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Both Biotic and Abiotic Factors Shape the Spatial Distribution of Aboveground Biomass in a Tropical Karst Seasonal Rainforest in South China

Fang Lu [1,2], Bin Wang [1,2], Jianxing Li [1,2], Dongxing Li [1,2], Shengyuan Liu [1,3], Yili Guo [1,2], Fuzhao Huang [1,2], Wusheng Xiang [1,2,*] and Xiankun Li [1,2]

1 Nonggang Karst Ecosystem Observation and Research Station of Guangxi, Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, Guilin 541006, China; lufang0814@gxib.cn (F.L.); wangbin@gxib.cn (B.W.); jxlee140820@163.com (J.L.); ldx@gxib.cn (D.L.); nonggang621@163.net (S.L.); yiliguo810414@163.com (Y.G.); fuzhaoh@gxib.cn (F.H.); xiankunli@163.com (X.L.)

2 Guangxi Key Laboratory of Plant Conservation and Restoration Ecology in Karst Terrain, Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, Guilin 541006, China

3 Administration of Nonggang National Nature Reserve of Chongzuo Guangxi, Chongzuo 532499, China

* Correspondence: xws@gxib.cn

Abstract: Forest biomass accumulation is fundamental to ecosystem stability, material cycling, and energy flow, and pit lays a crucial role in the carbon cycle. Understanding the factors influencing aboveground biomass (AGB) is essential for exploring ecosystem functioning mechanisms, restoring degraded forests, and estimating carbon balance in forest communities. Tropical karst seasonal rainforests are species-rich and heterogeneous, yet the impact mechanisms of biotic and abiotic factors on AGB remain incompletely understood. Based on the survey data of a 15 ha monitoring plot in a karst seasonal rainforest in Southern China, this study explores the distribution characteristics of AGB and its intrinsic correlation with different influencing factors. The results show that the average AGB of the plot is 125.7 Mg/ha, with notable variations among habitats, peaking in hillside habitats. Trees with medium and large diameters at breast height (DBH $\geq$ 10 cm) account for 83.94% of the aboveground biomass (AGB) and are its primary contributors; dominant tree species exhibit higher AGB values. Both biotic and abiotic elements substantially influence AGB, with biotic factors exhibiting the largest influence. Among abiotic factors, topographic factors have a strong direct or indirect influence on AGB, while soil physicochemical properties have the smallest indirect impact. This research provides a comprehensive understanding of AGB distribution and its influencing factors in tropical karst forests (KFs), contributing to the management of carbon sinks in these ecosystems.

Keywords: karst; seasonal rainforest; aboveground biomass; biotic factors; abiotic factors

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1. Introduction

Biomass plays a crucial role in forest ecosystems and serves as a vital measure for assessing forest productivity. It has substantial consequences for the stability and sustainable growth of the entire ecosystem [1]. AGB in tropical forests is essential for storing carbon and nutrients, and it significantly contributes to the global carbon cycle [2]. Therefore, it is imperative to attain a comprehensive understanding of the storage patterns of forest biomass to fully comprehend and assess the ecosystem services provided by forests and their capacity to adjust to climate variability [3]. The variation in AGB, apart from being influenced by various biotic and abiotic factors [4–6], is also influenced by the biological characteristics of trees themselves, which affect individual biomass and its allocation patterns [7].

AGB in forests may be influenced by the intricate interplay of abiotic and biotic elements. Topography can affect soil nutrients and tree composition, thus impacting AGB.

Prior research has indicated that topographic parameters, such as elevation and slope, play a significant role in shaping the distribution of AGB in forests [4,5], with higher biomass observed in sloping habitats [4] and a positive correlation with elevation [5]. However, some researchers have found that lower-elevation areas with more soil and water are better suited for forest growth, resulting in a significant negative correlation between elevation and biomass [8]. The distribution of AGB does not show significant differences across different slopes [9], and areas with flat terrain tend to have higher AGB values [10], indicating substantial variations in research results across different study regions. Additionally, soil also directly influences AGB [11], especially the nitrogen content, organic carbon content, and pH value of the soil, significantly impacting biomass distribution [12].

