Postprint of Leaf Traits in Old-Growth Loropetalum chinense Communities in Karst Rocky Mountains of Guilin

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Abstract

Taking 25 dominant plant species in the old-growth forest of a Loropetalum chinense community in Guilin karst hills as the research object, we measured leaf trait indicators including leaf dry mass (DW), leaf dry matter content (LDMC), leaf area (LA), leaf thickness (LT), specific leaf area (SLA), and leaf tissue density (LTD) to explore interspecific differences in leaf traits and the intrinsic relationships among traits, thereby investigating the mechanisms by which plants in the old-growth forest of the Loropetalum chinense community adapt to the karst hill habitat. The results showed that DW, LDMC, LA, LT, SLA, and LTD all exhibited highly significant differences ($P < 0.01$) among the 8 plant species in the tree layer and among the 17 plant species in the shrub layer, respectively. Leaves of tree layer plants had relatively larger DW, LDMC, and LT, while leaves of shrub layer plants had relatively larger SLA; differences in LA and LTD between tree and shrub layer plants were not significant. Pearson correlation analysis indicated that, except for the correlations between LTD and LDMC, LTD and LA, and SLA and LA, which were inconsistent between the two layers, correlations between other trait pairs were consistent between tree and shrub layer plants. Principal component analysis revealed that among the six leaf trait indicators, DW, LDMC, and LTD could serve as important leaf traits reflecting habitat adaptation of tree layer plants in the old-growth forest of the Loropetalum chinense community in karst hills, primarily characterizing the ability of plants to resist external disturbances and adverse environments and their capacity to adapt to the moisture regime of the growth environment, exhibiting characteristics of the "slow investment-return" leaf economics spectrum. SLA and LTD could serve as important leaf traits reflecting habitat adaptation of shrub layer plants in the old-growth forest of the Loropetalum chinense community in karst hills, primarily characterizing the ability of plants

to acquire resources, exhibiting characteristics of the "fast investment-return" leaf economics spectrum.

Full Text

Leaf Traits in Old-Growth Forest Plants of *Loropetalum chinense* Communities in Karst Hills of Guilin, China

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Abstract

This study examined 25 dominant plant species in old-growth *Loropetalum chinense* communities in the karst hills of Guilin, China, by measuring six key leaf traits: leaf dry weight (DW), leaf dry matter content (LDMC), leaf area (LA), leaf thickness (LT), specific leaf area (SLA), and leaf tissue density (LTD). Our objectives were to investigate interspecific differences in leaf traits, explore intrinsic relationships among these traits, and elucidate the adaptive mechanisms of plants to karst hill habitats at the old-growth forest stage. Results revealed highly significant differences ($P < 0.01$) in all six traits among the eight tree species and among the 17 shrub species. Tree layer species exhibited relatively higher DW, LDMC, and LT values, while shrub layer species showed greater SLA. No significant differences were detected between layers for LA and LTD. Pearson correlation analysis demonstrated consistent trait relationships between tree and shrub layers, except for the correlations of LTD with LDMC and LA, and SLA with LA. Principal component analysis indicated that DW, LDMC, and LTD serve as key leaf traits reflecting habitat adaptation in the tree layer, primarily representing resistance to disturbance and adaptation to moisture conditions—characteristics of a "slow investment-return" leaf economics spectrum. In contrast, SLA and LTD emerged as important indicators for shrub layer adaptation, mainly reflecting resource acquisition capacity and exhibiting a "fast investment-return" strategy.

Keywords: leaf traits, *Loropetalum chinense* communities, old-growth forest stage, karst hills of Guilin

Introduction

Plant functional traits are defined as a series of plant attributes that significantly influence plant establishment, survival, growth, and mortality (Díaz et al., 1999). These traits can individually or collectively indicate ecosystem responses to environmental changes and strongly influence ecosystem processes (Weiher et al., 1999; Cornelissen et al., 2003). Representing the outcome of long-term evolutionary adaptation to diverse environments, functional traits objectively express plant adaptability to external conditions (Xiao and Yu, 2012). They are also considered attributes related to resource acquisition, utilization, and conservation capacities, such as plant height, leaf size, leaf thickness, shade tolerance, and photosynthetic rate (Hu et al., 2014). Recent research on plant functional traits has predominantly focused on leaf characteristics (Zhou et al., 2016).

