Relationship Between Aboveground Biomass and Environmental Factors in Typical Karst Secondary Forests at Tianlong Mountain, Central Guizhou (Postprint)

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Abstract

To investigate the relationship between aboveground biomass and environmental factors in karst secondary forests, this study selected a typical secondary forest plot in Tianlong Mountain, Puding County, central Guizhou karst region as the research object. Aboveground biomass of dominant species and the community was calculated using single-species and different diameter class group models, spatial distribution maps were employed to describe the spatial distribution patterns of environmental factors and community aboveground biomass, and correlation test (Pearson), general linear model (GLM), and redundancy analysis (RDA) were utilized to discuss the relationships between community, life form, and species aboveground biomass and environmental factors. The results were as follows: (1) The total aboveground biomass of the karst secondary forest community was 106.94 $t \cdot hm^{-2}$, with dominant species accounting for 91.77% of the entire plot. Evergreen plants exhibited higher biomass than deciduous plants, with Lithocarpus confinis and Platycarya strobilacea showing the highest proportions in the community at 34.23% and 34.37%, respectively; (2) The spatial distribution of rock exposure rate showed distinct gradient differences between upper and lower slopes, being significantly greater on upper slopes, while the spatial distributions of slope gradient and soil thickness were discontinuous without obvious patterns; (3) Community aboveground biomass was significantly positively correlated with soil thickness, and their spatial distributions tended to be consistent. Soil thickness was the primary influencing factor for community aboveground biomass, while rock exposure rate and slope gradient had relatively minor effects; (4) For different life forms, rock exposure rate exerted the greatest influence on aboveground biomass, whereas soil thickness and slope gradient had more pronounced effects on evergreen plants than on deciduous plants; (5) For different species, the correlations between environmental factors and aboveground biomass were complex. Most species showed positive correlations with soil thickness, while Platycarya strobilacea and Zanthoxylum dimorphophyllum exhibited positive correlations with rock exposure rate and slope gradient, respectively. In summary, vegetation restoration in the secondary forest of this study area is proceeding slowly. Soil thickness is the main influencing factor of community aboveground biomass, but for different life forms and species, the response of aboveground biomass to environmental conditions is affected by biological factors such as life form differences, species habitat preferences, and interspecific relationships.

Full Text

Relationship Between Aboveground Biomass and Environmental Factors in a Typical Karst Secondary Forest in Tianlong Mountain, Central Guizhou

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Abstract: To explore the relationship between aboveground biomass and environmental factors in karst secondary forests, this study investigated a typical secondary forest plot in Tianlong Mountain, Puding County, central Guizhou. Aboveground biomass models for individual species and different diameter classes were used to calculate biomass of dominant species and the community. Spatial distribution maps described the spatial patterns of environmental factors and community aboveground biomass, while correlation tests (Pearson), general linear models (GLM), and redundancy analysis (RDA) were employed to examine relationships between aboveground biomass of communities, life forms, and species with environmental factors. The results showed: (1) Total community aboveground biomass in the karst secondary forest was 106.94 $t \cdot hm^{-2}$, with dominant species accounting for 91.77% of the total plot biomass. Evergreen plants exhibited higher biomass than deciduous plants, with *Lithocarpus confinis* and *Platycarya strobilacea* comprising the highest proportions at 34.23% and 34.37%, respectively. (2) Rock exposure rate showed distinct upper-lower slope gradient differences, being significantly greater on upper slopes, while slope and soil thickness showed discontinuous spatial distributions without clear patterns. (3) Community aboveground biomass was significantly positively correlated with soil thickness, and their spatial distributions tended to be consistent. Soil thickness was the primary factor influencing community aboveground biomass, while rock exposure rate and slope had relatively low impacts. (4) For different life forms, rock exposure

rate had the greatest influence on aboveground biomass, with soil thickness and slope affecting evergreen plants more than deciduous plants. (5) For different species, correlations between environmental factors and aboveground biomass were complex; most species were positively correlated with soil thickness, while *Platycarya strobilacea* and *Zanthoxylum dimorphophyllum* were positively correlated with rock exposure rate and slope, respectively. In conclusion, vegetation restoration in this secondary forest is slow, with soil thickness being the main factor influencing community aboveground biomass. However, for different life forms and species, the response of aboveground biomass to environmental conditions is affected by biological factors such as life form differences, species habitat preferences, and interspecific relationships.

