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**Research Article**

# Adaptive strategies in plant life forms: assessing the variations in leaf ecological stoichiometry and functional traits

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## Abstract

The study of leaf functional traits and leaf ecological stoichiometry is of great significance for understanding plant adaptation strategies and nutrient uptake and utilization. In order to explore the adaptation mechanism of different life types to humid and hot subtropical environment, this study analyzed the leaf functional traits and ecological stoichiometric characteristics and associations of different life types of plants (trees, shrubs and herbs) with 54 common subtropical plants as research objects. The results showed that there were significant differences in leaf functional traits among different life types, and specific leaf area and leaf water content were the key functional traits to regulate ecological stoichiometry. Different life types of plants have different regulation patterns, and they adopt different ecological strategies to adapt to the heterogeneity of subtropical environment. In general, herbs showed a "fast – return on investment" strategy, and trees tended to be "slow – return on investment" strategy.

***Keywords:*** adaptive strategies; ecological stoichiometry; leaf functional traits; plant life forms

## Introduction

Plants are crucial in terrestrial ecosystems, and their growth is directly affected by global climate and environmental changes (Wang *et al.*, 2020; Zhang, S *et al.*, 2020). Plants respond to these changes through physiological characteristics, leaf morphology, species distribution, element cycling and community composition, forming complex ecological networks (Reich *et al.*, 2003; Arndt, 2006; Hidalgo-Triana *et al.*,

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2018; Fanin *et al.*, 2020). Functional traits of plants are the core attributes that affect their growth, reproduction and ecological adaptability (Violle *et al.*, 2007). It can reflect, individually or jointly, plant responses to environmental changes and affect ecosystem functions (Wright *et al.*, 2004). Because these traits are easy to measure and have strong plasticity, they become important tools for studying plant resilience and species differences (Huang *et al.*, 2022). As the main part of plant contact with the environment, leaves are particularly sensitive to climate and environmental changes (Klich, 2000). Changes in leaf structure and chemical composition drive species functional differences, and thus affect species coexistence and ecological differentiation (Sack & Frole, 2006; Peppe *et al.*, 2011). Leaf functional traits are closely related to plant biomass and resource use efficiency, and their changes reflect plant environmental adaptation strategies (Osnas *et al.*, 2018). Therefore, leaf functional traits are a key perspective to study plant environmental adaptability, which helps to reveal plant survival strategies, ecological construction mechanisms and biodiversity maintenance processes (Kraft *et al.*, 2008; Laughlin *et al.*, 2017). Plant functional traits are closely related to ecological stoichiometry, which is an important ecological index reflecting plant structure, functional characteristics and nutrient restriction (Koerselman and Meuleman, 1996; Güsewell and Koerselman, 2002). The ecological stoichiometric characteristics of plants directly affect the distribution of plant nutrient elements, and are key factors affecting plant physiological and biochemical cycles, which have great significance for vegetation renewal and ecosystem function (Roa-Fuentes *et al.*, 2015). Therefore, the study of nutrient distribution, circulation and restriction of plant growth from the perspective of ecological stoichiometry is an important means to understand the influencing factors and mechanisms of ecosystem processes (McGroddy *et al.*, 2008; Rastetter *et al.*, 2013).

Plant functional traits and ecological stoichiometry in a typical habitat can characterize the characteristics of plant physiological and ecological processes in the region, and can represent important indicators of plant adaptation to the environment to the greatest extent (Feng *et al.*, 2008). Studies have indicated that leaf functional traits and ecological stoichiometry are influenced by large-scale climatic factors (Freschet *et al.*, 2010; Sundqvist *et al.*, 2011; Mason *et al.*, 2012). Temperature and precipitation have been shown to be the most important climatic factors, leading to changes in plant functional traits and ecological stoichiometry (Sellin *et al.*, 2013; Dong & Liu, 2017). The existing research results indicate that there may be obvious differences in the ecological stoichiometry of plants in different regions and climate types (Hooker and Compton, 2003; Zeng *et al.*, 2017; Liang *et al.*, 2018). Currently, there are many research reports on plant functional traits and ecological stoichiometry of forest ecosystems in cold and dry areas, such as Xinjiang and Three Rivers Headwaters Region (Hu *et al.*, 2012; Wang *et al.*, 2022), Northeast China (Ling *et al.*, 2022), arid and semi-arid region of Northwest China (Liu *et al.*, 2018; Yang *et al.*, 2020; Shui *et al.*, 2022), and Loess Plateau in Central China (Duan *et al.*, 2022), and arid forests in California of USA (Pezner *et al.*, 2020), arid regions in Southwestern Iberian Peninsula, Europe (Nunes *et al.*, 2017). However, there are few reports on the characteristics and variation of plant functional traits and ecological stoichiometry, and the relationship between them under high water and heat conditions. Nanning has a subtropical monsoon climate, abundant sunshine, abundant rainfall, relatively hot climate, high vegetation coverage, rich species diversity, is an important species gene pool. The functional traits and stoichiometric characteristics of different life types (trees, shrubs and herbs) were studied with 54 common plants in the Precious Plant Tree Species Garden of Qingxiu Mountain. To answer the following questions: (1) What are the differences in functional traits and ecological stoichiometry of different life type plants under the high humid and hot subtropical environment? (2) How do leaf functional traits affect plant ecological stoichiometry, and what are the differences in this effect on different life forms?

## Materials and Methods

### *Research area*

The study area is situated in the southeastern part of Nanning, Guangxi, China, with geographic coordinates ranging from 108° 21' to 108° 27' E and 22° 45' to 22° 48' N. This region is characterized by a southern subtropical monsoon climate, influenced by oceanic conditions, featuring year-round sunshine, plentiful rainfall, a mild climate with infrequent frost, and no snow, resulting in prolonged summers and brief winters. The region's average annual temperature registers at 21.6 °C, with January as the coldest month, averaging 12.5 °C, July as the warmest, averaging 28.7 °C, and the record maximum temperature reaching 40.4 °C. The region receives an average annual rainfall of 1304.2 millimeters, with the average relative humidity standing at 79%.