Biotic factors are important in influencing AGB. The distribution of AGB in forests can be influenced by both the community organization [6,13] as well as species composition [14]. Large-diameter trees have a considerable impact on community biomass [7], and the more complex the community structure, the stronger the impact on biomass [6,13]. Furthermore, AGB in KFs is substantially determined by abundance [5,15]. Species richness may show a positive or negative correlation with AGB [16,17]. Some researchers have also found that interspecific competition significantly affects plant size [18], and plant individuals can improve the surrounding environmental conditions through interactions, enabling neighboring species to survive in previously inhospitable environments. This enhances species diversity in the community [19], which may further affect the accumulation of AGB. Overall, biotic and abiotic factors may exhibit different patterns and mechanisms of influence in different ecosystems, study areas, and climatic conditions. Additionally, the relationship between ecological factors and AGB may be altered as a result of the intensification of global climate change [20]. Thus, further research is still needed to deepen our understanding of the interactions between these factors and their specific manifestations in different ecosystems. However, a comprehensive and in-depth analysis of the combined effects of biotic and abiotic factors and their interactions on AGB is still lacking.

Karst landscapes cover approximately 15% of the world's land area [21], particularly in China, where they account for about one-third of the country's land area [22]. Consequently, expansive regions of forests in karst terrains have a highly significant impact on the global process of carbon cycling and the storage of carbon. However, the steep terrain poses significant challenges in conducting surveys and sampling, leading to a relatively limited amount of research on biomass in KFs. Moreover, previous studies have mostly relied on allometric equations developed for non-karst habitats [23,24]. Karst vegetation is limited by its habitat and exhibits strong drought tolerance [25], and woody plants generally have higher wood density [26]. Therefore, using allometric equations developed for other regions may lead to significant estimation errors in AGB of KFs. Thus, the specific factors influencing AGB in KFs at a local scale are still unclear.

The karst rainforest in Southern China is considered to be the most exemplary tropical karst forest worldwide [27,28]. We created a model to estimate the amount of AGB in the tropical karst seasonal rainforest of South China using data collected from a 15-hectare plot. The model takes into account the wood density, height, and DBH of different tree species. We utilized structural equation modeling to undertake a thorough examination of the intricate relationships between biotic and abiotic factors that influence the spatial distribution of AGB. This work enhances our understanding of the mechanisms that drive AGB in tropical KFs at a small scale. This study seeks to investigate the following scientific inquiries: (1) How does the spatial distribution of AGB vary in the tropical karst seasonal rainforest? (2) How do biotic and abiotic factors influence the geographical distribution of AGB in the tropical karst seasonal rainforest? This project aims to enhance our comprehension of the mechanisms behind biomass generation in KFs and establish a basis for the creation of precise carbon cycling models for karst forests.

2. Materials and Methods

2.1. Study Area

This study was located in the Guangxi Nonggang National Nature Reserve (NNNR), at the border of Longzhou County and Ningming County in the Guangxi Zhuang Autonomous Region. The geographical coordinates are 106°42′28″–107°04′54″ E and 22°13′56″–22°33′09″ N, with a long, strip-shaped distribution from northwest to southeast. Due to its separation by residential areas, the entire reserve consists of three sections: Nonggang, Longhu, and Longrui. The main landforms in these areas are karst peak clusters and deep circular depressions (valleys), composed of multiple mountain peaks and embedded depression. The Longrui section in the east spans Longzhou and Ningming counties, with an area of 3645 ha. The Nonggang section in the central area has the largest area of 5425 ha, and the Longhu section in the west has the smallest area of 1008 ha. The Nonggang section is mostly characterized by peak–cluster–depression landforms, with a high density of peaks. The mountain peaks have an elevation of around 400–500 m, and the density of peaks can reach up to 80 per square kilometer. The depressions exhibit a bottom elevation ranging from approximately 150 to 200 m, with a peak recorded depth of 114 m and a maximum width spanning 450 m.

The vegetation in NNNR is a northern tropical native karst seasonal rainforest. The area is characterized by abundant heat and sufficient rainfall, with an average yearly temperature of approximately 22.52 °C and a yearly mean rainfall of 1329.59 mm. The majority of the rainfall occurs between the months of May and September. The average annual wind speed is 2.16 m/s. The climatic conditions are extremely favorable, nurturing a rich diversity of plant resources and varied vegetation types [29].