Keywords: karst, aboveground biomass, soil thickness, rock exposure rate, slope

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1. Study Area and Methods

1.1 Study Area Description The study site is located in Puding County, central Guizhou Province, on the watershed between the Yangtze River and Pearl River systems of the Guizhou Plateau, at an elevation of 1,460 m. The region has a mid-subtropical monsoon climate with warm, humid conditions and distinct seasonal alternation. The climate is mild year-round with low radiation energy, an annual mean temperature of 15.1°C, and average sunshine duration of 1,164.9 hours. The frost-free period is long, reaching 301 days, with abundant precipitation averaging 1,378.2 mm annually, concentrated mainly from May to September. The study area represents a typical karst secondary forest dominated by Fagaceae, Lauraceae, Juglandaceae, Pittosporaceae, Saxifragaceae, Rhamnaceae, Betulaceae, Rutaceae, and Ulmaceae families.

1.2 Plot Survey and Sample Collection In 2012, a permanent monitoring plot of 2 hm^2 was established on the southern slope of Tianlong Mountain in Puding County, Guizhou (105°45'06.65"E, 26°22'07.06"N). The plot was divided into 200 subplots of 10 m × 10 m. In 2020, we resurveyed all woody plants with DBH $\geq$ 1 cm in each subplot, recording species, quantity, height, DBH, and crown width. We also recorded slope gradient and rock exposure rate for each subplot, and measured soil thickness five times along the diagonal of each 10 m × 10 m subplot using a graduated steel rod, using the average value (Liu, 2020).

1.3 Data Analysis 1.3.1 Important Value Calculation

Important value characterizes species dominance (Li, 2020) and was calculated as follows:

Important Value = (Relative Density + Relative Frequency + Relative Dominance) / 3

Relative Frequency = (Frequency of a species / Total frequency of all species) × 100%
Relative Dominance = (Sum of basal area of a species / Sum of basal area of all species) × 100%
Relative Density = (Density of a species / Total density of all species) × 100%

1.3.2 Aboveground Biomass Estimation

Aboveground biomass calculation formulas used species-specific and diameter-class regression models developed by Liu et al. (2009) from the same plot based on relationships between dry weight, DBH, height, and crown width. Dominant species biomass was calculated using eight individual models (Table 1), while other species used different diameter-class regression models. Community aboveground biomass was obtained by summing all species values.

Table 1 Aboveground biomass estimation models for main tree species and different diameter classes

Model Object	Aboveground Biomass Model	R^2	P-value
Lithocarpus confinis	$y = 0.8967(D^2H)^{0.9636}$	0.9817	<0.01
Platycarya strobilacea	$y = 1.9611(D^2H)^{0.8921}$	0.9886	<0.01
Itea yunnanensis	$y = 1.9545(D^2H)^{0.8996}$	0.9568	<0.01
Machilus cavaleriei	$y = 2.6211(D^2H)^{0.8565}$	0.9730	<0.01

Note: D = diameter at breast height (cm), H = height (m), y = aboveground biomass (kg)

Community aboveground biomass for each subplot was calculated using these models. Spatial distribution maps of community aboveground biomass, soil depth, rock exposure rate, and slope were produced using Origin2021. Correlation heatmaps for soil thickness, rock exposure rate, slope, and aboveground biomass were generated using Corrplot in R. The explanatory power of environmental factors on community and different life form aboveground biomass was analyzed using general linear models in IBM SPSS Statistics. Redundancy analysis (RDA) in Canoco 4.5 was used to analyze relationships between dominant species aboveground biomass and environmental factors. In RDA ordination, solid arrows represent dominant species aboveground biomass, hollow arrows represent environmental factors, and correlation equals the cosine of the angle between vectors. Angles <90° indicate positive correlation, angles >90° and <180° indicate negative correlation, and angles approaching 90° indicate weaker correlations (Long et al., 2012).