As a crucial component of plant functional traits, leaf traits are most closely related to plant biomass and resource acquisition, utilization, and efficiency. They reflect survival strategies developed in response to environmental changes (Li et al., 2005). Leaf traits have garnered considerable attention from ecologists due to their convenience of measurement, strong operability, importance for plant carbon harvest, and consistent representation of trait relationships across various plant populations and communities. Consequently, leaf traits remain a central focus in ecological research. Recent studies have primarily investigated relationships between leaf traits and environmental factors under different site conditions (Yang et al., 2015; Zhou et al., 2015; Jiang et al., 2017; Pan et al., 2017), trait interrelationships and trade-off strategies (Ma et al., 2011; Funk and Cornwell, 2013; Yu et al., 2014), and variation patterns and correlations across different scales (Sánchez-Gómeza et al., 2013; Wang et al., 2016; Zhong et al., 2018).

Guangxi represents one of China' s typical karst landscapes, with a karst area of approximately 98,700 km^2, accounting for 41.57% of the region' s total land area. The Guilin-Yangshuo area features typical middle-stage karst geomorphology, characterized by peak-cluster depressions (valleys) and peak-forest plains formed primarily through carbonate rock dissolution, representing typical southern Chinese karst development features (Wei et al., 2016). Guilin' s karst region faces severe rocky desertification, manifested by steep slopes, high rock exposure rates, poor soil formation conditions, thin and discontinuous soil layers, extremely slow soil formation rates, and limited available water (Xiang et al., 2017). These harsh habitat conditions result in slow vegetation growth, reduced biomass production, and dramatically decreased forest cover, leading to fragile ecosystems with low stability, high sensitivity, diminished self-regulation capacity, and reduced resistance to natural disturbances. Once degraded, karst habitats are extremely difficult to restore, making vegetation ecological restoration the primary task for rocky desertification control and ecological reconstruction in karst regions (Li et al., 2008).

Loropetalum chinense communities represent a typical naturally secondary forest type widely distributed in Guilin's karst hill regions. Through natural succession, these communities have developed through shrub, shrub-tree, small-tree forest, and old-growth forest stages (Ma et al., 2013). Current ecological research on *L. chinense* communities has primarily focused on species composition (Ma et al., 2013), ecological niches (Ma et al., 2012a), litter decomposition (Qin et al., 2017), and biomass (Zhang et al., 2018), with limited investigation of leaf traits. This study examines old-growth *L. chinense* communities to explore interspecific differences in leaf traits and their relationships, thereby investigating adaptation strategies to karst hill habitats and providing guidance for species selection in vegetation restoration and reconstruction.

1.1 Study Site Description

The study area is located at Xingping Dock Scenic Area in Yangshuo County, Guilin City, Guangxi Zhuang Autonomous Region (110°31 E, 24°55 N) in northeastern Guangxi. The region experiences a mid-subtropical humid monsoon climate with mild temperatures and abundant rainfall, at elevations of 100–500 m. The annual mean temperature is 18.9 °C, with average temperatures of 7.8 °C in January (the coldest month) and 28 °C in July (the hottest month). The frost-free period extends to 300 days annually. Mean annual precipitation is 1,949.5 mm, unevenly distributed with dry conditions in autumn and winter. Annual evaporation ranges from 1,490 to 1,905 mm.