2.2. Establishment of Forest Plots and Tree Inventory

According to the CTFS-ForestGEO Forest Biodiversity Monitoring Protocol, a 15 ha (500 m × 300 m) forest plot was established in NNNR in 2011 (NG plot). The NG plot is part of the Chinese Forest Biodiversity Monitoring Network (CForBio) and The Forest Global Earth Observatory (ForestGEO) (https://forestgeo.si.edu/sites/asia/nonggang (accessed on 1 July 2024)). The plot consists of a relatively intact valley and a small peak, representing a series of complete "peak-clustered valley" habitat types, ranging from the valley bottom, hillsides, to the mountain top (Figure 1). The 15 ha plot was divided into 375 quadrats of 20 m × 20 m using a total station [30]. All trees with a DBH ≥ 1 cm within the plot were measured and recorded, including their species name, DBH, coordinates, and growth status.

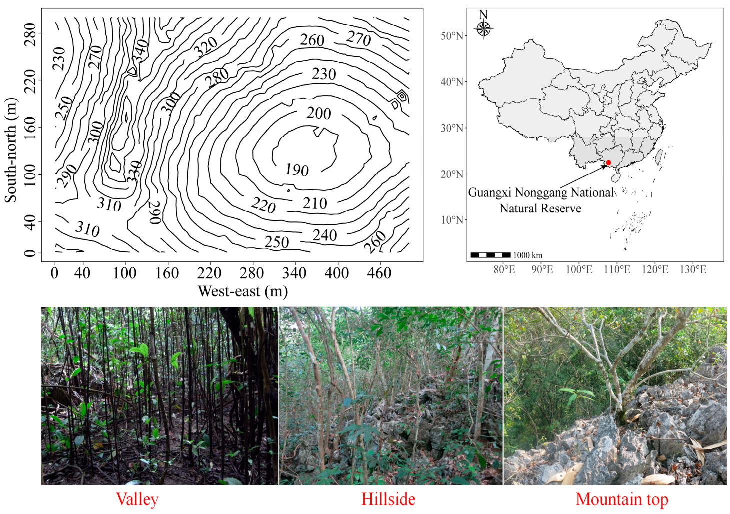

Figure 1. Elevation map, geographical location, and habitat outline of Nonggang 15 ha plot.

In 2021, we re-measured the DBH of all trees within the NG plot. In 2022, utilizing the developed functional trait manual [31], we determined the wood density of the species within the plot, as well as the height of 20,000 tree individuals.

2.3. Variables and Statistical Analysis Methods

2.3.1. Calculation of Aboveground Biomass

We estimated AGB using a model proposed by Chave [7]. The AGB of the forest was then determined by incorporating the DBH (cm), wood density ρ (g cm^{-3}), and height H (m) of the trees in the plot, utilizing the following formula:

$$ln(\mathrm{AGB}) = \alpha + \beta \ln(\rho \times DBH^2 \times H) + \varepsilon \quad (1)$$

The model coefficients, denoted as α and β, are obtained through least squares regression, whereas ε denotes the error term, which is presumed to adhere to a normal distribution with a mean of zero and a standard deviation of σ, implying that the random variables are identically and independently distributed according to N(0, σ^2). In the context of a model like Model (1), which possesses ρ parameters, the determination of σ is defined as follows:

$$\sigma = \sqrt{\frac{1}{N\ p}\sum_{i=1}^{N}\varepsilon_i^2} \quad (2)$$

where the sample size is denoted by N. In the field of statistics, the symbol σ represents the residual standard error, which is commonly referred to in the literature. The formula provided above serves as the maximum likelihood estimate for σ and is theoretically proven to be unbiased. When the parameter β is set to 1, an isometric relationship exists between the AGB and ρDBH^2H. To test the hypothesis of β equaling 1 within a likelihood-based framework, one can compare the Akaike Information Criterion (AIC) values between Model (1) and the nested model ln(AGB) = α + ln ($\rho \times DBH^2 \times H$) + ε. The AIC serves as a measure of the model's goodness-of-fit, penalizing complex models in line with the principle of parsimony [7].

