

Intra- and interspecific variation in leaf functional traits of four native valuable broad-leaved tree species: Postprint

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Abstract

Interspecific variation in plant functional traits reflects the life history strategies of different species, while intraspecific variation reflects the trait responses of individuals within the same species to different environments. The uniform environment of plantation forests facilitates in-depth analysis of intraspecific and interspecific variation among different tree species. This study investigated the intraspecific and interspecific variation in leaf functional traits of four native precious broad-leaved tree species (*Tsoongiodendron odorum*, *Castanopsis hystrix*, *Magnolia blumei*, and *Parashorea chinensis*) at Nanning Liangfengjiang Forest Farm, and the results showed that: (1) At the same height, most leaf functional traits differed significantly among the four species, with only a few traits showing no significant differences. Compared with the other three species, *Castanopsis hystrix* exhibited lower values for leaf fresh weight, leaf thickness, leaf area, leaf dry weight, specific leaf area, and leaf water content, but higher values for leaf mass per area, leaf dry matter content, and leaf tissue density. (2) Leaf functional traits varied with height, and different tree species exhibited different patterns of variation. The effect of height on leaf functional traits followed the order: *Magnolia blumei* > *Parashorea chinensis* > *Tsoongiodendron odorum* > *Castanopsis hystrix*. With changes in height, among the nine leaf functional traits, leaf thickness and leaf tissue density were the most stable, while leaf area and leaf dry weight showed greater variation; specific leaf area exhibited a decreasing trend, whereas leaf mass per area showed an increasing trend. (3) As tree age increased, *Magnolia blumei* showed the greatest variation in leaf functional traits, while *Castanopsis hystrix* exhibited the most stable traits; the influence of tree age on leaf functional traits followed the order: *Magnolia blumei* > *Tsoongiodendron odorum*/*Parashorea chinensis* > *Castanopsis hystrix*. Among the nine leaf functional traits, leaf thickness and leaf tissue density were most affected by tree age, while leaf fresh weight, leaf dry weight, and

leaf area were least affected; the leaf functional traits of the four species showed significant differences with tree age, but without clear regular patterns. (4) The correlation between leaf dry matter content and leaf thickness was not significant, nor was the correlation between leaf water content and leaf thickness, leaf area, leaf dry weight, and leaf mass per area; however, significant correlations existed among the remaining functional traits.

Full Text

Preamble

Interspecific and Intraspecific Variation in Leaf Functional Traits of Four Native Precious Hardwood Species

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Abstract

Interspecific trait variation in plant functional traits reflects the life history strategies of different species, while intraspecific variation reflects how individuals of the same species respond to different environments. The homogeneous environment of plantations provides an ideal setting for in-depth analysis of both intraspecific and interspecific variation among tree species. This study examined leaf functional trait variation in four native precious hardwood species (*Tsoongiodendron odorum*, *Castanopsis hystrix*, *Magnolia blumei*, and *Parashorea chinensis*) at the Liangfengjiang Forest Farm in Nanning. The results showed that: (1) Most leaf functional traits differed significantly among the four species at the same canopy height, with only a few traits showing no significant differences. Compared with the other three species, *C. hystrix* had lower values for leaf fresh weight, leaf thickness, leaf area, leaf dry weight, specific leaf area, and leaf water content, but higher values for leaf dry weight per unit area, leaf dry matter content, and leaf tissue density. (2) Leaf functional traits varied with canopy height, with different patterns among species. The effect of height on leaf functional traits followed the order: *M. blumei* > *P. chinensis* > *T. odorum* > *C. hystrix*. Among the nine leaf functional traits examined, leaf thickness and leaf tissue density were the most stable, while leaf area and leaf dry weight showed greater variation. Specific leaf area decreased with increasing height, while leaf dry weight per unit area increased. (3) As tree age increased, *M. blumei* showed the greatest changes in leaf functional traits, while *C. hystrix* was the most stable. The effect of tree age on leaf functional traits followed the order: *M. blumei* > *T. odorum* / *P. chinensis* > *C. hystrix*. Among the nine traits, leaf thickness and leaf tissue density were most affected by tree age, while leaf fresh weight, leaf dry weight, and leaf area were least affected. Leaf

functional traits of the four species varied significantly with tree age but showed no clear pattern. (4) Leaf dry matter content was not significantly correlated with leaf thickness, and leaf water content was not significantly correlated with leaf thickness, leaf area, leaf dry weight, or leaf dry weight per unit area, though significant correlations existed among other functional traits.

