layers and severe water-salt stress, so plants with strong stress resistance, such as those with well-developed root systems and salt/flood tolerance, should be prioritized. From the supratidal zone to areas near coastal backbone forests, which are typically affected by sand burial, drought, and human disturbance but have gradually improving soil conditions, plants with “respective advantages” in functional traits can be selected to increase species diversity, strengthen human protection, and promote rapid coastal vegetation restoration.

However, factors influencing plant functional traits are diverse and complex. In addition to external environmental factors, species genetics must also be considered.

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