Effects of Environmental Factors on Stem and Leaf Functional Traits of Island Plants (Postprint)

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Abstract

The relationship between plant functional traits and the environment constitutes a focal point of functional trait research. As unique ecosystems, islands inevitably exhibit differences in plant functional traits compared to mainland. Taking forest communities of Pingtan Island as the research object, and through measuring 10 functional traits of stems and leaves along with 9 environmental factors of topography and soil, this study explores the trade-off relationships among plant functional traits and analyzes the influence of environmental factors on island plant functional traits. The results showed that: (1) Specific leaf area (SLA) was positively correlated with leaf nitrogen content (LNC) and leaf phosphorus content (LPC), and negatively correlated with leaf thickness (LT), leaf dry matter content (LDMC), stem tissue density (STD), and leaf carbon content (LCC); LDMC was negatively correlated with LNC and stem nitrogen content (SNC); LT was positively correlated with STD, and negatively correlated with LNC and LPC; LPC was positively correlated with LNC and SNC; C and N contents in both stems and leaves were positively correlated. (2) Soil organic matter and pH were the main soil influencing factors for island plant functional traits. However, due to the deficiency of phosphorus content in soil, LNC, LPC, and SNC were all positively correlated with soil total phosphorus; LDMC and STD were positively correlated with soil organic matter and soil total nitrogen content; SLA increased with increasing soil pH. (3) Slope position and slope gradient were the main topographic influencing factors for island plant functional traits. SLA and stem phosphorus content (SPC) decreased with increasing elevation; STD and LDMC increased with increasing elevation and slope gradient; LNC and LPC were greater on shady slopes than on sunny slopes. This study clarifies the ecological adaptation mechanisms of island vegetation, aiming to provide a reference basis for island vegetation restoration and reconstruction.

Full Text

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Abstract

The relationship between plant functional traits and environmental conditions represents a central focus of functional trait research. As unique ecosystems, islands inevitably exhibit differences in plant functional traits compared to mainland systems. This study examined forest communities on Pingtan Island by measuring ten functional traits of stems and leaves alongside nine environmental factors related to topography and soil. Our objectives were to explore trade-off relationships among plant functional traits and analyze how environmental factors influence these traits in island plants. The results revealed: (1) Specific leaf area (SLA) was positively correlated with leaf nitrogen content (LNC) and leaf phosphorus content (LPC), but negatively correlated with leaf thickness (LT), leaf dry matter content (LDMC), stem tissue density (STD), and leaf carbon content (LCC). LDMC showed negative correlations with LNC and stem nitrogen content (SNC). LT was positively correlated with STD but negatively correlated with LNC and LPC. LPC exhibited positive correlations with both LNC and SNC. Carbon and nitrogen contents in stems and leaves were all positively correlated. (2) Soil organic matter and pH emerged as the primary soil factors influencing island plant functional traits. Due to phosphorus deficiency in the soil, LNC, LPC, and SNC all showed positive correlations with soil total phosphorus. LDMC and STD were positively correlated with soil organic matter and total nitrogen content. SLA increased with rising soil pH. (3) Slope position and gradient were the main topographic factors affecting island plant functional traits. SLA and stem phosphorus content (SPC) decreased with increasing elevation, while STD and LDMC increased with elevation and slope gradient. LNC and LPC were greater on shady slopes than on sunny slopes. This study clarifies the ecological adaptation mechanisms of island vegetation and provides a reference basis for island vegetation restoration and reconstruction.

Keywords: island, plant functional traits, topography, soil, ecological strategy

Introduction

Plant functional traits are a series of morphological, physiological, and phenological characteristics that represent plant ecological strategies, reflect changes in plant habitats, and significantly influence ecosystem functions. Examples include leaf lifespan, leaf size, leaf thickness, seed size, and dispersal patterns (Diaz & Cabido, 2001; Liu et al., 2017). Variation in plant functional traits primarily manifests as differences in morphological structure and nutrient elements among major organs, resulting in multiple relationships among traits. The most universal of these is the trade-off relationship, representing trait combinations shaped by natural selection (Liu & Ma, 2015; Hu et al., 2014).