Keywords: intraspecific variation, interspecific variation, coefficient of variation, height, tree age, correlation, leaf functional traits

Introduction

Plant functional traits are attributes that significantly influence plant establishment, survival, and adaptation. These traits substantially affect ecosystem functioning and reflect plant strategies for coping with environmental conditions (Liu et al., 2006; Ma et al., 2012; Liu and Ma, 2015). Among all plant traits, leaf functional traits are most closely related to plant biomass and the acquisition, utilization, and efficiency of resource use (Westoby, 1998; Vendramini et al., 2002). They are strongly correlated with individual plants, communities, and ecosystems, and can directly reflect the survival strategies formed by different species in response to environmental changes (Mao et al., 2012).

Variation in plant functional traits refers to changes in plants across different organizational levels and spatial scales, arising from the combined effects of genetic factors and external environments. Such variation exists widely within individual plants, within species, among species, and among communities (Xiong, 2015). Functional trait variation is primarily categorized into intraspecific and interspecific variation. Interspecific variation includes stable trait differences formed by species during long-term evolution and is also related to environmental filtering (Cornwell and Ackerly, 2009). Historically, scholars focused mainly on interspecific variation, assuming it far exceeded intraspecific variation (Fajardo and Piper, 2011; Jackson et al., 2013). However, increasing evidence suggests that interspecific trait variation studies have limitations, as plant trait variation is influenced not only by stable genetic factors but also by strong phenotypic plasticity in response to environmental changes (Albert et al., 2010; Messier et al., 2010; Paine et al., 2011). Jung et al. (2014) demonstrated that intraspecific variation contributes more substantially than interspecific variation, with intraspecific differences being ubiquitous in plant communities.

In natural communities, extreme spatial heterogeneity of environmental factors and their combined effects result in highly complex interspecific and intraspecific trait variation. In contrast, plantation communities have relatively uniform environmental factors, with light conditions changing systematically from ground level to canopy. Trees planted simultaneously also provide excellent experimental material for studying interspecific variation in functional traits. This study selected four native precious hardwood species (*Tsoongiodendron odorum*, *Castanopsis hystrix*, *Magnolia blumei*, and *Parashorea chinensis*) planted at Liangfengjiang Forest Farm. Based on individual-level analysis, we exam-

ined nine leaf functional traits: leaf fresh weight, leaf thickness, leaf area, leaf dry weight, specific leaf area, leaf dry weight per unit area, leaf dry matter content, leaf water content, and leaf tissue density. Our objectives were to investigate interspecific variation in leaf functional traits among different species under identical stand age and environmental conditions, and to explore intraspecific variation within each species by comparing different stand ages and light conditions. The results and methodology have theoretical significance and provide practical guidance for plantation management of native precious hardwood species.

1.1 Study Area Description

The study area is located in the Lianshan region of Liangfengjiang Forest Farm in Nanning (108°15'14" E, 22°34'31" N). Situated in the central part of the Nanning Basin, the area features low hills as the primary landform, with some terraces and platforms. The terrain slopes from high in the south to low in the north, with gentle undulations and open topography in the north and greater elevation differences in the south. The highest peak is Dayao Ridge in the south at 346.5 m elevation, while the lowest area near the Yongjiang River is 80 m, with relative elevation differences generally ranging from 80 to 200 m. Slope gradients are typically 20°–30°, with slopes and steep slopes accounting for over 80% of the area. Located south of the Tropic of Cancer, the region has a south subtropical monsoon climate with short winters and long summers, free from severe cold or extreme heat, and abundant heat and moisture resources. The mean annual temperature is 21.6°C, with average temperatures of 12.8°C in January and 28°C in July. Extreme maximum temperature reaches 40°C, while the minimum is -1.5°C. The annual accumulated temperature $\geq 10^{\circ}\text{C}$ is 7,600°C, and annual precipitation is 1,280 mm, concentrated mainly from May to September (71% of annual rainfall). The frost-free period is 342 days, with rare freezing conditions, creating extremely favorable conditions for forest growth.