### *Sample collection and measurement*

On March 15 2023, leaf samples were gathered from the Qingxiushan Mountain Precious Tree Species Exhibition Garden. A total of 54 plant species were sampled (31 tree species, 13 shrub species, and 10 herbs species), selecting 3 to 5 specimens per species based on robust growth and size uniformity. High branch shears were used to collect outermost branches from the eastern, southern, western, and northern sides of the plant. Complete, mature and healthy shoots of the current year were collected using high branch shears. Thirty leaves were collected from each species. To mitigate leaf dehydration, the collected samples were placed in Ziplock bags containing moist paper towels. After being sealed and labeled, they were stored in a dark environment and promptly transported to the laboratory for analysis.

Measurements of each functional trait were conducted in accordance with the Global Plant Functional Standardized Character Determination Manual (Perez-Harguindeguy *et al.*, 2016). The assessment of leaf functional traits encompassed chlorophyll content (CHL), leaf thickness (LT), leaf fresh weight (LFW), leaf area (LA), and leaf dry weight (LDW). Leaf ecological stoichiometry measurements included leaf carbon content (LCC), leaf nitrogen content (LNC), leaf phosphorus content (LPC), and leaf potassium content in leaves (LKC). Leaf thickness is measured at an intermediate position between the edge and midvein, between the tip of the leaf and the base, avoiding important secondary veins. Leaf area (LA) was assessed using the LI-COR3000C leaf area meter. Determination of leaf fresh weight (LFW) using a balance with a precision of 0.001 g. Leaves were placed in an oven at 105 °C for half an hour and subsequently dried at 75 °C until a constant weight was achieved to ascertain their dry weight. Chlorophyll content was gauged using a portable chlorophyll meter (SPAD-502), with the obtained SPAD values indicative of the chlorophyll levels. The dried leaves were pulverized using a multi-sample tissue grinder, and total carbon (TOC) levels were quantified using a MULTIN/C3100 total organic carbon analyzer. Following digestion with concentrated sulfuric acid, leaf total N content was assessed via the sodium salicylate colorimetric method (Willis *et al.*, 1996), total P through the molybdenum antimony colorimetric method, and total K using a flame photometer (Bao, 2000) .

SLA (specific leaf area) = LA/LDW
LWC (leaf water content) = (LFW－LDW)/LFW
LV (leaf volume) = LA×LT
LTD (leaf tissue density) = LDW/LV
C/N = LCC/LNC
C/P = LCC/LPC
N/P = LNC/LPC
P/K = LPC/LKC

### *Data analysis*

Basic information on the 54 plant species is presented in Supplementary Table 1. We calculated the coefficient of variation (cv = sd / mean) to quantify the variation of each trait at different levels. The measured data of all species were used for the individual level, the average value of each species was used for the interspecific level, and the average value of each life type was used for the interlife-type level. For tree level, the average of tree species is calculated, for shrub level, the average of shrub species is calculated, and for herb level, the average of herb species is calculated. The data of most indicators still do not conform to the normal distribution after corresponding transformation of the data, so the Wilcoxon test (P-values were corrected by using bonferroni) is used to assessed differences in leaf functional traits and ecological stoichiometry among plants with different life forms. Spearman correlation analysis was employed to examine the interrelationships between leaf functional traits and ecological stoichiometry. Redundancy analysis (RDA) was utilized to investigate the impact of leaf functional traits on ecological stoichiometry. Hierarchical partitioning (Lai *et al.*, 2022) was applied to quantify the individual contributions of each functional trait to the ecological stoichiometry of leaves. Path analysis using the PiecewiseSEM package was conducted to study the direct effects of functional traits on ecological stoichiometry (Lefcheck, 2016). All the aforementioned statistical analyses and corresponding graphical representations were performed in R version 4.2.2.

## **Results**

### *Patterns of leaf variation*

As shown in Table 1, the individual coefficients of variation for the 17 leaf functional traits and eco-chemometrics ranged from 12.01% to 135.70%. Interspecific variation was evident across all 17 indicators, both within and among life-types. The difference among tree species was the smallest (51.52), followed by shrub species (60.86), and herb species had the largest difference (63.90). Among these indicators, LV, LFW, LA, and LDW exhibited greater variation compared to other traits. LV demonstrated the highest interspecific variation (128.52%), while LCC exhibited the lowest (11.22%).

Among the 54 plant species studied, the tree plant *Quercus neglecta* had the lowest CHL and LPC, but the highest C/P and N/P. The tree plant *Podocarpus macrophyllus* exhibited the lowest values for LA, SLA, and LKC, but the highest CHL. The herb *Tradescantia zebrina* had the lowest LTD, but the highest LT and LWC. The herb *Ctenanthe oppenheimiana* showed the highest values for LFW, LA, and LV. The shrub plants *Megaskepasma erythrochlamys* had the lowest C/P ratio, but the highest LPC and LKC. In general, ecological stoichiometric minimums are mainly found in the upper layers of plants (trees), and ecological stoichiometric maximums are mainly found in the lower layers (herbs and shrubs).

### *Leaf functional traits among different plant life forms*

Leaf functional traits differed significantly between species (Supplementary Figures 1 to 9). There are significant differences in leaf functional traits among different plant life forms (Figure 1). Specifically, indicators such as SLA and LWC are highest in herbs and lowest in trees. LT, LFW, L), and LV also reach their maximum values in herbs, with no significant differences observed between trees and shrubs. Leaf tissue density (LTD) is highest in trees and lowest in herbs. Chlorophyll content (CHL) and leaf dry weight (LDW) are highest in trees, with no significant differences found between shrubs and herbs.

### *Ecological stoichiometry among different pant life forms*

Ecological Stoichiometry indicators differed significantly between species (Supplementary Figures 10 to 17). The P/K ratio shows no significant differences among trees, shrubs, and herbs, but all other indicators exhibit significant variations among different life types (Figure 2). Leaf nitrogen content (LNC) is higher in herbs than in trees. Leaf phosphorus content (LPC) and leaf potassium content (LKC) show no significant differences between shrubs and herbs, and LPC and LKC are the lowest values in trees. Leaf carbon content (LCC), C/P and N/P ratios show no significant differences between shrubs and herbs, and the highest values are found in trees. C/N ratio are highest in trees and lowest in herbs.