Leaf functional traits are closely related to plant growth strategies and resource utilization capabilities, reflecting the ecological strategies plants adopt in response to environmental changes. Stem functional traits correlate with plant defense and carbon sequestration capacities, serving as important indicators of plant growth and distribution. Investigating relationships between stem and leaf functional traits enhances understanding of species distribution and ecological adaptation processes.

In recent years, research on plant functional traits has extended to numerous ecological fields, with the relationship between functional traits and environment representing a key focus (Ding et al., 2011). Light, temperature, precipitation, and nutrients are the main environmental factors affecting plant functional traits, primarily manifested through differences in soil and topographic conditions (Diaz et al., 2010). Therefore, integrating the effects of soil and topographic factors on plant functional traits better reveals plant adaptation strategies to the environment. Soil acts as the dominant factor in forest communities, playing a crucial role in shaping plant functional traits (Li et al., 2016). Bu et al. (2013) noted that plant functional traits in tropical lowland rainforests are mainly influenced by soil pH and soil organic matter (SOM). Soil fertility shows positive correlations with specific leaf area (SLA), leaf nitrogen content (LNC), and leaf phosphorus content (LPC) (Jager et al., 2015), while soil infertility leads to smaller SLA and slower growth (Thuiller et al., 2004). Topographic factors influence plant functional traits primarily through variations in elevation, slope gradient, aspect, and position, which create differences in water, heat, and light conditions, thereby leading to different life strategies with distinct functional trait combinations (Liu & Ma, 2015). Related studies have found that SLA, LNC, and LT gradually increase with rising elevation (Craine & Lee, 2003). Pan et al. (2018) reported that SLA is greater on shady slopes than on sunny slopes, while LDMC and LT show the opposite pattern. Li et al. (2012) found that slope position primarily affects leaf size, LT, and LNC in forest communities. These findings demonstrate that relationships between soil, topography, and plant functional traits are complex, with plants coordinating various functional traits to adopt corresponding ecological strategies in different environments.

Islands represent relatively independent and complete ecosystems that are easily damaged and difficult to restore. As important components of island ecosystems, vegetation is significantly influenced by heterogeneous habitat factors and exhibits prominent functional traits (Huang et al., 2017). For instance, Huang et al. (2017) compared plant functional traits between islands and mainland, finding that island plants adapt to windy, dry, and nutrient-poor environments by being dominated by low shrubs and herbs with significantly smaller leaf sizes than mainland plants, featuring hairy leaves with lignified and succulent characteristics. However, current domestic research on islands has primarily focused on flora and diversity (Chi et al., 2015; Ye, 2017; Zheng et al., 2016), while studies based on island plant functional traits remain scarce. Therefore, this study examined forest vegetation on Pingtan Island by measuring ten functional trait indicators for stems and leaves, along with nine environmental factors related to topography and soil. Our objectives were to: (1) investigate the characteristics of trade-off relationships between stem and leaf functional traits in island forest communities; and (2) analyze the effects of soil and topographic factors on plant functional traits at the community level in island forests.

1. Materials and Methods

1.1 Study Area

Pingtan Island, the largest island in Fujian Province, is located in the central-northern part of the Taiwan Strait (119°32 -120°10 E, 25°15 -25°45 N) and represents the region of mainland China closest to Taiwan Province, with a highly special geographical position. The island experiences a humid, warm climate year-round with short winters and long summers, abundant rainfall, rare frost and snow, and a frost-free period of 326 days, characteristic of a south subtropical maritime monsoon climate. The average annual sunshine duration is 1,700–1,980 hours, with a mean annual temperature of 19.4°C. Precipitation concentrates mainly from February to June, with an average annual rainfall of 900–2,100 mm. The average annual evaporation (1,917.4 mm) far exceeds precipitation. Statistics indicate 125 days per year with winds exceeding level 7, with an average annual wind speed of 9.0 $\mathrm{m \cdot s^{-1}}$, and frequent tropical storms from July to September. The island suffers from scarce freshwater resources and limited river systems. Soils are sandy with low organic matter content, thin layers, and severe surface soil loss. The main soil types include lateritic red soil, saline soil, and aeolian sandy soil. The island' s vegetation features distinct dominant species, low species richness, highly fragile habitats, and simple community structure.