1.3 Functional Trait Measurement

In mid-August 2019, we selected four native precious hardwood species (*Tsoongiodendron odorum*, *Castanopsis hystrix*, *Magnolia blumei*, and *Parashorea chinensis*) from stands with similar management histories (the experimental plots were planted with *Pinus massoniana* before 2001, then with pure *Eucalyptus* stands from 2001–2012, before the current species were planted). For each species, we selected three individual trees planted in 2012, 2014, and 2017. From each tree, we collected samples from three canopy layers (upper, middle, and lower), gathering one healthy, current-year branch from each of the four cardinal directions per layer. Each branch (including stem and leaves) was placed in a separate bag, labeled, and stored in a cooler to maintain freshness. In the laboratory, stems and leaves were separated, and ten intact, undamaged leaves were selected from each layer per tree.

Leaf area (LA) was measured using a CanoScan LiDE 300 scanner combined with Photoshop software. Leaf thickness (LT) was measured at the front, middle, and end of each leaf (avoiding veins as much as possible) using an electronic vernier caliper with 0.01 mm precision, with the mean value used as leaf thickness. Leaf fresh weight (LFW) was measured using an electronic balance with 0.01 g precision. Leaves were then oven-dried at 70°C to constant weight before measuring leaf dry weight (LDW). The functional traits were calculated as follows:

- Specific leaf area (SLA, $\text{cm}^2 \cdot \text{g}^{-1}$) = LA / LDW
- Leaf dry weight per unit area (SLW, $\text{g} \cdot \text{m}^{-2}$) = LDW / LA
- Leaf dry matter content (LDMC, $\text{g} \cdot \text{g}^{-1}$) = LDW / LFW
- Leaf water content (LWC, %) = (LFW - LDW) / LFW × 100%
- Leaf tissue density (LTD, $\text{g} \cdot \text{mm}^{-3}$) = LDW / (LA × LT)

1.4 Data Processing

Data were recorded and calculated using Excel 2010. One-way ANOVA and Pearson correlation analysis were performed using SPSS 22.0 software. Figures were created using Origin 2018 software.

2.1 Interspecific Variation Analysis

One-way ANOVA of leaf functional traits among different species at the same canopy height revealed that most traits differed significantly among the four species, with only a few showing no significant differences. At all three canopy heights, *C. hystrix* had the lowest values for leaf fresh weight, leaf thickness, leaf area, leaf dry weight, specific leaf area, and leaf water content compared with the other three species, but the highest values for leaf dry weight per unit area, leaf dry matter content, and leaf tissue density. In the lower canopy layer, leaf fresh weight showed the highest coefficient of variation (86.56%), while leaf water content showed the lowest (25.85%). In the middle layer, leaf fresh weight again showed the highest variation (73.55%), with leaf water content the lowest (23.19%). In the upper layer, leaf fresh weight showed the greatest variation (76.74%), while specific leaf area was the most stable (27.26%). The coefficients of variation for all nine leaf functional traits in the middle canopy layer were lower than those in both the upper and lower layers.

GGM. *Tsoongiodendron odorum*; **HZ.** *Castanopsis hystrix*; **HML.** *Magnolia blumei*; **WTS.** *Parashorea chinensis*; **XC.** Lower layer; **ZC.** Middle layer; **SC.** Upper layer. Lowercase letters on bars indicate significant differences ($P < 0.05$). The same notation applies below.