2.3.2. The Classification of Diameter Classes and Habitat Types

Referring to Liu [5] and based on the characteristics of tree diameter distribution in the study area, the diameter classes were classified into the following categories: small-diameter class (1–5 cm, 5–10 cm); medium-diameter class (10–15 cm, 15–20 cm, 20–25 cm, 25–30 cm); and large-diameter class (30–35 cm, 35–40 cm, 40–45 cm, 45–50 cm, ≥50 cm).

Based on the relative elevation, slope, aspect, convexity, and species importance values of each quadrat in the 15 ha, the plots were divided into different habitat types (Table 1, Figure 1) [32]. The formula for calculating species importance values (IV) is as follows [33]:

$$IV = (Relative\ \ abundance + Relative\ \ frequency + Relative\ \ dominance)/3 \quad (3)$$

$$Relative\ abundance = \begin{array}{l}(Number\ of\ individuals\ of\ a\ species/\\ Total\ number\ of\ individuals\ in\ the\ community) \times 100\end{array} \quad (4)$$

$$Relative\ frequency = \begin{array}{l}(Number\ of\ quadrat\ swhere\ a\ species\ occurs/\\ Total\ number\ of\ quadrats\ sampled) \times 100\end{array} \quad (5)$$

$$Relative\ dominance = \begin{array}{l}(Total\ basal\ area\ of\ a\ species/\\ Total\ basal\ area\ of\ all\ species\ in\ the\ community) \times 100\end{array} \quad (6)$$

Table 1. Dominant tree species and their habitat conditions in different habitat types.

Habitat Type	Dominant Tree Species	Habitat Conditions
Valley	*Saraca dive*, *Sterculia monosperma*, *Ficus hispida*, *Albizia odoratissima*, *Erythrina stricta*	The humidity in both the soil and air is relatively high, with some areas experiencing seasonal waterlogging.
Hillside	*Vitex kwangsiensis*, *Excentrodendron tonkinense*, *Cephalomappa sinensis*, *Diplodiscus trichosperma*, *Cleistanthus sumatranus*, *Sterculia monosperma*	Most regions have moderately dry soil moisture and relatively steep slopes.
Mountain top	*Boniodendron minius*, *Memecylon scutellatum*, *Sinosideroxylon pedunculatum* var. *Pubifolium*, *Pistacia weinmanniifolia*	These areas are subjected to the longest duration of direct sunlight, maximum exposure of bare rocks, dry air temperatures, and severe soil moisture deficits.

2.3.3. Biotic Factors

In terms of biotic factors, we considered species diversity, structural diversity, and individual interactions. Based on plot survey data, we calculated species richness and abundance for 375 quadrats measuring 20 m × 20 m to reflect species diversity. Additionally, we used the Gini coefficient (GC), coefficient of variation (CV), and standard deviation (SD) as three common indices to measure the structural diversity of the community using DBH and H. The coefficient of variation of DBH is a commonly used indicator to describe the distribution frequency of the forest stand, where a higher value indicates a greater degree of size differentiation among trees. The Gini coefficient serves as a measure of the dispersion of individual tree DBH or H from perfect uniformity. When there is no difference between individuals, the value is 0, and when the difference is maximized, the value approaches 1 [34]. The calculation formulas are as follows [35]:

$$CV_{ba} = 100 \times \frac{SD_{ba}}{\overline{x}_{ba}}; CV_h = 100 \times \frac{SD_h}{\overline{x}_h} \tag{7}$$

$$GC_{ba} = \frac{\sum_{j=1}^{n} (2 \times j - n - 1) \times ba_j}{\sum_{j=1}^{n} (n-1) \times ba_j} \tag{8}$$

$$GC_h = \frac{\sum_{j=1}^{n} (2 \times j - n - 1) \times h_j}{\sum_{j=1}^{n} (n-1) \times h_j} \tag{9}$$

In the equation, ba_j represents the DBH of the j-th tree in the quadrat, ordered in ascending order by size, while h_j represents the H of the j-th tree in the quadrat (m). $\overline{x}_{ba}$ refers to the average basal area of all individuals in the quadrat, and $\overline{x}_h$ refers to the average H of all trees in the quadrat. j represents the rank of the tree, ranging from 1 to n.