1.2 Field Sampling

Field sampling was conducted on Pingtan Island communities from June to October 2017. Based on extensive surveys of forest vegetation on the island, we randomly selected 16 sample plots, including 12 plots of 20 m × 20 m and 4 plots of 10 m × 10 m. All trees with diameter at breast height (DBH) $\geq$ 1 cm were measured, with DBH, tree height, and crown width recorded. Within each tree plot, four 5 m × 5 m shrub plots were established along the diagonal to survey shrub species, plant height, individual number, basal diameter, and coverage. At the center of each 5 m × 5 m shrub plot, one 1 m × 1 m herb plot was selected to investigate herbaceous species, coverage, and plant height. For each plot, we recorded the main vegetation type, species names, species count, plant height, slope gradient, slope aspect, slope position, longitude, latitude, and elevation. Basic information and community structure for each plot are presented in Table 1 .

Table 1 Basic information and community structure of sample plots

Sample plot	Elevation	Slope	Aspect	Slope position	Community structure
1	Sagereti athea-Panicum repens				
2	Urena procumbens-Paspalum thunbergii				
3	Rubus hirsutus-Miscanthus floridulus-Axonopus compressus				
4	Elaeagnus pungens-Miscanthus floridulus				
5	Pinus elliottii-Celtis sinensis-Urena procumbens				
6	Pinus elliottii-Litsea rotundifolia-Gardenia jasminoides				

Sample plot	Elevation	Slope	Aspect	Slope position	Community structure
7	Pinus thunbergii-Eurya emarginata-Dodonaea viscose				
8	Pinus elliottii-Casuarina equisetifolia-Urena procumbens				
9	Pinus thunbergii-Acacia confuse-Dodonaea viscose				
10	Litsea rotundifolia-Eurya emarginata-Melastoma candidum				
11	Eurya emarginata-Dodonaea viscose-Melastoma candidum				
12	Chukrasia tabularis-Murraya exotica-Ligustrum sinense				

Sample plot	Elevation	Slope	Aspect	Slope position	Community structure
13	Acacia confuse-Cinnamomum camphora-Litsea rotundifolia				
14	Casuarina equisetifolia-Psychotria rubra-Miscanthus floridulus				
15	Eurya emarginata-Litsea rotundifolia-Ardisia crenata				
16	Acacia confuse-Syzygium buxifolium-Litsea rotundifolia				

Note: Elevation and slope data are expressed as actual observed values. Aspect data start from east (0°) and rotate clockwise, classified into grades at 45° intervals: 1. North slope (247.5°-292.5°); 2. Northeast slope (292.5°-337.5°); 3. Northwest slope (202.5°-247.5°); 4. East slope (337.5°-22.5°); 5. West slope (167.5°-202.5°); 6. Southeast slope (22.5°-67.5°); 7. Southwest slope (112.5°-167.5°); 8. South slope (67.5°-112.5°). Larger numbers indicate more sun-exposed, hotter, and drier conditions (Zhang & Zhang, 2003). Slope position data: 1. Upper slope; 2. Middle slope; 3. Lower slope.

1.3 Plant Functional Trait Collection and Measurement

1.3.1 Plant Functional Trait Collection We calculated the importance values of tree, shrub, and herbaceous species in the 16 plots and collected stems and leaves from dominant species (importance value > 0.1). After identifying dominant species, we selected 5 or 10 healthy, mature individuals (5 for trees and shrubs, 10 for herbs) and collected fully expanded current-year leaves. To eliminate the effect of sun position on leaf nitrogen content, leaves were collected from four directions (east, south, west, north). For trees, leaves were taken from outer canopy branches; for shrubs, larger sun-exposed leaves were collected. Trees and shrubs were sampled by first cutting branches and then removing leaves with scissors, while herbs were sampled by directly cutting leaves (all without petioles). For each plant individual, 5-10 mature, well-developed leaves and 5-10 branches (1 cm $\leq$ DBH $\leq$ 2 cm) were collected. Sampling was conducted from July to September 2017.