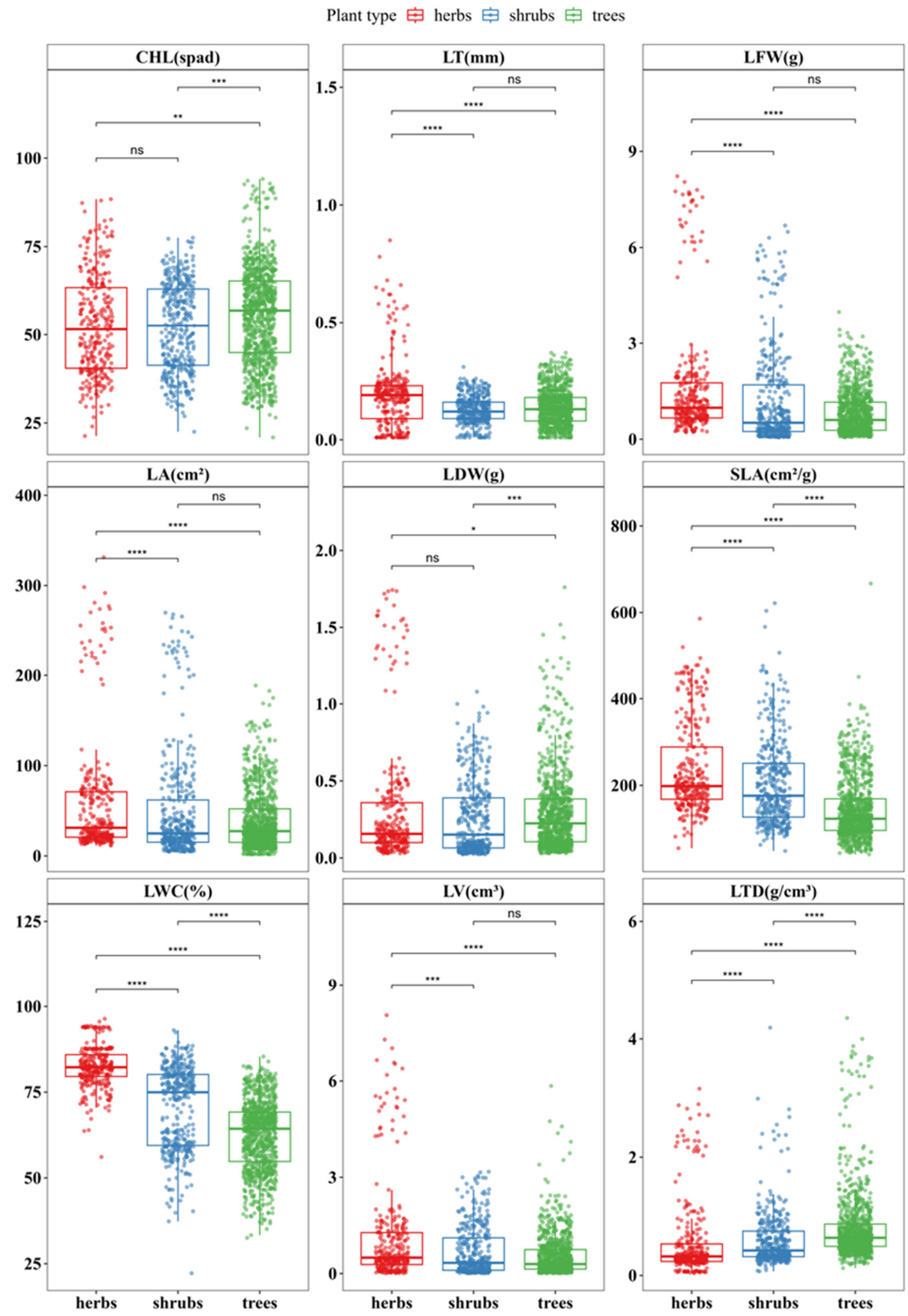


**Figure 1.** Differences in leaf functional traits among herbs, shrubs, and trees

CHL: chlorophyll content, LT: leaf thickness, LFW: leaf fresh weight, LA: leaf area, LDW: leaf dry weight, SLA: specific leaf area, LWC: leaf water content, LV: leaf volume, LTD: leaf tissue density. ns: non-significant; *$0.01 < p < 0.05$; **$0.001 < p < 0.01$; ***$0.0001 < p < 0.001$; ****$0.0001 < p$.