The Hegyi individual competition index was employed to characterize the individuals' interactions [36]. Based on the formula proposed by Hegyi [36], we calculated the individual interaction index for 375 quadrats measuring 20 m × 20 m:

$$C_i = \sum_j \frac{{DBH_j}^2 / DBH_i}{R_{ij}} \tag{10}$$

Here, DBH_i denotes the DBH of the focal tree, DBH_j denotes the DBH of rival j, and R_{ij} denotes the distance between trees i and j. The total is taken over the "competitors" j of tree i. Hegyi's index defines rivals as any trees located within a certain distance R_{max} from the target tree.

2.3.4. Abiotic Factors

We utilized the techniques employed by Harms and Valencia [37,38] to acquire topographic characteristics, including elevation, convexity, slope, and aspect, for a total of 375 plots measuring 20 m × 20 m. The aspect was converted using a formula to transform compass measurements ranging from 0 to 360° into values between 0 and 1. The formula is as stated by Tian [39]:

$$TRASP = \{1 - cos[(\pi/180)(aspect - 30)]\}/2 \quad (11)$$

In the equation, *TRASP* denotes the aspect index, and aspect denotes the aspect direction angle. After the conversion, *TRASP* values range from 0 to 1, where 0 represents the north–northeast direction and 1 represents the south–southwest direction. The larger the *TRASP* value, the drier and hotter the habitat is.

The equation uses *TRASP* to represent the aspect index, whereas aspect represents the angle of the aspect direction. Following the conversion, *TRASP* values span from 0 to 1, with 0 denoting the north–northeast route and 1 denoting the south–southwest route. A greater *TRASP* number signifies a more arid and warmer ecosystem.

Surface soil samples (0–20 cm) were collected from the 375 quadrats (20 m × 20 m) in 2022. A total of nine soil physicochemical properties were analyzed, including soil water content (SWC), soil organic carbon content (SOC), total carbon (C), total nitrogen (N), total phosphorus (P), total potassium (K), calcium (Ca), magnesium (Mg), and pH. The dehydrating method was employed to ascertain the soil's water content (SWC) [40]. The vario MACRO cube elemental analyzer was employed to analyze the total nitrogen (N) and total carbon (C) content, while the potentiometric method was employed to measure the soil's pH. Using molybdenum–antimony anti-colorimetry, the total phosphorus (P) content was ascertained using the NaOH fusion method. Flame photometry was implemented to quantify the total potassium (K) content. Hydrochloric–nitric–perchloric acid digestion was employed to ascertain the calcium (Ca) and magnesium (Mg) contents. The potassium dichromate–sulfuric acid heating method was employed to ascertain the soil organic carbon content (SOC) [41].

2.3.5. Statistical Analysis

The AGB data underwent a log transformation in order to satisfy the requirement of a normal distribution. A one-way analysis of variance (ANOVA) was used to examine the variations in AGB among various environments. The "LSD Test" function in the "agricolae" package of R version 4.3.1 was used to perform multiple comparisons.

A variation partitioning analysis (VPA) was performed to quantitatively assess the impacts of biotic and abiotic variables on AGB. VPA can quantify the proportion of shared or individual explanatory power of multiple variables or variable sets in the response variable. In the case of multivariate analysis, redundancy analysis (RDA) can be combined to partition the variation in the response variable [42]. However, in specific analysis scenarios, collinearity among factors and the overlap of explanatory power pose significant challenges in assessing the importance of different factors. To address this issue, the R package ''rdacca.hp" introduces the concept of hierarchical partitioning (HP), which assigns separate effects to each explanatory variable (or set of explanatory variables) in all possible model subsets. This provides a new quantitative measure for assessing the relative importance of collinear explanatory variables in the analysis [43].