1.3.2 Plant Functional Trait Measurement Plant functional traits were measured as follows. Fresh leaf samples were oven-dried at 60°C to constant weight (generally 72 hours) and then weighed for leaf dry mass. Leaf area was measured using a leaf area meter (LI-COR 3100C Area Meter, LI-COR, USA). Leaf thickness was measured using a vernier caliper (precision 0.01 mm) at three uniformly selected points 0.25 cm from the main vein, with the average of the three measurements taken as leaf thickness. Stem samples were peeled, and their volume was determined using the water displacement method before being oven-dried at 103°C to constant weight (generally 72 hours) and weighed. Dried leaf and stem samples were then analyzed for carbon, nitrogen, and phosphorus content. Carbon and nitrogen contents were determined using an elemental analyzer (Isoprime vario ISOTOPE cube, Germany), while phosphorus content was measured using the molybdenum-antimony anti-colorimetric method. The ten measured plant functional trait indicators, formulas, and ecological significance are listed in Table 2 .

Table 2 Ten plant functional traits and their formulas and ecological significance

Plant functional trait	English name and abbreviation	Formula and unit	Ecological meaning
Specific leaf area	SLA (m^2/kg) = leaf area (m^2) / leaf dry mass (kg)	Reflects plant ability to acquire light resources and self-protection under strong light	
Leaf dry matter content	LDMC (g/kg) = leaf dry mass (g) / leaf fresh mass (kg)	Reflects plant resource acquisition ability and resistance to physical damage	

Plant functional trait	English name and abbreviation	Formula and unit	Ecological meaning
Leaf thickness	LT (mm) = $(N_1+N_2+N_3)/3$	Reflects plant resource acquisition and water conservation	
Leaf phosphorus content	LPC (g/kg) = leaf total phosphorus (g) / leaf dry mass (kg)	Related to plant resource acquisition, metabolism, and growth	
Leaf nitrogen content	LNC (g/kg) = leaf total nitrogen (g) / leaf dry mass (kg)	Related to maximum photosynthetic rate, plant metabolism, and growth capacity	
Leaf carbon content	LCC (g/kg) = leaf total carbon (g) / leaf dry mass (kg)	Construction cost of leaf tissue, related to plant growth capacity	
Stem tissue density	STD (kg/mm^3) = stem dry mass (kg) / stem volume (mm^3)	Related to vertical structural support, material transport, and defense	
Stem nitrogen content	SNC (g/kg) = stem total nitrogen (g) / stem dry mass (kg)	Related to maximum photosynthetic rate, metabolism, growth, and defense	

Plant functional trait	English name and abbreviation	Formula and unit	Ecological meaning
Stem phosphorus content	SPC (g/kg) = stem total phosphorus (g) / stem dry mass (kg)	Related to plant resource acquisition, metabolism, and growth	
Stem carbon content	SCC (g/kg) = stem total carbon (g) / stem dry mass (kg)	Construction cost of leaf tissue, related to growth, development, and defense	

1.4 Soil Sampling

Soil samples were collected using a soil auger, with five soil cores (diameter 4 cm, length 20 cm) taken from each plot using the five-point sampling method. Samples were brought to the laboratory for chemical property analysis, including soil water content (WC), pH value, organic matter (SOM), total nitrogen (TN), and total phosphorus (TP).

1.5 Data Processing

Community-weighted mean functional trait values (CWM) were calculated by weighting species-level functional trait values by species abundance to obtain average plant functional trait values at the community level. Community functional trait values were computed using the FD package in R 3.5.0. Pearson correlation analysis was employed to explore relationships between stem and leaf functional traits. Redundancy analysis (RDA) was performed to further verify relationships between plant functional traits and environmental factors using the Vegan package in R 3.5.0.

2. Results and Analysis

2.1 Variation in Plant Functional Traits

As shown in Table 3 , plant functional traits on Pingtan Island varied considerably, particularly SLA, STD, and SPC, which ranged from 33.01-1.01 $m^2 \cdot kg^{-1}$, 0.13-5.60 $kg \cdot mm^{-3}$, and 0.01-0.88 $g \cdot kg^{-1}$, respectively.