This study focused on old-growth *Loropetalum chinense* communities, selecting species with importance values greater than 1. The 17 shrub layer species included *Mallotus philippensis*, *Osmanthus fragrans*, *Bauhinia championii*, *Micromelum integerrimum*, *Ficus tinctoria*, *Millettia cinerea*, *Mussaenda erosa*, *Cinnamomum burmanni*, *Decaspermum esquirolii*, *Trachelospermum jasminoides*, *Cinnamomum saxatile*, *Jasminum seguinii*, *Albizia kalkora*, *Ardisia crenata*, *Akebia trifoliata*, *Loropetalum chinense*, and *Canthium dicoccum*. The eight tree layer species included *Mallotus philippensis*, *Osmanthus fragrans*, *Loropetalum chinense*, *Cinnamomum burmanni*, *Swida wilsoniana*, *Liquidambar formosana*, *Choerospondias axillaris*, and *Canthium dicoccum*.

1.2 Leaf Trait Measurements

For each species, three healthy mature individuals were selected, and ten mature, intact leaves were collected from each plant. After removing petioles, leaves were placed between two moist filter papers, sealed in plastic bags, and transported to the laboratory. Leaves were moistened and stored in darkness at 5 °C for 12 hours, then surface moisture was rapidly absorbed with filter paper before weighing on a 1/10,000 g electronic balance to obtain saturated fresh weight (FW, g). Leaf thickness (LT, mm) was measured using digital calipers. Leaf area (LA, cm^2) was determined with a leaf area meter. Leaf samples were oven-dried at 70 °C for 72 hours before measuring dry weight (DW, g). Specific leaf area (SLA, $cm^2 \cdot g^{-1}$) was calculated as the ratio of leaf area to dry weight. Leaf dry matter content (LDMC, $g \cdot g^{-1}$) was calculated as the ratio of dry weight to saturated fresh weight. Leaf tissue density (LTD, $kg \cdot m^{-3}$) was calculated as the ratio of dry weight to the product of leaf area and thickness.

1.3 Data Analysis

SPSS 22.0 software was used for descriptive statistics, Pearson correlation analysis, and principal component analysis. Sigmaplot 12.5 software was used for figure preparation.

2.1 Leaf Traits in Tree and Shrub Layers

As shown in Figure 1 [Figure 1: see original paper], ANOVA revealed highly significant differences ($P < 0.01$) in DW, LDMC, LA, LT, SLA, and LTD among the eight tree species and among the 17 shrub species. For tree layer species, DW ranged from 0.056 to 0.442 g (mean = 0.193 g), while shrub layer species ranged from 0.023 to 0.424 g (mean = 0.161 g). *Osmanthus fragrans* exhibited the maximum DW in both layers, while *Canthium dicoccum* and *Albizia kalkora* showed the minimum values in tree and shrub layers, respectively.

LDMC ranged from 0.244 to 0.431 $g \cdot g^{-1}$ (mean = 0.323 $g \cdot g^{-1}$) in the tree layer and from 0.138 to 0.396 $g \cdot g^{-1}$ (mean = 0.271 $g \cdot g^{-1}$) in the shrub layer. *Osmanthus fragrans* showed the highest LDMC in both layers, while *Choerospondias axillaris* and *Albizia kalkora* had the lowest values in tree and shrub layers, respectively.

LA varied from 7.825 to 53.443 cm^2 (mean = 28.374 cm^2) in tree species and from 9.540 to 57.262 cm^2 (mean = 26.850 cm^2) in shrub species. *Mallotus philippensis* and *Bauhinia championii* showed maximum LA in tree and shrub layers, respectively, while *Canthium dicoccum* had the minimum LA in both layers.

LT ranged from 0.139 to 0.333 mm (mean = 0.232 mm) in tree species and from 0.109 to 0.358 mm (mean = 0.209 mm) in shrub species. *Liquidambar formosana* and *Osmanthus fragrans* exhibited maximum LT in tree and shrub layers, respectively, while *Choerospondias axillaris* and *Albizia kalkora* showed minimum values.

SLA varied from 91.833 to 261.481 $cm^2 \cdot g^{-1}$ (mean = 165.050 $cm^2 \cdot g^{-1}$) in tree species and from 99.160 to 498.884 $cm^2 \cdot g^{-1}$ (mean = 199.107 $cm^2 \cdot g^{-1}$) in shrub species. *Swida wilsoniana* and *Albizia kalkora* had maximum SLA in tree and shrub layers, respectively, while *Osmanthus fragrans* showed the minimum value in both layers.