Our research incorporated species diversity, structural diversity, and individuals' interactions as biotic factors. Additionally, we considered topographic characteristics such as elevation, slope, aspect, and convexity, as well as soil physicochemical properties including SOC, SWC, C, N, P, K, pH, Ca, and Mg as abiotic factors. Principal component analysis (PCA) was employed to decrease the dimensionality of structural diversity indices and soil physicochemical characteristics in order to mitigate the impact of collinearity across variables. When analyzing structural diversity indices, the first principal component (PC1) explained 69.98% of the variance and included GC_h, CV_h, SD_{ba}, and GC_{ba} as the main characteristic vectors. These vectors contained most of the information and were representative; thus, PC1 was selected to represent structural diversity (Figure A1a). Similarly, in the PCA analysis of soil physicochemical properties, PC1 explained 43% of the variance and was predominantly distributed in the mountaintop habitat. PC2 explained 25% of the variance and was mainly distributed in the valley habitat. Together, they accounted for 68% of the variance and encompassed most of the information in the measured data. Thus, PC1 and PC2 were selected to represent the soil physicochemical properties (Figure A1b). The variation partitioning analysis was executed utilizing the "rdacca.hp" package in R version 4.3.1, while the PCA analysis was carried out using the "vegan" package.

In order to assess the direct and indirect impact of different ecological factors on AGB, we developed a conceptual model (Figure 2) that illustrates the influence of both biotic factors and abiotic factors on AGB. Biotic factors exhibit structural diversity, species diversity (in terms of abundance and richness), and interactions among individuals. The abiotic elements were manifested through the soil and topography attributes. The presence of various structures, the abundance and variety of species, and the interactions between neighboring plants have a direct impact on how light and water are distributed and used in a forest. These factors also play a role in the accumulation and distribution of AGB. Additionally, the high or low levels of structural and species diversity may influence the competitive interactions among trees, and species richness may also influence the distribution of species abundance to some extent. Soil physicochemical properties may directly affect the distribution of AGB and may also indirectly influence the distribution of AGB through their effects on biotic factors. Topographic factors may directly influence the distribution of AGB and may also indirectly affect the accumulation and distribution of AGB through their effects on soil physicochemical properties and biotic factors (Figure 2). This study utilized the "piecewiseSEM" package in the R 4.3.1 software to build a SEM for the purpose of estimating the direct and indirect impacts of various factors on the spatial variability of AGB. To account for the potential spatial autocorrelation among ecological components, the "gls" function was employed to handle the problem of spatial autocorrelation during the fitting of the SEM.

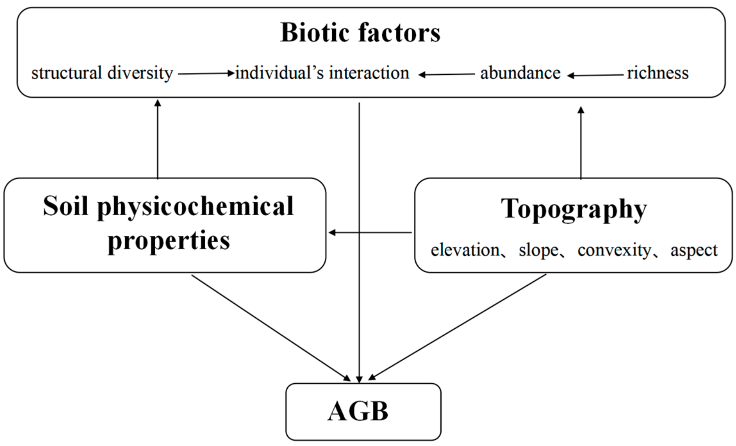

Figure 2. Initial SEM analysis of the impacts of biotic factors, soil physicochemical properties, and topographic factors on the amount of biomass above the ground.

3. Results

3.1. Distribution of Aboveground Biomass

The average AGB in the study area was 125.7 Mg/ha, and the distribution of AGB shows a certain degree of spatial heterogeneity (Figure 3a). Some quadrats (20 m × 20 m) in the valley reached as high as 21.04 Mg, while some quadrats on the hillsides reached 13.92 Mg. Additionally, there were some quadrats with AGB values below 1.5 Mg (Figure 3a).

The results of one-way analysis of variance and multiple comparisons indicate that the AGB on hillsides is significantly higher than that in valleys and peaks, while the difference in AGB between valleys and peaks is not significant (Figure 3b).