Table 3 Variation in plant functional traits on Pingtan Island

Functional trait	Min	Max	Mean ± SE
SLA ($m^2 \cdot kg^{-1}$)	1.01	33.01	11.39 ± 0.59
LDMC ($g \cdot kg^{-1}$)	168.00	625.00	386.00 ± 10.37
LT (mm)	0.13	1.02	0.32 ± 0.17
LPC ($g \cdot kg^{-1}$)	0.12	1.38	0.53 ± 0.06
SPC ($g \cdot kg^{-1}$)	0.01	0.88	0.22 ± 0.29
LNC ($g \cdot kg^{-1}$)	7.21	18.56	10.90 ± 2.19
LCC ($g \cdot kg^{-1}$)	416.23	492.12	461.66 ± 3.30
SNC ($g \cdot kg^{-1}$)	3.21	8.56	5.32 ± 0.18
SCC ($g \cdot kg^{-1}$)	0.12	2.89	0.66 ± 0.29
STD ($kg \cdot mm^{-3}$)	0.21	0.65	0.32 ± 0.02

Note: SLA = Specific leaf area; LDMC = Leaf dry matter content; LT = Leaf thickness; STD = Stem tissue density; LPC = Leaf phosphorus concentration; SPC = Stem phosphorus concentration; LNC = Leaf nitrogen concentration; LCC = Leaf carbon concentration; SNC = Stem nitrogen concentration; SCC = Stem carbon concentration.

2.2 Variation in Soil Factors

As shown in Table 4 , soil TN content on Pingtan Island was higher than the national average (0.65 $g \cdot kg^{-1}$), while soil TP content was lower than the national average (0.56 $g \cdot kg^{-1}$), indicating phosphorus deficiency and acidic soil conditions.

Table 4 Variation in soil characteristics on Pingtan Island

Soil factor	Min	Max	Mean ± SE
SOM ($g \cdot kg^{-1}$)	3.21	28.56	19.99 ± 3.73
TN ($g \cdot kg^{-1}$)	0.56	4.23	2.45 ± 0.155
TP ($g \cdot kg^{-1}$)	0.01	0.98	0.22 ± 0.29
WC (%)	3.21	18.56	10.90 ± 2.19
pH	4.21	6.89	5.32 ± 0.18

Note: SOM = Soil organic matter; TN = Total nitrogen; TP = Total phosphorus; WC = Water content; pH = pH value.

2.3 Relationships Between Stem and Leaf Functional Traits

Pearson correlation analysis of stem and leaf functional traits for dominant species across all plots revealed significant patterns (Table 5). SLA was extremely significantly positively correlated with LPC and LNC, significantly positively correlated with SNC, extremely significantly negatively correlated with LT, LCC, and SCC, and significantly negatively correlated with LDMC and

STD. LDMC was significantly positively correlated with SCC, extremely significantly negatively correlated with SNC, and significantly negatively correlated with LNC. LT was significantly positively correlated with STD, extremely significantly negatively correlated with LNC, and significantly negatively correlated with LPC. LPC was extremely significantly positively correlated with both LNC and SNC. SPC was extremely significantly positively correlated with SNC. LNC was extremely significantly positively correlated with SNC. LCC was extremely significantly positively correlated with SCC. In summary, carbon and nitrogen contents in leaves and stems were all positively correlated.

Table 5 Correlations among stem and leaf functional traits

Functional trait	SLA	LDMC	LT	STD	LPC	SPC	LNC	LCC	SNC	SCC
SLA	1									
LDMC	-0.196*	1								
LT	-0.471**	-0.277*	1							
STD	-0.283**	0.281**	0.329**	1						
LPC	0.217*	-0.458**	-0.227*	-0.234*	1					
SPC	0.443**	0.336**	-0.212*	-0.282**	0.395**	1				
LNC	-0.295**	0.227*	0.443**	0.498**	0.491**	0.336**	1			
LCC	-0.283**	0.281**	0.329**	0.217*	-0.234*	-0.282**	0.443**	1		
SNC	-0.458**	-0.277*	0.329**	0.498**	0.491**	0.395**	0.336**	0.217*	1	
SCC	0.227*	-0.234*	-0.283**	-0.282**	0.395**	0.443**	0.336**	0.498**	0.491**	1

*Note: **P < 0.01, *P < 0.05.*

2.4 Relationships Between Plant Functional Traits and Environmental Factors

Redundancy analysis (RDA) was used to analyze correlations between plant functional traits and environmental factors (Figure 1 [Figure 1: see original paper]). Results showed that soil factors explained 54.44% of the variation, with soil SOM having the greatest influence, followed by pH, TP, TN, and WC. Topographic factors explained 35.26% of the variation, with slope position having the greatest influence, followed by slope gradient, aspect, and elevation.

