Postprint: Response of Kapok Tree Architecture and Leaf Traits to Habitat Factors

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Abstract

Plant morphological structure results from the combined effects of intrinsic plant characteristics and external environmental factors. Analyzing the correlation between kapok tree architecture and leaf traits, and exploring the impacts of topographic, soil, and meteorological factors on kapok growth, are of great significance for revealing the growth strategies and adaptive mechanisms of kapok trees. This study examined 230 kapok trees in Xishuangbanna National Nature Reserve, Yunnan Province, measuring six tree architecture indices, eight leaf trait indices, and habitat factors including regional topography, meteorology, and soil nutrients. Structural equation modeling and variation partitioning were employed to analyze the effects and explanatory power of these habitat factors on kapok tree architecture and leaf traits. The results showed that: (1) significant correlations existed among the measured indices of kapok tree architecture and among those of leaf traits ($P<0.05$); (2) the measured habitat factors strongly influenced kapok growth, with annual average rainfall, slope, and mean temperature showing high explanatory rates for kapok growth indices, representing the primary habitat factors affecting kapok growth; (3) based on standardized path coefficients, the three habitat factor types exhibited consistent effects on kapok tree architecture and leaf traits, all showing the pattern of topographic factors > meteorological factors > soil factors; and (4) the three habitat factors cumulatively explained 43.5% and 12.3% of the variation in tree architecture and leaf traits, respectively, demonstrating that tree architecture responds more strongly to habitat conditions than leaf traits. These findings preliminarily elucidate the adaptive strategies of different kapok growth indices to environmental factors, providing theoretical basis and practical reference for the cultivation, propagation of kapok in heterogeneous habitats, and efficient management of kapok plantations.

Full Text

Preamble

Bombax ceiba Tree Structure and Leaf Traits Response to Habitat Elements

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Abstract: Plant morphology and structure result from the joint action of intrinsic biological factors and external environmental conditions. Analyzing the correlation between tree structure and leaf traits of *Bombax ceiba* and exploring the influence of topographic, soil, and meteorological elements on its growth are crucial for revealing the species' growth strategies and adaptation mechanisms. This study examined 230 *B. ceiba* trees in Xishuangbanna National Nature Reserve, Yunnan Province, measuring six tree structure indices, eight leaf trait indices, and associated habitat elements including topography, meteorology, and soil nutrients. Structural equation modeling and variation partitioning were used to analyze the effects and explanatory power of various habitat elements on tree structure and leaf traits. The results showed that: (1) Significant correlations existed among tree structure indices and among leaf trait indices ($P < 0.05$). (2) Habitat element indices strongly influenced *B. ceiba* growth, with mean annual precipitation, slope, and average temperature showing the highest explanatory rates as the dominant habitat factors. (3) Standardized path coefficients revealed consistent effects of the three habitat elements on both tree structure and leaf traits, following the pattern: topographic elements > meteorological elements > soil elements. (4) The combined effects of the three habitat elements explained 43.5% of variation in tree structure and 12.3% in leaf traits, demonstrating that tree structure responds more strongly to habitat conditions than leaf traits. These findings clarify the adaptive strategies of different growth indices to environmental factors in *B. ceiba*, providing theoretical basis and practical guidance for cultivation, propagation, and efficient plantation management in heterogeneous habitats.

Keywords: *Bombax ceiba*, habitat elements, tree structure, leaf traits, redundancy analysis, structural equation model

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Introduction

Over the past century, global climate has shown a significant warming trend, altering mean temperature and precipitation patterns worldwide (Yuan et al., 2020). The IPCC Special Report on Global Warming of 1.5°C indicates that future global temperatures will continue rising, with intensified drought conditions (IPCC, 2018). These climatic changes affect tree growth to varying degrees (Deslauriers et al., 2007), consequently altering forest ecosystem structure and function (Bonan, 2008). Therefore, understanding tree growth responses to environmental factors under climate change is essential for predicting forest ecosystem trends and providing theoretical foundations for plant conservation and management.