2. Results

2.1 Aboveground Biomass Characteristics of Tianlong Mountain Secondary Forest The main species in the karst secondary forest of Tianlong Mountain include *Lithocarpus confinis*, *Platycarya strobilacea*, *Itea yunnanensis*, *Machilus cavaleriei*, *Pittosporum brevicalyx*, *Carpinus pubescens*, *Lindera communis*, *Zanthoxylum dimorphophyllum*, *Celtis sinensis*, *Stachyurus obovatus*, *Ilex corallina*, *Rhamnella martini*, *Rhamnus heterophylla*, *Fraxinus chinensis*, and *Cinnamomum bodinieri*. Based on actual community composition, the top eight species by important value were designated as dominant species.

Total community aboveground biomass in Tianlong Mountain secondary forest was 106.94 $t \cdot hm^{-2}$, with dominant species accounting for 91.77% of community biomass (Table 2). Deciduous plants contributed 41.42 $t \cdot hm^{-2}$, while evergreen plants contributed 56.72 $t \cdot hm^{-2}$. *Lithocarpus confinis* alone accounted for 34.23% of community aboveground biomass with an important value of 24.6%, serving as the constructive species. *Platycarya strobilacea* had the highest proportion at 34.37% of aboveground biomass.

Table 2 Characteristics of dominant species in Tianlong Mountain

Species	Life Form	Living Habit	Importance Value	Biomass ($t \cdot hm^{-2}$)	Biomass Proportion
Lithocarpus confinis	Evergreen	Mesophyte	24.6%	36.60	34.23%
Platycarya strobilacea	Deciduous	Heliophyte	15.8%	36.75	34.37%
Itea yunnanensis	Evergreen	Heliophyte	9.2%	8.42	7.88%
Machilus cavaleriei	Evergreen	Mesophyte	7.8%	7.85	7.34%
Pittosporum brevicalyx	Evergreen	Shade-tolerant	6.5%	5.21	4.87%
Carpinus pubescens	Deciduous	Heliophyte	5.9%	4.68	4.38%
Lindera communis	Evergreen	Shade-tolerant	4.3%	2.13	1.99%

Species	Life Form	Living Habit	Importance Value	Biomass (t · hm^{-2})	Biomass Proportion
Zanthoxylum dimorphophyllum	Deciduous	Heliophyte	3.8%	1.30	1.22%

2.2 Spatial Distribution Characteristics of Aboveground Biomass and Environmental Factors Mean soil thickness in the Tianlong Mountain plot was 15.59 cm (Table 3), with a maximum of 35.40 cm and minimum of 5.80 cm, showing a coefficient of variation of 68.03%. According to slope classification for karst regions, the plot is steep slope (Li, 2004) with relatively low coefficient of variation (34.88%). Mean rock exposure rate was 44.69%, with spatial distribution showing obvious upper-lower slope gradient differences (Figure 1). Areas with high rock exposure were primarily distributed on upper slopes. Slope showed discontinuous spatial distribution, while community aboveground biomass distribution tended to align with soil thickness.

Table 3 Data characteristics of environmental factors in Tianlong Mountain

Environmental Factor	Minimum	Maximum	Mean	Standard Deviation	Coefficient of Variation (%)
Soil thickness (cm)	5.80	35.40	15.59	10.60	68.03
Slope (°)	10.00	45.00	26.88	9.37	34.88
Rock exposure rate (%)	10.00	85.00	44.69	18.61	41.64

Figure 1 [Figure 1: see original paper] Spatial distribution of biomass and environmental factors in Tianlong Mountain. (A) Spatial distribution of rock exposure rate; (B) Spatial distribution of slope; (C) Spatial distribution of soil thickness; (D) Spatial distribution of community aboveground biomass.