Regarding relationships between soil and functional traits (Figure 1a), LNC, LPC, and SNC were positively correlated with soil TP. LT and LCC were positively correlated with soil TN. LDMC and STD were positively correlated with soil SOM and TN but negatively correlated with pH. SLA was positively correlated with soil pH.

Regarding relationships between topographic factors and functional traits (Figure 1b), SLA and SPC were positively correlated with slope position but negatively correlated with elevation and slope gradient. LNC and LPC were positively correlated with aspect. STD, LDMC, and LCC were positively correlated with elevation and slope gradient but negatively correlated with slope position.

Note: Redundancy analysis (RDA) of correlations between plant functional traits and environment: The arrow length and angle between two line segments indicate the correlation strength between plant functional traits and environmental factors. Longer arrows indicate stronger correlations, and vice versa. An angle of 0°-90° indicates positive correlation, 90°-180° indicates negative correlation, and 90° indicates no significant correlation (Ding et al., 2011).

Figure 1 Redundancy analysis of plant functional traits with soil parameters (a) and topographic variations (b)

3. Discussion

3.1 Trade-off Relationships Between Stem and Leaf Functional Traits in Island Vegetation

Trade-off relationships represent the most universal connections among plant functional traits, also termed "ecological strategies," referring to optimal trait combinations shaped by natural selection (Westoby et al., 2002; Diaz et al., 2004). These trade-offs primarily include relationships between leaf and stem traits. Our study found that island plant functional trait SLA was significantly positively correlated with LPC and LNC, and significantly negatively correlated with LT, LDMC, STD, and LCC, consistent with findings by Wright et al. (2001) and Reich et al. (2001). SLA is related to plant potential growth rate and photosynthetic rate (Mao et al., 2012). Nitrogen is a crucial component of photosynthetic proteins and closely related to photosynthesis (Zhou et al., 2015). Phosphorus is an essential element of ATP for energy transfer and participates in photosynthate transport (Zhao et al., 2016). Therefore, SLA, LNC, and LPC are positively correlated, collectively reflecting plant capacity to acquire light resources. Conversely, SLA is negatively correlated with LDMC; increased LDMC (i.e., decreased SLA) increases the distance and resistance for internal water diffusion to the leaf surface, thereby reducing water loss (Liu et al., 2017). LT plays an important role in plant growth and is closely related to resource acquisition and water conservation. STD is an important stem functional trait reflecting plant growth rate and resistance capacity. Plants with low SLA are adapted to nutrient-poor, dry environments, featuring thicker leaf margins or greater tissue density (Wright et al., 2004). These plants allocate more photosynthate to leaf defense structures, manifested in the ecological strategy of increasing LT and STD while reducing leaf area (Wright et al., 2002). Additionally, LDMC was negatively correlated with LNC, consistent with results from Li et al. (2012), indicating a trade-off between plant structural tissue and resource allocation, particularly protein allocation involved in cellular processes, most importantly photosynthesis (Xu et al., 2016). Our study also found significant positive correlations between carbon and nitrogen contents in stems and leaves, and between LPC and LNC/SNC, indicating that nitrogen and phosphorus are synergistic elements whose interactions influence plant ecological trade-offs (He & Han, 2010).

3.2 Effects of Soil on Island Plant Functional Traits

Soil constitutes an important component of forest ecosystems, affecting plant survival and distribution and playing a crucial role in shaping plant functional traits (Chai, 2016). Our study identified soil SOM, pH, and TP as the main factors influencing island plant functional traits, consistent with Chytry et al. (2008). Pingtan Island frequently experiences natural disasters such as storm surges and salt spray, resulting in severe soil salinization. Consequently, soil pH became one of the main factors affecting island plant functional traits, directly influencing element transformation in soil, affecting not only plant nutrient absorption but also community species composition and functional trait variation (Zhang, 2014). Soil SOM, as an important component of ecosystem carbon cycling, plays a significant role in forming leaf dry matter and structural composition (Kang et al., 2017), resulting in positive correlation between LDMC and SOM.