Current research on plant functional traits has expanded beyond single or grouped trait analyses to focus increasingly on intrinsic linkages and trade-off relationships among traits (Kosaka et al., 2004). Clarifying the relationships between plant functional traits and environmental conditions helps reveal plant growth strategies and resource allocation patterns, elucidates underlying physiological and ecological mechanisms, and provides reliable background data for studying ecosystem energy flow and material cycling while enabling more accurate predictions of climate change impacts on plant communities (Wright et al., 2004; He et al., 2019). Tree structure describes forest growth status and reflects natural processes such as growth, competition, and regeneration, as well as human influences, with diameter at breast height (DBH) and tree height being key indicators for predicting community development trends (Li et al., 2023). *Bombax ceiba* morphology is significantly influenced by external environmental factors during its development. Temperature is a critical climatic factor affecting tree structure (Delpierre et al., 2019), as radial growth benefits from elevated early-growing-season temperatures. On one hand, radial growth depends on non-structural carbohydrates produced through photosynthesis, which relies on chlorophyll and photosynthetic enzymes. Increased growing-season temperatures accelerate enzyme function (Shi et al., 2015), enhancing carbohydrate accumulation for xylem growth. Fertile soils provide more nutrients (especially available N and P), influencing plant productivity and biological processes that promote tree growth. Altitude gradients cause dramatic changes in temperature, humidity, light, and other environmental factors, making elevation an important indicator affecting tree growth (Cai et al., 2017). As the basic structural and functional unit of plants, leaves are crucial organs for energy and material exchange among plants, soil, and atmosphere. The sensitivity of leaf traits to environmental changes directly or indirectly affects plant physiological and ecological processes. Soil nutrients serve as the material and energy source for leaf trait construction, while altitude changes indirectly affect the redistribution of temperature, precipitation, and light, creating spatial heterogeneity in climate that influences plant growth and indirectly affects functional trait variation (Cornelissen et al., 2003). Since minor environmental changes can produce different external morphological expressions, investigating environmental effects on different traits of the same species is significant. Although previous studies have examined relationships between plant functional traits and environment, they have focused primarily on a few species such as *Populus euphratica* (Wei et al., 2021; Shi et al., 2023) and *Caragana* spp. (Luo et al., 2022; Yang et al., 2023). Therefore, expanding research to different species is necessary for more accurate understanding of these relationships.

This study examined 230 *B. ceiba* trees in Xishuangbanna National Nature Reserve, Yunnan Province, measuring six tree structure indices, eight leaf trait indices, and habitat elements including topography, meteorology, and soil nutrients. Through correlation analysis, redundancy analysis, structural equation modeling, and variation partitioning, we addressed three questions: (1) Do correlations exist among tree structure indices and among leaf trait indices? (2) How do different habitat indices differentially affect *B. ceiba* growth? (3) How do tree structure and leaf traits respond differently to the same habitat elements? These investigations provide scientific basis for establishing and protecting wild *B. ceiba* populations.

1.1 Study Area

The study area is located in Xishuangbanna National Nature Reserve, Yunnan Province (100°50 –101°06 E, 21°08 –22°25 N), with elevations ranging from 480 to 1,400 m. The terrain features intermountain basins and hilly valleys. The region has a warm and humid climate with abundant light and heat resources, annual precipitation of 1,200–1,600 mm, mean annual temperature of 21.8°C, and 2,293.4 sunshine hours. Xishuangbanna is an important region for concentrated tropical rainforest distribution in China, with soils primarily composed of latosol and red soil that are acidic (Ma et al., 2020) and rich in total phosphorus and nitrate nitrogen. Situated in a biogeographic transition zone between tropical and subtropical biota (Zhu et al., 2015), the reserve features complex forest vegetation with rich species diversity in both canopy and understory layers, forming a unique tropical rainforest ecosystem. Major associated tree species include *Celtis timorensis*, *Antiaris toxicaria*, *Hedyotis auricularia*, and *Prismatomeris connata*.