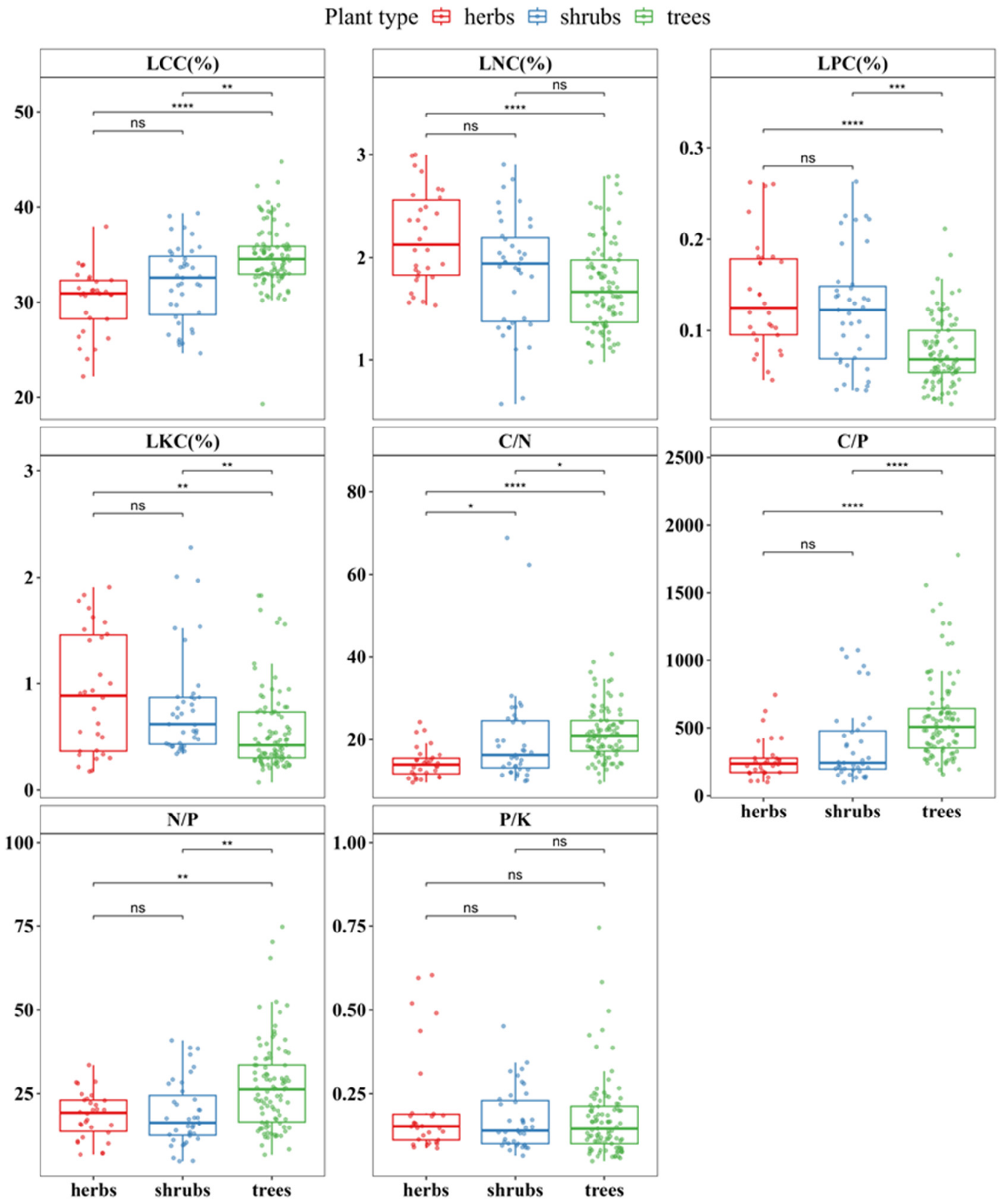


**Figure 2.** Differences in leaf ecological stoichiometry among herbs, shrubs, and trees

LCC: leaf carbon content, LNC: leaf nitrogen content, LPC: leaf phosphorus content, LKC: leaf potassium content, C/N: LCC/LNC, C/P: LCC/LPC, N/P: LNC/LPC, P/K: LPC/LKC. ns: non-significant; *0.01 < $p$ < 0.05; **0.001 < $p$ < 0.01; ***0.0001 < $p$ < 0.001; ****0.0001 < $p$.

**Table 1.** Coefficient of variation (CV) in leaf functional traits and leaf ecological stoichiometry

| Variable | Mean | SD | Median | Min | Max | Individual cv (%) | Interspecific cv (%) | Life forms cv (%) | Tree species cv (%) | Shrub species cv (%) | herb species cv (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| CHL | 54.15 | 13.49 | 55.2 | 20.9 *Quercus neglecta* | 94.1 *Podocarpus macrophyllus* | 24.91 | 22.85 | 3.51 | 22.86 | 21.24 | 25.94 |
| LT | 0.15 | 0.09 | 0.14 | 0.01 *Averrhoa carambola* | 0.85*Tradescantia zebrina* | 63.48 | 60.37 | 21.91 | 52.87 | 43.33 | 75.46 |
| LFW | 1.06 | 1.23 | 0.69 | 0.06 *Calliandra haematocephala* | 8.23 *Ctenanthe oppenheimiana* | 115.92 | 112.88 | 34.53 | 76.73 | 126.04 | 113.99 |
| LA | 45.2 | 48.57 | 27.43 | 1.68 *Podocarpus macrophyllus* | 331.26 *Ctenanthe oppenheimiana* | 107.45 | 104.67 | 21.47 | 79.86 | 122.9 | 113.76 |
| LDW | 0.29 | 0.28 | 0.2 | 0.02 *Reinwardtia indica* | 1.76 *Woonyoungia septentrionalis* | 98.84 | 93.42 | 10.26 | 80.12 | 90.11 | 130.34 |
| SLA | 176.46 | 93.56 | 151.38 | 40.73 *Podocarpus macrophyllus* | 666.97 *Yulania soulangeana* | 53.02 | 49.62 | 24.06 | 46.54 | 43.96 | 42.85 |
| LWC | 68.15 | 12.57 | 67.95 | 22.22 *Aglaia odorata* | 96.38 *Tradescantia zebrina* | 18.44 | 17.78 | 13.98 | 15.52 | 16.15 | 7.06 |
| LV | 0.68 | 0.93 | 0.36 | 0.01 *Reinwardtia indica* | 8.05 *Ctenanthe oppenheimiana* | 135.70 | 128.52 | 38.17 | 102.81 | 108.59 | 141.18 |
| LTD | 0.71 | 0.58 | 0.56 | 0.04 *Tradescantia zebrina* | 4.35 *Hovenia acerba* | 82.40 | 73.1 | 20.46 | 66.52 | 69.09 | 102.71 |
| LCC | 33.22 | 3.99 | 33.33 | 19.3 *Camellia japonica* | 44.78 *Callistemon rigidus* | 12.01 | 11.22 | 7.1 | 8.39 | 12.6 | 11.21 |
| LNC | 1.84 | 0.49 | 1.85 | 0.57 *Rhododendron lapponicum* | 3 *Piper sarmentosum* | 26.70 | 25.78 | 12.52 | 23.18 | 29.59 | 20.93 |
| LPC | 0.1 | 0.06 | 0.09 | 0.02 *Quercus neglecta* | 0.26 *Megaskepasma erythrochlamys* | 56.24 | 54.73 | 28.4 | 44.9 | 51.92 | 44.64 |
| LKC | 0.68 | 0.47 | 0.5 | 0.07 *Podocarpus macrophyllus* | 2.28 *Megaskepasma erythrochlamys* | 69.56 | 69.56 | 24.44 | 69.53 | 63.58 | 64.16 |
| C/N | 19.87 | 8.24 | 18.19 | 9.63 *Piper sarmentosum* | 68.85 *Rhododendron lapponicum* | 41.49 | 38.94 | 20.31 | 27.98 | 56.7 | 25.88 |
| C/P | 472.81 | 312.68 | 395.64 | 98.11 *Megaskepasma erythrochlamys* | 1778.76 *Quercus neglecta* | 66.13 | 64.15 | 37.64 | 52.65 | 77.84 | 56.83 |
| N/P | 23.75 | 12.19 | 21.99 | 4.98 *Aglaia odorata* | 74.74 *Quercus neglecta* | 51.33 | 48.95 | 22.86 | 45.73 | 49.58 | 36.82 |
| P/K | 0.18 | 0.12 | 0.15 | 0.05 *Averrhoa carambola* | 0.75 *Brachychiton rupestris* | 65.20 | 60.69 | 10.86 | 59.68 | 51.37 | 72.47 |
| Mean of each variable | 52.90 | 29.97 | 45.63 | 12.85 | 187.37 | 61.01 | 20.73 | 51.52 | 60.86 | 63.90 | 64.05 |