LTD ranged from 185.968 to 504.604 $\mathrm{kg \cdot m^{-3}}$ (mean = 311.382 $\mathrm{kg \cdot m^{-3}}$) in tree species and from 184.668 to 486.357 $\mathrm{kg \cdot m^{-3}}$ (mean = 297.395 $\mathrm{kg \cdot m^{-3}}$) in shrub species. *Cinnamomum burmanni* and *Cinnamomum saxatile* exhibited maximum LTD in tree and shrub layers, respectively, while *Swida wilsoniana* and *Trachelospermum jasminoides* showed minimum values.

T-tests (Table 1) revealed that tree layer species had significantly greater DW, LDMC, and LT, and significantly lower SLA compared to shrub layer species, while LA and LTD did not differ significantly between layers. For shared species, *M. philippensis* showed significantly higher DW, LDMC, LA, and LT in the tree layer; *O. fragrans* had higher LDMC and LTD; *C. burmanni* showed higher DW and LTD; *L. chinense* had higher DW, LA, and LT; and *C. dicoccum* exhibited higher LDMC and LTD in the tree layer. Conversely, *M. philippensis* had significantly lower SLA and LTD; *O. fragrans* showed lower LT and SLA; *C. burmanni* had lower LDMC, LT, and SLA; and *C. dicoccum* exhibited lower LA and SLA in the tree layer. No significant differences between layers were found for *O. fragrans* DW and LA, *C. burmanni* LA, *L. chinense* LDMC, SLA, and LTD, or *C. dicoccum* DW and LT.

2.2 Relationships Among Leaf Traits

Pearson correlation analysis of six leaf traits for eight tree species and 17 shrub species (Table 2) showed consistent patterns between layers. DW was significantly positively correlated with LDMC, LA, LT, and LTD, but negatively correlated with SLA in both layers. LDMC was significantly positively correlated with LA and LT, and negatively correlated with SLA in both layers. The correlation between LDMC and LTD was non-significant in the tree layer but highly significant in the shrub layer. LA was significantly positively correlated with LT in both layers, but showed a significant negative correlation with LTD in the tree layer and a significant positive correlation in the shrub layer. LT was significantly negatively correlated with SLA and LTD in both layers. SLA was significantly negatively correlated with LTD in both layers.

2.3 Principal Component Analysis of Leaf Traits

Principal component analysis of eight tree species (Table 3) showed that the first and second principal components explained 51.94% and 30.58% of total variance, respectively, with a cumulative contribution of 82.52%. The first component, with the highest coefficients for x1 (DW) and x2 (LDMC), primarily reflected comprehensive resistance to external disturbance and adverse environments. The second component, with the largest absolute coefficient for x6

(LTD), mainly reflected adaptation to moisture conditions.

For the 17 shrub species, the first and second principal components explained 52.35% and 23.55% of variance, respectively (cumulative = 75.90%). In the first component, x3 (LA), x4 (LT), and x6 (LTD) had relatively small coefficients, while x1 (DW), x2 (LDMC), and x5 (SLA) had larger coefficients. Notably, x5 (SLA) had a negative coefficient, indicating that it reduces the component value. Since SLA reflects light-capturing area per unit dry mass investment, the first component comprehensively represents resource acquisition capacity. The second component, with the highest coefficient for x6 (LTD), primarily reflected moisture environment adaptation.

The principal component equations for tree species were: $y_1 = 0.952x_1 + 0.955x_2 + 0.718x_3 + 0.634x_4 - 0.612x_5 + 0.064x_6$ $y_2 = -0.111x_1 + 0.001x_2 + 0.298x_3 + 0.570x_4 + 0.664x_5 - 0.984x_6$

Composite scores (F) were calculated as $F = (3.116y_1 + 1.834y_2)/(3.116 + 1.834)$, yielding the following ranking for disturbance resistance and moisture adaptation: *Osmanthus fragrans* > *Mallotus philippensis* > *Liquidambar formosana* > *Cinnamomum burmanni* > *Loropetalum chinense* > *Swida wilsoniana* > *Choerospondias axillaris* > *Canthium dicoccum*.