2.3 Relationships Between Aboveground Biomass and Environmental Factors Correlation analysis revealed that community aboveground biomass was significantly positively correlated with soil thickness ($P<0.01$). Rock exposure rate was significantly positively correlated with slope ($P<0.01$), while soil thickness was significantly negatively correlated with slope ($P<0.01$) and rock exposure rate ($P<0.05$) (Figure 2).

Figure 2 [Figure 2: see original paper] Correlation between environmental factors and community aboveground biomass. BIO: Community aboveground biomass; TOS: Soil thickness; RE: Rock exposure rate; SLO: Slope. * Significantly correlated at the 0.05 level; ** Significantly correlated at the 0.01 level.

As shown in Table 4, soil thickness had the highest explanatory power for community aboveground biomass (R^2=0.505), while rock exposure rate and slope had lower effects. For different life forms, rock exposure rate showed the highest explanatory power for both evergreen and deciduous plants (R^2=0.386 and R^2=0.412, respectively). Soil thickness and slope had greater effects on evergreen than deciduous plants, while rock exposure rate had slightly less effect on evergreens than deciduous species.

Table 4 Explanatory power of environmental factors on plant aboveground biomass

	Soil Thickness	Rock Exposure Rate	Slope
Community	0.505	0.089	0.067
Evergreen	0.203	0.386	0.158
Deciduous	0.112	0.412	0.089

RDA ordination showed different correlations among the three environmental factors and eight dominant species (Figure 3). *Lithocarpus confinis*, *Zanthoxylum dimorphophyllum*, *Carpinus pubescens*, and *Pittosporum brevicalyx* were positively correlated with soil thickness. *Platycarya strobilacea* was positively correlated with rock exposure rate, while *Zanthoxylum dimorphophyllum* was positively correlated with slope.

Figure 3 [Figure 3: see original paper] RDA ordination diagram of aboveground biomass of dominant species and environmental factors. SPE1: *Lithocarpus confinis*; SPE2: *Platycarya strobilacea*; SPE3: *Itea yunnanensis*; SPE4: *Machilus cavaleriei*; SPE5: *Pittosporum brevicalyx*; SPE6: *Carpinus pubescens*; SPE7: *Lindera communis*; SPE8: *Zanthoxylum dimorphophyllum*; TOS: Soil thickness; RE: Rock exposure rate; SLO: Slope.

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3. Discussion

3.1 Dominant Species Determine Community Aboveground Biomass

Total aboveground biomass in Tianlong Mountain secondary forest was 106.94 $t \cdot hm^{-2}$, significantly lower than the *Lithocarpus xylocarpus* forest in Ailao Mountain, Yunnan (348.7 $t \cdot hm^{-2}$) in the same climate zone (Qiu et al., 1984) and the Maolan primary karst forest (168.02 $t \cdot hm^{-2}$) (Zhu et al., 1991). Although the Tianlong Mountain karst secondary forest was selectively logged in the 1950s-1960s and has undergone long-term recovery, its aboveground biomass remains low, indicating slow vegetation restoration under these special environmental conditions.

Karst soils are poor with harsh site conditions. Dominant species filtered by environmental pressures are well-adapted to karst environmental stresses and can maintain advantages in competition, growing extensively and accumulating nutrients under similar conditions (Chen, 2015; Wang et al., 2020). Dominant species accounted for 91.77% of community aboveground biomass, playing a decisive role consistent with the selection effect hypothesis (Slik et al., 2010). Evergreen plants in this study had greater aboveground biomass than deciduous plants, possibly because evergreens are better suited to the humid karst environment of southern China. With low sunshine rates in central Guizhou (only 26.3%) (Ni et al., 2017), light-demanding deciduous plants are at a competitive disadvantage (Givnish, 2001; Che et al., 2020).