### *Relationship between leaf functional traits and stoichiometric characteristics*

Spearman correlation analysis of leaf functional traits and ecological stoichiometry across all plant species revealed several significant correlations (Figure 3). Notable negative correlations were found between:

LFW and LCC, SLA and LCC, LWC and LCC; CHL and LNC, LT and LNC; LTD and LPC, LT and LKC; LFW and C/N, LA and C/N, SLA and C/N ratio, LWC and C/N ratio; SLA and C/P ratio, LWC and C/P ratio; SLA and N/P ratio, LWC and N/P ratio; LTD and P/K ratio. Significant positive correlations were observed between: LTD and LCC; SLA and LNC, LWC and LNC; SLA and LPC, LWC and LPC; SLA and LKC, LWC and LKC; LTD and C/P; LTD and N/P; LT and P/K ratio, LV and P/K.

**Figure 3.** The relationship between leaf functional traits and leaf ecological stoichiometry
CHL: chlorophyll content, LT: leaf thickness, LFW: leaf fresh weight, LA: leaf area, LDW: leaf dry weight, SLA: specific leaf area, LWC: leaf water content, LV: leaf volume, LTD: leaf tissue density, LCC: leaf carbon content, LNC: leaf nitrogen content, LPC: leaf phosphorus content, LKC: leaf potassium content, C/N: LCC/LNC, C/P: LCC/LPC, N/P: LNC/LPC, P/K: LPC/LKC. *0.01 < $p$ < 0.05; **0.001 < $p$ < 0.01; ***$p$ < 0.001.

### *Influence of leaf functional traits on ecological stoichiometry*

To understand how leaf functional traits influence ecological stoichiometry, redundancy analysis (RDA) was employed to examine the extent to which functional traits explain the variation in ecological stoichiometry, with functional traits as explanatory variables and ecological stoichiometry as response variables. The RDA results for all plants revealed that the first and second axes explained 73.80% and 16.31% of the total variation, respectively, accounting for 90.11% of the total variation in ecological stoichiometry. Hierarchical partitioning indicated that leaf water content and specific leaf area have the top two importance values compared to other functional trait variables. RDA analysis for trees, shrubs, and herbs showed that functional traits explained 83.08%, 76.81%, and 76.51% of the total variation in ecological stoichiometry, respectively (Supplementary Figures 18,19, and 20). Contributions of SLA and LWC were higher in all three life types, thus they are more important functional trait factors. The RDA analysis grouped different life forms of tree species into distinct clusters. Tree species were predominantly grouped on the upper right quadrant of the coordinate origin, characterized by lower SLA, LNC, LPC, and LKC (Figure 4). In contrast, herbaceous species were primarily clustered on the left side of the origin, exhibiting higher SLA, LNC, LPC, and LKC (Figure 4). Shrubs were positioned between these two groups. Additionally, the contributions of various indicators to the first two principal component axes varied among the three life forms, while the correlations between these indicators remained consistent (Supplementary Figures 18, 19, and 20).