1.2 Measurement of *B. ceiba* Growth Indices

Field surveys were conducted on 230 naturally growing *B. ceiba* trees across the reserve, measuring morphological structures and habitat elements. Tree height (H), diameter at breast height (DBH), crown breadth (CB), and height to crown base (HCB) were measured using tape measures. Branch number (NB) was counted from four cardinal directions, and taperingness (T) was calculated using proportional relationships. From each tree, 20 fully expanded, healthy, and intact leaves were collected from the middle outer canopy in four directions. Leaf length (LL), width (LW), area (LA), and perimeter (P) were measured using a CID portable laser leaf area meter (CID CI-202, USA). Fresh weight (LFW), saturated weight (LSW), and dry weight (LDW) were measured using a Shimadzu analytical balance (ATY124, Japan). Leaf water content (LWC) was calculated as: LWC = (fresh weight - dry weight) / dry weight × 100%.

1.3 Measurement of Habitat Elements

Handheld GPS devices recorded latitude, longitude, altitude, and aspect for each tree location, while geological compasses measured slope. Aspect data were quantified by measuring clockwise from east to northeast, assigning values from 1 to 8, followed by standardization and normalization (Chen et al., 2019). Soil samples were collected using a five-point sampling method from the 0–20 cm topsoil layer in each plot, mixed uniformly, and brought to the laboratory in cloth bags. After air-drying, grinding, and sieving, samples were analyzed for total nitrogen (TN), total phosphorus (TP), available phosphorus (AP), ammonium nitrogen (AN), and nitrate nitrogen (NN) (Liu et al., 2021), with three replicates for each indicator. Meteorological data (average temperature [AT], mean relative humidity [MRH], and mean annual precipitation [MAP] from 2009–2018) were obtained from the Mengla meteorological station (101°35 E, 21°28 N) (http://data.cma.cn/). Basic plot characteristics are shown in Table 1 .

1.4 Data Processing

Data were analyzed using Excel 2016, SPSS 22.0, Amos 21.0, and Canoco 5.0. Pearson correlation analysis was performed on tree structure and leaf trait indices at $\alpha = 0.01$ significance level. Principal component analysis (PCA) was conducted separately for tree structure indices, leaf trait indices, soil elements, topographic elements, and meteorological elements. The coefficient for each observed variable was calculated as the loading on the first principal component axis divided by the square root of the corresponding eigenvalue. Structural equation modeling (SEM) was performed in Amos 21.0, with model fit assessed using chi-square/degrees of freedom (^{2}/df), where CFI and GFI values > 0.9 indicate good fit (Dong et al., 2021). Finally, redundancy analysis (RDA) and variation partitioning were conducted in Canoco 5.0 to quantify the effects and explanatory power of different habitat elements on *B. ceiba* morphology.

Results

2.1 Correlation Analysis of Tree Structure and Leaf Trait Indices

Pearson correlation analysis revealed that tree height was extremely significantly positively correlated with DBH, crown breadth, HCB, and branch number ($P < 0.01$). DBH showed extremely significant positive correlations with crown breadth, HCB, and branch number, while crown breadth was extremely significantly positively correlated with HCB and branch number. Taperingness was extremely significantly negatively correlated with tree height and HCB, indicating strong overall correlations among tree structure indices. For leaf traits, leaf area, length, and width were extremely significantly negatively correlated with leaf dry weight but extremely significantly positively correlated with other indices. Perimeter was significantly negatively correlated with leaf dry weight but extremely significantly positively correlated with other indices. Fresh weight, saturated weight, dry weight, and water content were extremely significantly negatively correlated with each other but extremely significantly positively correlated with other indices (Figure 1 [Figure 1: see original paper]).

2.2 Weight Analysis of Habitat Elements and *B. ceiba* Indices

Redundancy analysis of the three habitat element indices and *B. ceiba* morphology explained 60.52% and 8.01% of total variance on the first two axes (cumulative 68.53%), indicating reliable RDA results. The explanatory power of environmental factors on *B. ceiba* growth followed the order: mean annual precipitation (46.4%) > slope (7.9%) > average temperature (5.7%) > altitude (4.3%) > total nitrogen (1.9%) > available phosphorus (1.5%) > nitrate nitrogen (1.4%) > ammonium nitrogen (1.3%) > mean relative humidity (1.2%) > aspect (0.5%) (Figure 2 [Figure 2: see original paper]).