[Figure 1: see original paper] Multiple comparisons of leaf functional traits among different tree species at the same height (LSD)

2.2 Intraspecific Variation in Leaf Functional Traits at Different Heights

Leaf functional traits varied significantly with canopy height, with different patterns among species. With changing height, all nine leaf functional traits of *M. blumei* differed significantly, with specific leaf area, leaf dry weight per unit area, leaf dry matter content, leaf water content, and leaf tissue density showing extremely significant differences. In contrast, only leaf tissue density differed significantly in *C. hystrix* across heights. The overall effect of height on functional traits followed the order: *M. blumei* > *P. chinensis* > *T. odorum* > *C. hystrix*. Among the nine traits, leaf thickness and leaf tissue density were the most stable (showing significant differences in only one species), while leaf area and leaf dry weight showed greater variation (differing significantly in *T. odorum*, *M. blumei*, and *P. chinensis*). Across all species, specific leaf area decreased with increasing height, while leaf dry weight per unit area increased. Leaf fresh weight, leaf thickness, leaf area, leaf dry weight, leaf dry matter content, leaf water content, and leaf tissue density showed no consistent patterns, with different species exhibiting different trends [Figure 2: see original paper].

[Figure 2: see original paper] Multiple comparisons of leaf functional traits at different heights (LSD)

2.3 Intraspecific Variation in Leaf Functional Traits at Different Tree Ages

As tree age increased, *M. blumei* showed the greatest changes in leaf functional traits, with only leaf area showing no significant difference while all other traits differed significantly. *Castanopsis hystrix* was the most stable, with only leaf thickness, leaf dry matter content, leaf water content, and leaf tissue density showing significant differences. The effect of tree age on leaf functional traits followed the order: *M. blumei* > *T. odorum* / *P. chinensis* > *C. hystrix*. Among the nine traits, leaf thickness and leaf tissue density were most affected by tree age (showing significant differences in all four species), while leaf fresh weight, leaf dry weight, and leaf area were least affected (showing significant differences in only two species). As shown in [Figure 3: see original paper], leaf functional traits of the four species varied significantly with tree age but showed no clear pattern. Combined with the results from [Figure 2: see original paper], tree age had a greater influence on leaf functional traits than canopy height.

[Figure 3: see original paper] Multiple comparisons of leaf functional traits at different tree ages (LSD)

2.4 Correlation Analysis of Functional Traits

Correlation analysis revealed that leaf fresh weight was extremely significantly positively correlated with leaf thickness, leaf area, leaf dry weight, leaf water content, and specific leaf area ($P < 0.01$), and extremely significantly negatively correlated with leaf dry weight per unit area, leaf dry matter content, and leaf

tissue density. Leaf thickness was extremely significantly positively correlated with leaf area and leaf dry weight, extremely significantly negatively correlated with leaf dry weight per unit area and leaf tissue density, and significantly correlated with specific leaf area ($P < 0.05$). Leaf area was extremely significantly positively correlated with leaf dry weight and specific leaf area, extremely significantly negatively correlated with leaf dry weight per unit area and leaf tissue density, and significantly negatively correlated with leaf dry matter content. Leaf dry weight was extremely significantly positively correlated with specific leaf area, extremely significantly negatively correlated with leaf dry weight per unit area and leaf tissue density, and significantly negatively correlated with leaf dry matter content. Specific leaf area was extremely significantly negatively correlated with leaf dry weight per unit area, leaf dry matter content, and leaf tissue density, and significantly positively correlated with leaf water content. Leaf dry weight per unit area was extremely significantly positively correlated with leaf dry matter content and leaf tissue density. Leaf dry matter content was extremely significantly positively correlated with leaf water content and extremely significantly negatively correlated with leaf tissue density. Leaf water content was significantly negatively correlated with leaf tissue density.

Correlation analysis of leaf functional traits

Note: "*" and "***" indicate significant correlation at the 0.05 and 0.01 levels, respectively.

3.1 Interspecific Variation Characteristics of Leaf Functional Traits Among Different Tree Species

Significant differences in leaf functional traits among different tree species of the same age and height reflect different environmental adaptation strategies and inherent genetic characteristics (Liu and Ma, 2015). In this study, *C. hystrix* had the lowest values for leaf fresh weight, leaf thickness, leaf area, leaf dry weight, specific leaf area, and leaf water content, but the highest values for leaf dry weight per unit area, leaf dry matter content, and leaf tissue density. Generally, higher leaf dry matter content and leaf tissue density indicate greater nutrient investment in leaf construction, while higher leaf dry weight per unit area suggests smaller water storage space, leading to lower leaf water content and specific leaf area, implying slower plant growth. Among the four species, *C. hystrix* showed the smallest variation in leaf functional traits, indicating relatively stable characteristics and strong resistance to harsh environments.