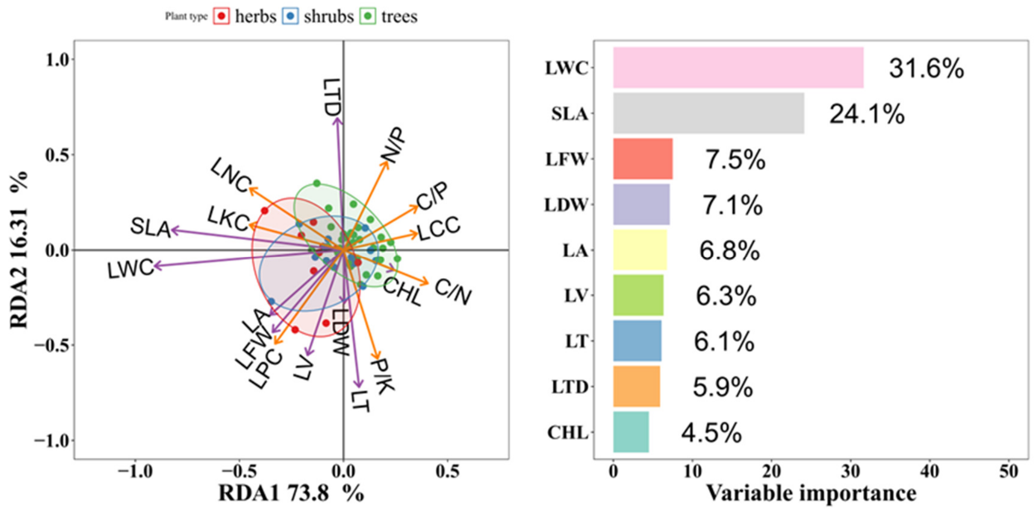
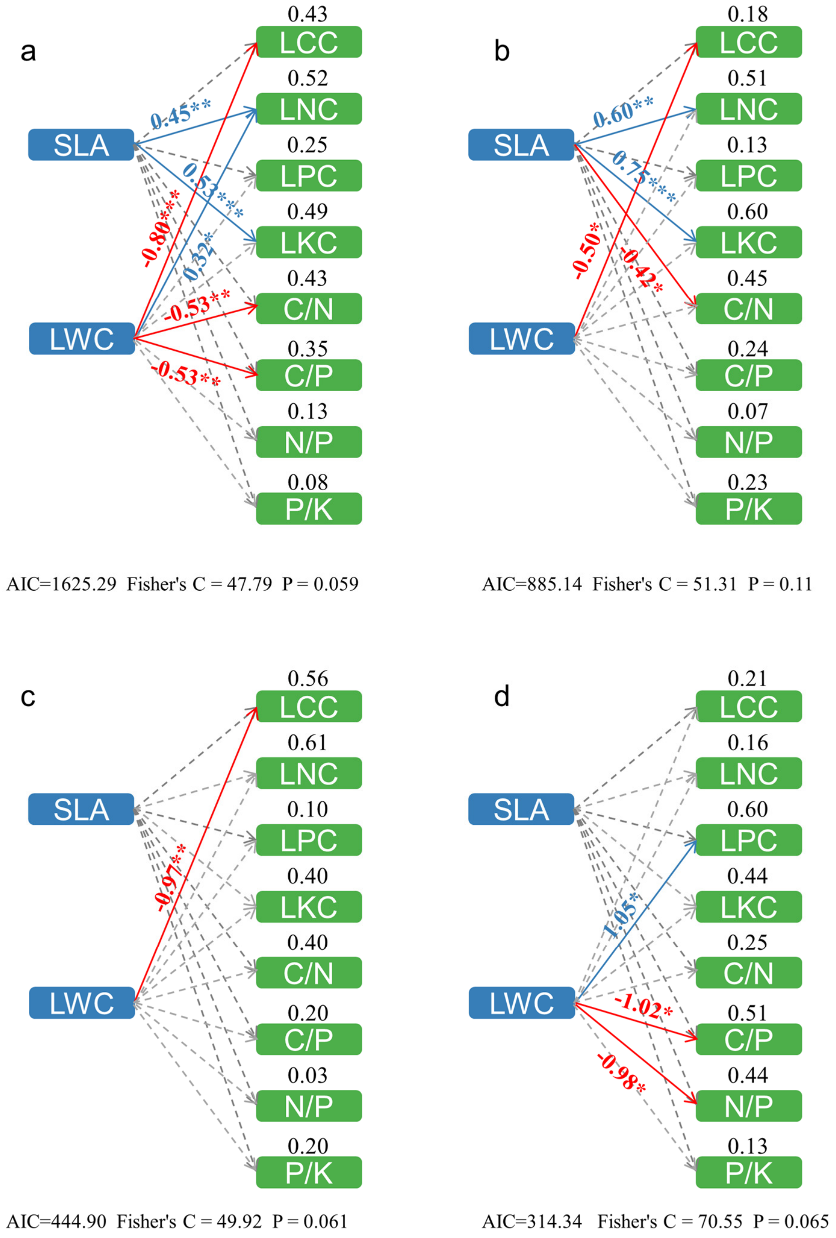


**Figure 4.** Redundancy analysis (RDA) of leaf functional traits with ecological stoichiometry and the importance of leaf functional traits in explaining leaf ecological stoichiometric variation (all plants)
CHL: chlorophyll content, LT: leaf thickness, LFW: leaf fresh weight, LA: leaf area, LDW: leaf dry weight, SLA: specific leaf area, LWC: leaf water content, LV: leaf volume LTD: leaf tissue density; LCC: leaf carbon content, LNC: leaf nitrogen content, LPC: leaf phosphorus content, LKC: leaf potassium content, C/N: LCC/LNC, C/P: LCC/LPC, N/P: LNC/LPC, P/K: LPC/LKC. *0.01 < $p$ < 0.05; **0.001 < $p$ < 0.01; ***$p$ < 0.001

To further investigate the direct effects of SLA and LWC on ecological stoichiometry, and whether these effects differ among life forms, we performed path analyses using SLA and LWC as explanatory variables and ecological stoichiometry as the response variable. The results of the path analysis showed the following explanatory power for the model across all plants (Figure 5a): 0.43, 0.52, 0.25, 0.49, 0.43, 0.35, 0.13, and 0.08. Positive effects were observed for SLA on LNC and LKC, while negative effects were noted for LWC on LCC, C/N, and C/P, with positive effects for LWC on LNC. In trees (Figure 5b), the model's explanatory power for ecological stoichiometry was 0.18, 0.51, 0.13, 0.60, 0.45, 0.24, 0.07, and 0.23. Positive effects were observed for SLA on LNC and LKC, while SLA had a negative effect on C/N, and LWC had a negative effect on LCC. In shrubs (Figure 5c), the model explained ecological stoichiometry with powers of 0.56, 0.61, 0.10, 0.40, 0.40, 0.20, 0.03, and 0.20, with negative effects of LWC on LCC. In herbs (Figure 5d), the model's explanatory power was 0.21, 0.16, 0.60, 0.44, 0.25, 0.51, 0.44, and 0.13, showing positive effects of LWC on LPC and negative effects of LWC on C/P and N/P. Detailed results of the path analysis are provided in Supplementary Table 2.



AIC=1625.29 Fisher's C = 47.79 P = 0.059

AIC=885.14 Fisher's C = 51.31 P = 0.11

AIC=444.90 Fisher's C = 49.92 P = 0.061

AIC=314.34 Fisher's C = 70.55 P = 0.065

**Figure 5.** Effect of SLA, LWC on ecological stoichiometry for all plants (a), trees (b), shrubs (c) and herbs (d)

Solid blue and red lines indicate significant positive and negative correlations, respectively, and dashed gray lines indicate non-significant relationships. *$0.01 < p < 0.05$; **$0.001 < p < 0.01$; ***$p < 0.001$.

## Discussion

### *Causes of interspecific variation in leaf traits*

In this study, the functional traits and ecological stoichiometric characteristics of tree species in the Qingxiushan Mountain Precious Tree Species Exhibition Garden exhibited lower interspecific variability, while those of the shrubs and herbaceous plants had higher interspecific variability. Similar results have been observed in studies of savannas in Brazil and southwestern China, indicating that environments characterized by nutrient deficiencies or abiotic stress tend to promote conservatism in trait metrics (Scalon *et al.*, 2017; Liu *et al.*, 2022). Under the conditions of high water and heat in subtropical monsoon area, plants are susceptible to light suppression and even damage due to intense solar radiation in summer and autumn and drought in winter (Zhang *et al.*, 2012). Research has demonstrated that phenotypic variability in plants is significantly constrained under stress conditions (Liu *et al.*, 2022). The photoinhibition experienced by tree species in the upper canopy is most pronounced, leading to the lowest degree of interspecific variation. In contrast, shrubs and herbs in the understory exhibit a higher degree of interspecific variability.