Principal component analysis effectively characterized relationships between observed variables and latent variables in SEM. Weight coefficients were calculated for the three habitat elements and two growth indices. Tree height, DBH, and crown breadth contributed most to tree structure weight (coefficients: 0.241, 0.287, and 0.316, respectively). Leaf area, length, width, and water content contributed most to leaf trait weight (coefficients: 0.254, 0.255, 0.217, and 0.221, respectively). Total nitrogen, total phosphorus, and available phosphorus contributed most to soil element weight (coefficients: 0.252, 0.243, and 0.250, respectively). Mean relative humidity contributed most to meteorological element weight (coefficient: 0.467), while slope contributed most to topographic element weight (coefficient: 0.58) (Table 2).

2.3 Path Analysis of Habitat Elements on Tree Structure and Leaf Traits

Structural equation modeling revealed optimal model fit (GFI = 0.998; AGFI = 0.968; SRMR < 0.005). Tree structure and leaf traits showed extremely significant negative correlation ($P < 0.01$, coefficient = -0.47). Topographic, meteorological, and soil elements were strongly intercorrelated (extremely significant positive correlation, $P < 0.01$). Path analysis showed that all three habitat elements positively affected tree structure, with topographic and meteorological elements having extremely significant positive effects (path coefficients: 0.47 and 0.39, respectively), while soil elements had a smaller effect (path coefficient: 0.12). The three habitat elements differentially affected tree structure and leaf traits: topographic elements had an extremely significant negative effect on leaf traits (path coefficient: -0.32), while meteorological and soil elements showed no significant effects (Figure 3 [Figure 3: see original paper]).

2.4 Explanatory Analysis of Habitat Elements on Tree Structure and Leaf Traits

Topographic, meteorological, and soil elements are crucial components of habitat conditions for plant growth. Variation partitioning quantified the individual and interactive contributions of these elements to tree structure and leaf traits (Figure 4 [Figure 4: see original paper]).

The combined effects of the three habitat elements explained 43.5% of variation in tree structure. Among individual factors, topographic elements explained the largest portion (18.6%), followed by meteorological elements (17.5%), while soil elements explained the smallest portion (12.4%). In contrast, the total explanatory power for leaf traits was substantially lower at 12.3%. The individual explanatory powers of topographic, soil, and meteorological elements on leaf traits were 6.0%, 20.1%, and 4.7%, respectively.

Discussion

3.1 Tree Structure Response to Habitat Elements

Tree structure shows strong relationships with environmental habitat elements. In this study, the three habitat elements substantially influenced tree structure, with topographic elements showing the highest explanatory power, followed by meteorological elements, and soil elements the lowest. This indicates that topography most strongly affects *B. ceiba* growth in tropical rainforests. Lei et al. (2012) found that climate factors limiting radial growth of *Picea crassifolia* shifted from precipitation to temperature along altitude gradients, with seasonal limiting factors also changing. This differs from our results, possibly because topographic changes alter moisture and humidity in *B. ceiba* habitats. At lower elevations, trees can access more water and soil nutrients, but as elevation increases, temperature decreases, atmospheric pressure drops, and light intensity increases, directly affecting plant metabolism and limiting growth (Pan et al., 2009), resulting in greater topographic influence. Our findings align with Hu and Fan (2016), who reported positive correlations between stem radial increment and relative humidity/precipitation but negative correlation with daily maximum temperature. Tree height, DBH, and crown breadth showed significant positive correlations ($P < 0.01$), demonstrating consistent responses to environmental conditions, likely resulting from combined genetic and external environmental factors. Wang et al. (2010) found that elevated temperatures in May-June increased evaporation, causing soil water deficits that affected *Pinus armandii* growth in Funiu Mountain. This differs from our study, possibly because spring-summer high temperatures significantly limit *P. armandii* growth, whereas our tropical study area has both high temperatures and abundant moisture. Water affects cell division and growth by influencing cell compression (Muller et al., 2011), while higher temperatures enhance photosynthesis in *B. ceiba*, generating more carbohydrates for tree growth and structural development.