Similarly, shrub layer rankings for resource acquisition and moisture adaptation were: *Osmanthus fragrans* > *Bauhinia championii* > *Cinnamomum burmanni* > *Cinnamomum saxatile* > *Mallotus philippensis* > *Ficus tinctoria* > *Millettia cinerea* > *Micromelum integerrimum* > *Ardisia crenata* > *Decaspermum esquirolii* > *Loropetalum chinense* > *Jasminum seguinii* > *Akebia trifoliata* > *Canthium dicoccum* > *Mussaenda erosa* > *Trachelospermum jasminoides* > *Albizia kalkora*.

3.1 Comparison of Leaf Traits Between Tree and Shrub Layers

Tree layer species in old-growth *Loropetalum chinense* communities exhibited significantly greater DW, LDMC, and LT compared to shrub layer species. Mean DW was higher than that of common shrub species in both karst hills (Ma et al., 2011) and soil mountains (Ma et al., 2012b) in the same region, while mean LDMC was lower. These findings indicate that tree layer plants in old-growth *L. chinense* communities possess stronger resistance to external disturbance and adverse environmental conditions compared to shrub layer plants and relative to common shrubs in local karst and soil mountain habitats.

At the old-growth stage, *L. chinense* communities form a climax community with tall trees, open canopies, and high canopy closure, creating favorable microclimatic conditions. Tree layer plants receive direct sunlight, while understory shrubs experience shaded conditions, resulting in thicker leaves in the tree layer. However, mean LT in this study was lower than that of common shrubs in local karst hills (Ma et al., 2011) and soil mountains (Ma et al., 2012b), suggesting relatively moderate microclimatic conditions (water, heat, light) in old-growth *L. chinense* communities compared to other local habitats. Mean LDMC and LT were lower and higher, respectively, than those of karst woody plants in central Guizhou (Zhong et al., 2018) and main woody species in limestone areas of Chongqing (Liu et al., 2015).

Tree layer SLA was significantly lower than shrub layer SLA, while both layers showed higher mean SLA than common shrubs in local karst hills (Ma et al., 2011) and soil mountains (Ma et al., 2012b). This indicates that tree layer plants are better adapted to resource-poor conditions, whereas shrub layer plants exhibit greater light-capturing area per unit dry mass investment and stronger resource acquisition capacity (Li et al., 2005), suggesting higher productivity than local karst and soil mountain shrub communities. SLA values were higher than those of karst woody plants in central Guizhou (Zhong et al., 2018) and Chongqing limestone areas (Liu et al., 2015). No significant differences in LA and LTD were observed between layers, though both showed higher mean LA than common shrubs in local karst and soil mountain habitats (Ma et al., 2011; Ma et al., 2012b), indicating consistent hydrothermal environments between layers and relatively balanced water-heat conditions in old-growth *L. chinense* communities. Mean LA and LTD were higher and lower, respectively, than those of central Guizhou karst woody plants (Zhong et al., 2018).

Among the five shared species (*Mallotus philippensis*, *Osmanthus fragrans*, *Cinnamomum burmanni*, *Loropetalum chinense*, and *Canthium dicoccum*), most leaf traits showed highly significant differences between layers, except for *O. fragrans* DW and LA, *C. burmanni* LA, *L. chinense* LDMC, SLA, and LTD, and *C. dicoccum* DW and LT. This demonstrates both consistency and variability in adaptive strategies of shared species to local environments at the individual level, exhibiting functional convergence and divergence among co-occurring species (Zhang et al., 2010; Yao et al., 2010; Zhong et al., 2018).