### *Leaf functional traits and ecological stoichiometry characteristics*

Differences in the functional traits of plants of various life forms within the same habitat drive the ecological niche differentiation of these plants, reflecting their resource acquisition strategies in response to environmental conditions (Ling *et al.*, 2022; Qin *et al.*, 2022). In this study, herbs, shrubs, and trees sequentially occupied the lower, middle, and upper strata of the ecological niche within the community. The results indicate that SLA significantly decreased from herbs to shrubs to trees, while CHL gradually increased. This suggests that trees occupying higher ecological niches had higher photo contracting efficiency. The shrubs and herbs exhibited lower CHL but higher SLA and LNC compared to trees, that likely contributes to more efficient light resource utilization. Leaves with high SLA have a larger light capture area and can make more effective use of light energy for photosynthesis (Shipley *et al.*, 2005). LNC can improve the activity of Rubisco enzyme, thus improving the efficiency of photosynthesis (Feng *et al.*, 2009). Relevant studies have found that there is a negative correlation between CHL and LNC of plants in karst forest (Wu *et al.*, 2023). Plants in a low CHL may promote photosynthesis by raising their SLA and LNC. Due to direct exposure to sunlight, the LWC and LFW of trees were significantly lower than those of shrubs and herbs. To mitigate water loss and maintain leaf tissue structural stability, trees had higher LTD and LDW compared to shrubs and herbs, which may help prevent heat-induced leaf damage. Additionally, a smaller LA reduces the cost of respiration and transpiration, while increases LCC, thereby minimizes damage from intense light during the dry season (Bosabalidis and Kofidis, 2002; Pringle *et al.*, 2011; Long *et al.*, 2023).

Leaf C, N, P, and K are essential synergistic elements for plant growth. Carbon serves as the primary energy source for various plant activities, while N and P are critical for synthesizing proteins and amino acids. Potassium is pivotal in plant protein synthesis, water regulation, and nutrient absorption (Herbert *et al.*, 2003; Zeng *et al.*, 2016). Nutrient distribution varies significantly among plants of different life forms. Regarding nutrient content, LCC follows the order: herbs < shrubs < trees. Conversely, LNC, LPC, and LKC exhibit the reverse trend: herbs > shrubs > trees. This suggests that herbs, adapting to environmental changes, consume more organic carbohydrates for faster growth and quicker life cycle completion. In contrast, trees prioritize long-term survival, accumulating organic carbohydrates. Complementary research in the Maolan Karst area reveals a consistent pattern: LNC, LPC, and LKC in plants of different life forms exhibit a sequence of herbs > shrubs > trees (Wu *et al.*, 2020). In the Hainan tropics, LCC of different life types exhibit a sequence of tree > shrub > herb, and this is consistent with the results of this study (Zhang *et al.*, 2020). The leaf ecological stoichiometric ratio offers a refined reflection of a plant's ecological strategy (Niklas and Cobb, 2005). The N/P ratio in plant leaves serves as an indicator of vegetative growth limitations. Typically, an N/P ratio above 16 signifies a phosphorus deficiency phenomenon (Güsewell, 2004). This study revealed that the N/P ratios of the three life forms exceeded 16, suggesting a prevalent phosphorus limitation. Appropriate amount of P fertilizer can be applied to promote plant growth in the late garden maintenance management. Notably, trees exhibited the highest N/P ratio, denoting a pronounced P limitation and underscoring the need for careful management of P fertilization in trees. The C/N and C/P ratios are indicative of a plant's carbon assimilation capacity (Zhao and Huang, 2022). In this study, herbs exhibited higher leaf nitrogen content (LNC) and lower

C/N and C/P ratios, characteristic of rapid organic carbohydrate consumption, while trees demonstrated the inverse trend. Similar patterns in the leaf ecological stoichiometry of trees, shrubs, and herbs were also observed in the Kanas natural forest (Bagedeng *et al.*, 2023). Ecological niche constraints resulted in a carbon sequestration capacity hierarchy in this study: herbs < shrubs < trees, establishing trees as the predominant species for ecological carbon sequestration in the Qingxiushan Mountain Precious Tree Species Exhibition Garden. Within a given habitat, herbs and trees commonly exhibit distinct ecological adaptations for the acquisition and allocation of resources (Zhu *et al.*, 2023). Herb plants display higher LT, LWC, LFW, and nutrient content, which is a "fast return on investment" strategy. On the other hand, tree plants possess lower SLA and higher LTD, LCC, and C/N, aligning with a "slow return on investment" strategy (Wright *et al.*, 2004; Chen and Xu, 2014).

### *Relationship between functional traits and stoichiometric characteristics of plant leaves*

The results of correlation analysis showed that there was a strong correlation between the functional traits and ecological stoichiometry of plant leaves. In the same habitat, different plant species exhibit certain correlations between their functional traits and ecological stoichiometric characteristics, which collectively influence their roles and interactions within the ecosystem, thereby facilitating adaptation to specific environmental conditions (Freschet *et al.*, 2010). Leaf functional traits reflect the acquisition and utilization strategies of light energy, water and nutrients, and thus affect the carbon fixation capacity, absorption and distribution of nutrients (Wright *et al.*, 2004; Liu *et al.*, 2023). These strategies directly influence the ecological stoichiometry of plants, and the relationship between functional traits and ecological stoichiometry is also the result of long-term evolution and environmental adaptation (Feng *et al.*, 2008). The resource utilization strategy of plants can be reflected by the size of SLA. The resource utilization strategy of plants can be reflected by their SLA. Plants with higher SLA usually exhibit rapid growth strategies, while plants with lower SLA grow more slowly, live longer, and are more tolerant to resource-poor environments (Wright *et al.*, 2004). As the medium for nutrient solubilization and transport, water plays a crucial role in leaf water content, which affects nutrient transport and distribution within the plant, subsequently influencing plant growth and development. Both SLA and LWC significantly impact the resource utilization and nutrient acquisition strategies of plants, affecting not only individual plants but also altering the structure and function of plant communities, which in turn influences nutrient balance and biogeochemical cycles in ecosystems. The redundancy analysis results further demonstrate that the functional traits of plant leave's significantly explain the variation in ecological stoichiometry. In this study, tree species occupyed the upper canopy layer, and hindered the light availability for the underlying herbaceous plants, thereby restricted their photosynthetic capacity. Characterized by larger SLA and higher LNC and LKC, herb plants exhibit enhanced resource acquisition capabilities. In contrast, tree species subjected to intense light stress and developed smaller LA, higher LTD and LCC, which contributed to reducing water loss, and maintaining leaf tissue structural integrity, and mitigating damage from intense light during the dry season (Bosabalidis and Kofidis, 2002; Pringle *et al.*, 2011; Long *et al.*, 2023). Similar trade-offs between plant functional traits and ecological adaptations have been reported in both sandy and natural forest ecosystems (Chen *et al.*, 2011; Peng *et al.*, 2016).