3.2 Leaf Trait Response to Habitat Elements

Leaf traits are influenced by both genetic factors and environmental regulation (Rathgeber et al., 2016). Soil elements explained the largest portion of leaf trait variation, followed by topographic elements, while meteorological elements explained the least. Path analysis indicated that topographic and meteorological elements negatively affected leaf traits, with topographic effects greater than meteorological effects. Leaf area, perimeter, water content, width, and length were positively correlated with nitrate nitrogen, total nitrogen, and available phosphorus, reflecting that *B. ceiba* allocates more soil nutrients to leaf trait construction. This aligns with Huang et al. (2021) regarding Chinese fir growth and soil nutrients. Higher soil nutrient availability (e.g., available phosphorus in this study) tends to increase leaf perimeter, area, and specific leaf area, indicating that *B. ceiba* in Xishuangbanna adopts a fast investment growth strategy under nutrient-rich conditions, consistent with many studies (Luo et al., 2021; Liu et al., 2021; Huang et al., 2022). Meteorological effects on leaf traits vary with environmental conditions. In this study, leaf area, perimeter, water content, length, and width were positively correlated with mean annual precipitation and relative humidity but negatively correlated with mean temperature. This suggests that air and soil moisture promote leaf traits while high temperatures inhibit them. Elevated temperatures cause stomatal closure, reducing photosynthesis and biomass accumulation. The study area experiences tropical monsoon climate, and mid-April corresponds to the late dry season with abundant sunlight and high temperatures that significantly affect leaves, demonstrating temperature inhibition of leaf traits. However, tree structure is less sensitive to environmental changes than leaf traits, as summer temperature increases have minimal impact on nutrient transport and morphological construction, resulting in positive standardized path coefficients. These findings are consistent with previous research showing that drought conditions inhibit plant growth (Shi et al., 2019).

3.3 Correlation Between Tree Structure and Leaf Traits and Adaptive Strategies

Plant morphology objectively expresses adaptation to external environments. At large scales, climate determines functional trait distribution; at intermediate scales, land use and disturbance are primary factors; while at small or local scales, topography and soil determine trait expression (Venn et al., 2011). This study shows that meteorological, topographic, and soil elements are extremely significantly correlated ($P < 0.01$) but exert different effects on *B. ceiba* morphology, with topographic elements having the greatest influence, followed by meteorological elements, and soil elements the least. This indicates that *B. ceiba* growth is jointly controlled by temperature, moisture, and soil nutrients from its origin, rather than by temperature or water alone (Barboni et al., 2004). Meteorological elements determine required temperature and moisture, topographic elements (altitude, slope, aspect) affect water, heat, and light distribution to alter regional temperature and humidity, while soil— influenced by temperature, precipitation, biological activity, and geological changes—creates a material layer providing nutrients, energy, and suitable pH for growth (Huang et al., 2018; Liu et al., 2021). The extremely significant negative correlation between tree structure and leaf traits, combined with higher explanatory power for tree structure (43.5%) than leaf traits (12.3%), suggests resource allocation varies across growth stages. This aligns with previous research: during seedling stages, *B. ceiba* enhances photosynthetic capture by increasing leaf area and specific leaf area while absorbing substantial water to support vigorous growth and improve survival (Yang et al., 2022). During stable or stagnant growth periods, trees reduce leaf area and specific leaf area to decrease transpiration and nutrient/water consumption, while reduced leaf water content decreases metabolism, ensuring more resource accumulation to facilitate tree structure expansion and competitive advantage (Wright et al., 2002; Ding et al., 2014; Liu et al., 2020). Future studies should incorporate additional growth indices such as ring traits reflecting light absorption and water collection, and branch-stem angles that play important roles in growth, to provide more comprehensive understanding of environmental responses.

This study demonstrates widespread and mostly extremely significant correlations among *B. ceiba* tree structure and leaf trait indices, reflecting similar adjustment patterns within the same habitat. The three environmental elements differentially affect tree structure and leaf traits, with greater influence on tree structure. During growth, *B. ceiba* employs negative correlations between tree structure and leaf traits as a strategy to cope with environmental changes through different trait combinations.

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Note: Figure translations are in progress. See original paper for figures.