Lithocarpus confinis and *Platycarya strobilacea* accounted for 34.23% and 34.37% of community aboveground biomass, respectively, serving as main tree species in the karst secondary forest community with strong drought and poor-soil tolerance, numerous individuals, wide distribution, and broad ecological amplitude (Li, 2021). *Lithocarpus confinis* acts as both a constructive species and primary producer in Tianlong Mountain. As a mesophytic plant, it has considerable growth potential in future community succession. Although *Platycarya strobilacea* had lower important value than *Lithocarpus confinis*, its aboveground biomass was slightly higher, possibly because the biomass calculation model used in this study was based on multiple regression relationships between plant dry weight and DBH, height, and crown width (Liu et al., 2009). *Platycarya strobilacea* has relatively high individual dry weight, meaning that at the same individual size, its aboveground biomass exceeds that of *Lithocarpus confinis*.

3.2 Community Aboveground Biomass Distribution Aligns with Soil Thickness Spatial distribution analysis revealed obvious upper-lower slope gradient differences in rock exposure rate, likely because upper slopes experience more rainwater erosion, exposing substantial bedrock at the plot's upper section. Slope and soil thickness showed discontinuous spatial distributions, with soil thickness closely related to microtopography, reflecting the high heterogeneity of karst habitats. Research shows that environmental factors affect plant spatial distribution patterns (Sheng et al., 2018). Soil thickness is an important factor influencing community species diversity and plant biomass (Liu, 2020). In this study, community aboveground biomass showed discontinuous distribution, with high biomass areas corresponding to thick soils, and their spatial distributions tended to be consistent. This reflects the high dependence of plant aboveground biomass on soil thickness, consistent with most related studies (Li et al., 2012; Wang et al., 2007). This relationship likely occurs because deeper soils provide higher soil quality and more abundant soil microorganisms (Zhou et al., 2018), while also offering more space for root growth and enhancing soil water and mineral nutrient retention capacity (Belcher et al., 1995; Li et al., 2012), thereby affecting plant growth and development and resulting in higher biomass.

3.3 Different Ecological Groups and Species Respond Differently to Environment General linear models and Pearson correlation tests showed that soil thickness had the highest explanatory power for community aboveground biomass, consistent with previous research (Liang, 2016; Liu, 2020), indicating that soil thickness is the main driver of community aboveground biomass. Slope and rock exposure rate had relatively low explanatory power for community aboveground biomass, possibly related to the ecological adaptability of karst plants. Species with climbing characteristics (e.g., *Dalbergia hancei*) can still grow in high-slope environments (Wei et al., 2014). Additionally, plants have developed unique nutrient absorption strategies to adapt to karst environments (Huang et al., 2011). For example, *Platycarya strobilacea* has well-developed root systems that can grow in rock crevices to absorb nutrients and moisture (Xu et al., 1997). The negative correlation between rock exposure rate, slope, and soil thickness is a common phenomenon, as soil erosion resistance generally decreases with increasing slope, and bedrock exposure can reduce soil cohesion, causing soil loss (Heimsath et al., 1997; Zhang et al., 2007). Therefore, slope and rock exposure rate may indirectly affect community aboveground biomass by influencing soil thickness.

The same life form represents similar environmental requirements and adaptive capacities (Gao & Chen, 1998; Yang et al., 2017). In this study, rock exposure rate had the highest explanatory power for aboveground biomass, indicating that habitat differentiation dominated by rock exposure rate is an important factor causing spatial distribution differences and coexistence of evergreen and deciduous plants in Tianlong Mountain secondary forest. Soil thickness had greater explanatory power for evergreen than deciduous plants, possibly due to differences in ecological habits between life forms. Evergreen plants tend to select for soil fertility and moisture, while deciduous plants reduce consumption through regular leaf shedding, enabling survival in soil-resource-scarce environments. Deciduous plants also have higher light requirements (Che et al., 2020), and areas with high rock exposure have relatively sparse forests with larger canopy gaps, allowing deciduous plants to grow in high rock exposure areas to obtain more light resources. Xie et al. (2012) found that topographic factors affect evergreen plants more than deciduous plants. In this study, slope had greater explanatory power for evergreen than deciduous plants, indicating that evergreen species are more limited by slope due to their life habits. Although slope showed discontinuous distribution in the plot, its variation was limited, restricting its capacity to intensify resource heterogeneity and resulting in low explanatory power for aboveground biomass of different life forms.