The hierarchical partitioning analysis showed that SLA and LWC played an important role in the influence of functional traits on ecological stoichiometry, and the results of path analysis revealed the mechanism of the influence of SLA and LWC on ecological stoichiometry. The path analysis of all plants showed that LWC had negative effects on LCC, C/N ratio, and C/P ratio, while it had positive effects on LNC. That is because when the LWC increases, the tissue growth resulting in the cell expansion and cell wall thinning, cell mass in the cells, and relatively reduced carbon content (Boucher *et al.*, 1995; Emery, 2016; Lehmann *et al.*, 2018; Berry *et al.*, 2019). Additionally, when the LWC increases, respiration may increase, consuming more photosynthetic products, resulting in lower carbon content (Galmés *et al.*, 2007). Under high hydrothermal conditions with abundant water supply, plants may prioritize rapid growth and resource-use efficiency over carbon storage (Lu *et al.*, 2023). This strategy aids in acquiring light and nutrients in competitive environments but lowers LWC, requiring substantial N and P for protein and nucleic acid synthesis. In contrast, SLA and LNC had positive effects, as did SLA and LKC. SLA is closely related to the net photosynthetic rate of plants. The increase of SLA promotes the increase of the surface area of chloroplasts thylakoids, which is conducive to the absorption of light and the higher photosynthetic efficiency of chloroplasts (Shipley *et al.*, 2005; Long *et al.*, 2011). Nitrogen is crucial for chlorophyll synthesis and increases Rubisco enzyme activity, thereby boosting photosynthetic rates (Feng *et al.*, 2009; Zhang *et al.*, 2022). In hot and humid conditions, plants often exhibit larger LA, which improves competitiveness and adaptability, necessitating higher N levels to enhance ecological fitness (Moles and Westoby, 2000; Lehmann *et al.*, 2018). Larger leaves generally have more cells, and K plays a critical role in cell wall synthesis, maintenance of cellular osmotic pressure, and enzyme synthesis for photosynthesis (Pan *et al.*, 2015). Thus, LKC may increase to support rapid growth and metabolic activities (Wright *et al.*, 2001; Huo *et al.*, 2023). Comparing the results of path analyses for trees, shrubs, and herbs revealed differences in the effects of LWC and SLA on ecological stoichiometry across these life forms. In trees, SLA primarily influences N, K, and C/N ratios, and LWC mainly affects carbon content. In shrubs, LWC primarily affects LCC, whereas in herbs, LWC mainly influences LPC and C/P ratios. SLA plays a particularly crucial role in regulating ecological stoichiometry in trees. Trees are positioned in the upper layers of the ecosystem's vertical structure, receiving more light energy and being more exposed to intense light radiation. SLA reflects the ability of leaves to intercept light and protect themselves from high light intensity (Li *et al.*, 2007). Adjusting SLA helps optimize light energy use and reduce water transpiration, thereby improving photosynthetic efficiency and carbon uptake and fixation (Liu *et al.*, 2022). Therefore, SLA can improve resource utilization efficiency by influencing N, K and C/N ratio in trees. In contrast, shrubs and herbs occupy lower levels in the community and are shaded by the trees above them. As a result, light intensity has less impact on their growth and development in low light environments. The roots of shrubs and herbaceous plants are located in less water-scarce topsoil layers, and efficient water use is more critical for their survival and reproduction (Dodd *et al.*, 1998). By improving water use efficiency, shrubs can accumulate more carbon in the case of limited water (Wang and Liu, 2000). For herbs, a rapid growth strategy results in higher P demands, as P is a key element in energy metabolism and DNA/RNA synthesis (Zeng and Wang, 2015). High LWC enhances photosynthesis and energy conversion, thereby improving P utilization efficiency.

## Conclusions

The results of this study showed that leaf functional traits could affect the ecological stoichiometric characteristics of plants, and specific leaf area and water content were the key functional trait factors affecting the ecological stoichiometric characteristics of plants, and there were significant differences in leaf functional trait indexes of herbs, shrubs and trees. In general, herbs showed a "fast - return on investment" strategy, with higher investment in rapid growth and environmental adaptability. Trees adopts a relatively conservative "slow - investment income" strategy, which is conducive to the long-term sustainability of growth; Shrub growth strategies fall somewhere in the middle. This study is helpful to further understand the growth strategies and ecological adaptation mechanisms of plants under high water and heat conditions in subtropical monsoon areas. Different life-type plants adapt to specific environmental conditions to meet growth needs by adjusting corresponding functional traits and ecological stoichiometric characteristics and optimizing resource allocation. The results of the study will help park managers better understand the adaptability of plants under specific environmental conditions, so as to better protect and manage plant populations, which is crucial for maintaining plant population health and plant diversity.

## Authors' Contributions

Material preparation, data collection, data analysis was performed by JS. The design and arrangement of the experiment was done by ZO, and WT. The first draft of the manuscript was written by JS and WT revised it carefully. The experiment data was measured with the help of LD, LK, HL, YL, SH, and LH. The project funding was supported by relevant topics chaired by TW. All authors read and approved the final manuscript.

## **Ethical approval** (for researches involving animals or humans)

Not applicable.

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## Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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