Across the three canopy heights, leaf fresh weight showed the greatest variation, which is inherent to its nature as it changes with variations in other functional traits, reflecting its close relationship with other leaf functional traits. In the middle and lower canopy layers, leaf water content showed the smallest variation, while in the upper layer, specific leaf area was most stable. This may be because light is relatively limited in the middle and lower layers of plantation communities, resulting in less water production through photosynthesis and

weaker transpiration, leading to more stable leaf water content. In the upper canopy, better light conditions enable leaves to produce sufficient nutrients to meet growth requirements without needing to increase photosynthetic efficiency by altering specific leaf area. Additionally, stronger transpiration in the upper canopy may contribute to the stability of specific leaf area.

3.2 Variation Characteristics of Leaf Functional Traits at Different Heights

Leaf functional traits differed among canopy heights, with variation patterns varying among species. Only leaf tissue density showed significant differences across heights in *C. hystrix*, while all nine leaf functional traits differed significantly with height in *M. blumei*. Since our study plots were located in the same region with highly similar planting histories, environmental factors such as rainfall, temperature, and elevation likely had minimal effects on leaf functional traits. The most important factor varying with height in these communities was stand density, which affects light conditions. Therefore, we infer that the effect of light on leaf functional traits follows the order: *M. blumei* > *P. chinensis* > *T. odorum* > *C. hystrix*.

Specific leaf area directly reflects a plant's ability to absorb light resources and acquire carbon, while leaf dry matter content indicates nutrient conservation capacity; both are key leaf traits for habitat adaptation (Bodegom et al., 2014). With increasing canopy height, specific leaf area decreased while leaf dry weight per unit area increased in all four species. As height increases, light penetration improves, providing better illumination for leaves on higher branches and reducing the need for high specific leaf area. This result aligns with Wright et al. (2004). The ranking of specific leaf area and leaf water content across the four species was: *M. blumei* > *P. chinensis* > *T. odorum* > *C. hystrix*, indicating that higher specific leaf area corresponds to higher leaf water content. This is because higher specific leaf area enhances photosynthetic efficiency and increases water demand, resulting in higher leaf water content, consistent with findings by Song et al. (2016). Higher leaf dry matter content indicates greater investment in leaf construction, higher leaf tolerance, and stronger nutrient accumulation capacity (Cheng et al., 2019). In this study, leaf dry matter content of *M. blumei* and *P. chinensis* differed significantly with height but showed different trends: *M. blumei* showed an initial increase followed by a decrease with increasing sampling height, while *P. chinensis* showed a gradual decrease. This reflects different nutrient allocation strategies: in *M. blumei*, middle-canopy leaves allocate more nutrients to leaf construction, while upper and lower canopy leaves allocate more nutrients to whole-plant growth; in *P. chinensis*, lower-canopy leaves allocate more nutrients to leaf construction, while upper-canopy leaves allocate more to plant growth.

3.3 Variation Characteristics of Leaf Functional Traits at Different Tree Ages

Our results indicate that leaf functional traits of the four native precious hardwood species varied significantly with tree age, with greater variation than that observed across height gradients, though no clear patterns emerged. Only specific leaf area showed no significant difference with age in *C. hystrix*, while leaf dry matter content increased significantly with age. Generally, high specific leaf area and low leaf dry matter content represent high light-capture capacity and rapid nutrient acquisition, favoring high productivity; low specific leaf area and high leaf dry matter content suggest potential nutrient acquisition limitations (Wright et al., 2005). This indicates that *C. hystrix* growth stabilizes with age, with photosynthates allocated primarily to leaf construction to enhance leaf tolerance. The other three species showed no clear patterns with age, likely because they remain in rapid growth phases across the three age classes, with unstable trait expression. Their higher specific leaf area and lower leaf dry matter content compared with *C. hystrix* confirm that their leaves allocate more nutrients to whole-plant growth. Leaf dry weight per unit area, representing the light-intercepting surface area per unit dry mass investment, is directly related to light interception efficiency and significantly affects relative growth rate (Wilson et al., 1999). Only *C. hystrix* showed no significant difference in leaf dry weight per unit area across ages, indicating relatively stable growth rates that support the above interpretation. Across the four species, only leaf thickness and leaf tissue density showed clear differences with tree age, but without consistent patterns. This may reflect different nutrient allocation strategies adopted by plants at different growth stages in response to environmental conditions, with changes in leaf thickness and tissue density representing external manifestations of these shifting strategies. These two traits appear particularly sensitive to environmental changes.