For different species, correlations between plant aboveground biomass and environmental factors were more complex. Karst plants have unique environmental preferences (Hu et al., 2017), enabling different tree species to occupy specific resources and spaces for species coexistence (Nakashizuka, 2001). Aboveground biomass of *Lithocarpus confinis*, *Carpinus pubescens*, *Pittosporum brevicalyx*, and *Zanthoxylum dimorphophyllum* was positively correlated with soil thickness, indicating these species tend to select areas with relatively rich soil resources to absorb more soil nutrients for growth. Different correlations with environmental factors may result from differences in plant habits and resource utilization capacities. For example, *Zanthoxylum dimorphophyllum* has relatively low dominance and weaker resource utilization capacity than other dominant species, and its shade-preferring habit tends toward environments with smaller canopy gaps. Areas with thicker soils have relatively lush vegetation, resulting in stronger correlation between *Zanthoxylum dimorphophyllum* and soil thickness. *Itea yunnanensis* does not have strict soil resource requirements, and to maintain its dominant position in the community, its habitat selection diverges from other dominant species. *Lindera communis* has relatively small individuals and shallow root systems; environments with high rock exposure and slope restrict horizontal root growth, and its strong water utilization capacity (Deng et al., 2015) reduces its demand for soil thickness, resulting in no correlation between its aboveground biomass and soil thickness.

Platycarya strobilacea aboveground biomass was positively correlated with rock exposure rate, possibly because areas with high rock exposure lack water and soil, have relatively sparse vegetation, and larger canopy gaps. With strong karst environment adaptation capacity (Xu et al., 1997), *Platycarya strobilacea* tends to grow extensively in high rock exposure areas to obtain more light resources. Yang et al. (2022) found that *Platycarya strobilacea* has a mutually exclusive ecological relationship with *Lithocarpus confinis* and *Machilus cavaleriei*. In this study, rock exposure rate was negatively correlated with aboveground biomass of *Lithocarpus confinis* and *Machilus cavaleriei*, indicating that plant environmental preferences and interspecific relationships jointly influence how plant aboveground biomass responds to environmental conditions.

Although *Carpinus pubescens* and *Platycarya strobilacea* are both heliophilous deciduous species, their relationships with environmental factors differ significantly. *Carpinus pubescens* is a pioneer species in community succession that occupies upper forest layers in early development stages in areas with high soil thickness. Due to its competitive strategy, this species only regrows to supplement the upper layer after upper forest destruction (Liang, 1992), resulting in small horizontal spatial variation and different environmental response patterns from *Platycarya strobilacea*. This demonstrates that plant life history strategies also affect aboveground biomass-environment relationships.

In summary, as the research focus shifts from community to species level, plant aboveground biomass responses to environmental factors become increasingly complex due to biological factors such as environmental adaptability of different life forms, species life history, interspecific relationships, and habitat preferences. However, this study has not specifically analyzed the effect intensity of biological factors on plant aboveground biomass. Future research should further discuss the combined influence mechanisms of biological and abiotic factors on karst ecological functions.

4. Conclusion

This study examined relationships between aboveground biomass and environmental factors in a typical karst secondary forest, reaching the following conclusions:

1. Community aboveground biomass in Tianlong Mountain secondary forest was 106.94 $t \cdot hm^{-2}$, indicating slow vegetation restoration that is significantly lower than non-karst forests and regional karst primary forests in the same climate zone decades ago. Soil thickness is the main factor influencing community aboveground biomass.
2. Differentiation in rock exposure rate is an important factor causing spatial distribution differences and coexistence of evergreen and deciduous plants. Evergreen species are more limited by soil thickness and slope than deciduous plants.
3. For different species, relationships between species aboveground biomass and environmental factors are more complex than at community or life form levels due to biological interference such as interspecific relationships, plant life history strategies, and species habitat preferences.

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