Additionally, soil TP content on Pingtan Island is extremely deficient, possibly because highly weathered soils in subtropical regions have large amounts of phosphorus adsorbed and fixed by iron and aluminum oxides, making plant uptake difficult. Furthermore, high temperatures and abundant rainfall on Pingtan Island cause leaching and loss of soil phosphorus (Zeng et al., 2018). This makes phosphorus one of the limiting nutrient elements for forest communities on the island, rendering plant functional traits highly sensitive to soil TP content (Ding et al., 2011). Plant functional traits serve as effective tools for reflecting plant utilization mechanisms of soil nutrients (Orwin & Bardgett, 2010). Generally, plants in nutrient-poor environments have smaller SLA, while those in resource-rich environments have larger SLA (Wright et al., 2002). However, our study found weak correlation between SLA and soil nutrients, possibly because drought, strong solar radiation, and frequent typhoons on Pingtan Island (Zhang et al., 2017) have led island plants to adapt by forming small leaves to reduce wind damage and water loss. This suggests that SLA is influenced by complex factors, including not only soil nutrients but also topography, climate, and species biological characteristics (Pan, 2018). In our study, STD was positively correlated with soil SOM and TN content, consistent with Kang et al. (2017), possibly because soil TN is mainly used for synthesizing cellulose and lignin to enhance stem hardness (Wright et al., 2001). Additionally, frequent strong winds on Pingtan Island have selected for species with slower growth rates and higher wood density, which can improve habitat conditions and increase soil nutrients.

3.3 Effects of Topography on Island Plant Functional Traits

Topography represents a composite of multiple environmental factors, with changes in temperature, water, and soil nutrients concentrated in topographic gradients, which are reflected in variations in plant functional traits (Loreau et al., 2001). Our study found that slope position had the greatest influence on island plant functional traits, followed by slope gradient, aspect, and elevation. Elevation had the smallest effect on Pingtan Island plant functional traits, possibly because the relative elevation difference among surveyed plots was small (232 m), with no significant decrease in water and heat conditions limiting plant growth. Our results showed that slope gradient and elevation were positively correlated with STD, LDMC, and LCC, but negatively correlated with SLA and SPC. Slope gradient affects runoff and soil erosion intensity, indirectly influencing soil nutrient and water distribution. Elevation affects plant functional traits mainly by influencing temperature, water, CO_2, and other factors required for plant growth, leading to changes in ecological adaptation (Westoby et al., 2002). With increasing slope gradient and elevation, plants tend to reduce SLA and increase LDMC and STD, allocating more resources to defensive tissues to enhance leaf resistance against nutrient loss caused by erosion. In undulating forest land, different slope positions create different habitats: upper slopes have intense solar radiation, high temperatures, thin soil layers, and low soil nutrient and water content, while middle and lower slopes have higher soil nutrient content than upper slopes (Yang et al., 2014). Consequently, SLA gradually increases from upper to lower slopes, while STD and LDMC gradually decrease, consistent with Qi et al. (2008). Slope aspect mainly causes differences in wind direction and solar radiation, affecting the distribution of light, heat, water, soil, and vegetation. Wright & Westoby (2001) noted that more sun-exposed and drier areas have higher LNC and LPC, consistent with our study. Additionally, to prevent leaf water loss, leaves typically feature hairy, thick leathery characteristics, manifested as positive correlations between aspect and LNC/LPC and negative correlation with LT.

In conclusion, compared to mainland areas, islands are more vulnerable to natural disasters and have fragile ecosystems that are difficult to restore once damaged. To adapt to their special environment, island plants coordinate stem and leaf functional traits to adopt corresponding ecological strategies. Soil SOM and slope position are the main environmental factors affecting island plant functional traits. This study extends research on mainland plant functional traits to island forest vegetation, better revealing adaptation strategies of island plants under land-sea interactions and providing a reference basis for species selection in island vegetation restoration and reconstruction.

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