Combined with [Figure 2: see original paper] and [Figure 3: see original paper], tree age had a greater influence on leaf functional traits than canopy height. This may be because plants have different requirements and adopt different survival strategies at different growth stages. For example, young trees require rapid growth to enhance environmental adaptability and thus typically have high specific leaf area and low leaf dry matter content, while mature trees generally have low specific leaf area and high leaf dry matter content. Additionally, correlations among functional traits (see below) cause substantial changes in traits with tree age, whereas height affects only some functional traits, with the degree of influence varying among species with different life habits.

3.4 Correlation Analysis of Plant Leaf Functional Traits

Plant functional traits do not function independently; correlations among traits enable plants to adjust and balance trait combinations to adapt to specific habitats (Baraloto et al., 2010; Freschet et al., 2010). Multiple associations exist among leaf functional traits, with trait combinations acting simultaneously to

achieve environmental adaptation, reflecting convergent plant adaptation strategies (Cheng et al., 2019).

Specific leaf area and leaf dry matter content reflect resource use efficiency and are key characteristics of plant adaptation to various habitats with important ecological significance. In this study, specific leaf area was significantly negatively correlated with leaf dry matter content, consistent with Wright et al. (2001) and Roche et al. (2004). Lower specific leaf area and higher leaf dry matter content indicate high resource use efficiency and adaptation to harsh environments, while higher specific leaf area and lower leaf dry matter content indicate lower resource use efficiency and poor resistance to adverse conditions (Feng et al., 2009). Leaf dry matter content and leaf tissue density reflect nutrient investment in leaf construction; higher values indicate greater allocation of photosynthates to leaf building, leading to increased tissue density, reduced water content, and greater resistance to internal water diffusion, thereby enhancing drought resistance (Wilson et al., 1999; Wang et al., 2016). Our results confirm this: leaf dry matter content was extremely significantly positively correlated with leaf tissue density ($P < 0.01$), while leaf water content was extremely significantly negatively correlated with leaf dry matter content and significantly negatively correlated with leaf tissue density ($P < 0.05$). Leaf thickness is important for water storage and drought resistance; thicker leaves have stronger water storage and drought resistance. In this study, leaf thickness was not significantly correlated with leaf dry matter content or leaf water content, indicating that variation in leaf thickness was primarily influenced by other leaf functional traits. This may be because Liangfengjiang Forest Farm is located in a subtropical region with humid climate, high temperatures, and abundant rainfall, providing suitable conditions for plant survival. Since leaf dry matter content reflects adaptation to harsh environments and is extremely significantly negatively correlated with leaf water content, leaf thickness is not directly affected by leaf dry matter content or leaf water content.

Correlations among plant functional traits are ubiquitous, reflecting plant survival strategies for environmental adaptation. Under different environmental conditions, plants adapt through different functional trait combinations, forming coevolutionary relationships with their environment.

3.5 Conclusion

Intraspecific and interspecific variation in plant functional traits is ubiquitous, influenced by diverse factors. Our results demonstrate that in plant communities within the same region, leaf functional traits are affected by both canopy height and tree age, with different species showing different degrees of sensitivity. Therefore, Liangfengjiang Forest Farm can improve forest productivity by adopting appropriate management strategies for different species. For species like *C. hystrix* that are less affected by height and age, higher planting densities can be used, with mixed planting of different age classes and vertical stratification. For species like *M. blumei* that are more strongly affected, lower planting

densities are recommended, with stands maintained at uniform ages. This study confirmed correlations among functional traits, with traits coordinating to adapt to environmental changes, further supporting the general pattern of leaf trait relationships in terrestrial ecosystems. Future research should incorporate soil and other environmental factors for deeper analysis of environmental influences on leaf functional traits in this region.

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