3.2 Correlations Among Leaf Traits

During ecological restoration of Guilin’ s karst hill environment, plants continuously adjust resource allocation and physiological processes, manifesting characteristic morphological changes (Zhou et al., 2015). This study found consistent correlations between tree and shrub layers for most trait pairs, except for LTD with LDMC and LA, and SLA with LA.

DW showed significant positive correlations with LDMC, LA, and LT in both layers, consistent with studies on common plants in Guilin’ s soil mountains (Ma et al., 2012b). SLA was significantly negatively correlated with LDMC, LT, and LTD in both layers, aligning with findings from 52 plant species in the Horqin Sandy Land (Zhao et al., 2010), common plants in Guilin’ s soil mountains (Ma et al., 2012b), 14 dominant species in Guilin’ s karst hills (Ma et al., 2011), and plants in desertified grasslands of northwest Sichuan (Jiang et al., 2017). This indicates that decreasing SLA corresponds to increasing LDMC, LT, and LTD, which increases the distance or resistance for internal water diffusion to the leaf surface, thereby reducing water loss and producing thicker, denser leaves.

LDMC was significantly positively correlated with LT, similar to findings in the Daqinggou Nature Reserve (Liu et al., 2017), and with LA, consistent with studies on central Guizhou karst woody plants (Zhong et al., 2018). LT was significantly positively correlated with LA and negatively correlated with LTD, matching results from 25 subtropical plants (Zeng et al., 2006) and desertified grassland plants in northwest Sichuan (Jiang et al., 2017).

3.3 Adaptive Strategies of Tree and Shrub Layers

Principal component analysis identified DW, LDMC, and LTD as key leaf traits for tree layer adaptation, indicating strong resistance to disturbance and moisture stress. The significantly higher DW and LDMC in tree layer species suggest greater "defensive" investment, characteristic of a "slow investment-return" or "conservative" leaf economics spectrum (Wright et al., 2005; Chen and Xu, 2014). In contrast, SLA and LTD emerged as key traits for shrub layer adaptation, reflecting strong resource acquisition and moisture adaptation capacities. The significantly higher SLA in shrub layer species indicates lower "defensive" investment, representing a "fast investment-return" or "acquisitive" strategy (Wright et al., 2005; Chen and Xu, 2014).

While LDMC and SLA are widely recognized as the two most important leaf traits (Hutchison et al., 1986; Wilson et al., 1999; Zhang et al., 2008), this study highlights the additional importance of LTD for both layers, suggesting that adaptation strategies in old-growth karst forest habitats prominently feature resource acquisition, conservation, and moisture adaptation.

3.4 Ecological Niche of *Loropetalum chinense* in Old-Growth Forests

Loropetalum chinense communities play a crucial role in natural vegetation restoration succession in this region' s karst habitats, progressing from shrub to shrub-tree, small-tree forest, and old-growth stages (Ma et al., 2012a). In the tree layer, *L. chinense* ranked relatively low in DW content but intermediate in LDMC and LTD, placing fifth in comprehensive adaptation scores. In the shrub layer, *L. chinense* showed intermediate SLA and LTD values, ranking 11th in resource acquisition and moisture adaptation. These results objectively reflect *L. chinense*' s ecological niche in old-growth communities, consistent with Ma et al. (2012a), which demonstrated that *L. chinense*' s dominant position declines through natural succession, potentially developing into a mixed evergreen-deciduous broadleaf forest with multiple co-dominant species. Comprehensive evaluation of *L. chinense*' s ecological niche and adaptive capacity requires integrated consideration of photosynthetic ability, nutrient utilization, and water use efficiency.

In summary, this study analyzed differences and relationships in leaf traits between tree and shrub layers in old-growth *Loropetalum chinense* communities. DW, LDMC, and LTD emerged as key indicators for tree layer adaptation, while SLA and LTD were critical for shrub layer adaptation. These findings enhance understanding of plant adaptation to karst hill habitats and provide valuable guidance for species selection and functional group configuration in Guilin' s karst vegetation restoration and reconstruction efforts.

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