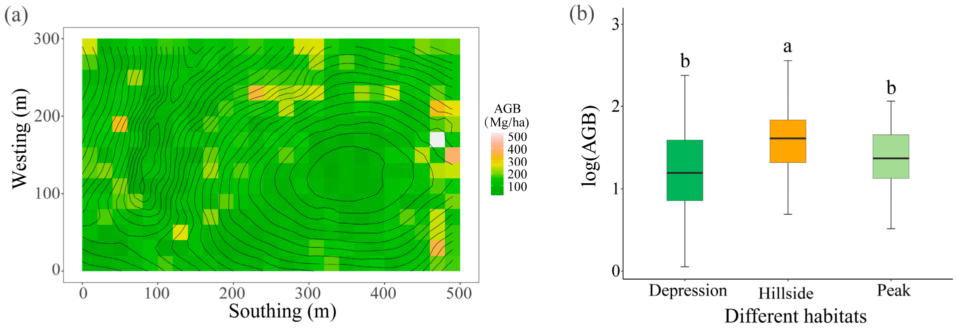

Figure 3. Distribution of aboveground biomass: map of distribution (**a**) and across different habitats (**b**). Lowercase letters denote statistically significant variations between distinct habitats ($p < 0.05$).

3.2. Distribution of Aboveground Biomass Across Different Diameter Classes and Species

The AGB of trees with DBH in the range of 1–5 cm and 40–45 cm is relatively low, accounting for only 3.63% and 3.59% of the total AGB, respectively. The AGB of trees in the diameter class of 10–15 cm reaches its peak at 302.93 Mg. Trees having a DBH $\geq$ 10 cm make up a significant share of 83.94%. In general, the data indicate a fast rise in AGB as the diameter class increases, followed by a slow decline (Figure 4a).

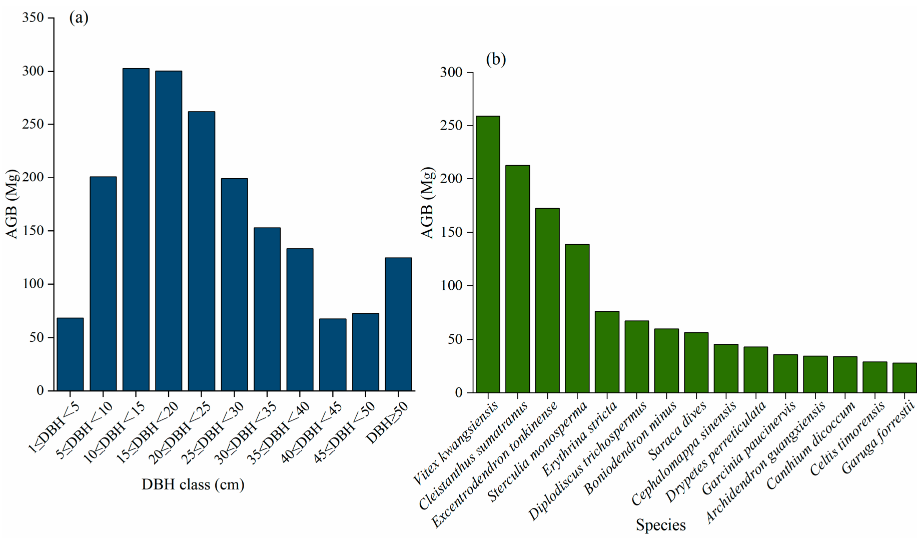

Figure 4. The distribution of aboveground biomass analyzed based on different DBH classes (**a**) and the top 15 species (**b**).

In the three habitats of the study area, the depression habitat supports 6738 individuals representing 174 species; the hillside habitat harbors 56,931 individuals of 678 species; and the peak habitat is home to 11,102 individuals belonging to 141 species.

In terms of overall levels, the AGB of the important species *Vitex kwangsiensis* (ranked second in importance value) reaches a maximum of 258.97 Mg. The species *Cleistanthus sumatranus*, ranked first in importance value, also has a high AGB of 212.77 Mg. Together, these two species accounts for 25.02% of the total AGB. The AGB of the top 10 dominant tree species accounts for 53.20% of the total AGB. The top 15 species in terms of AGB contribute a combined 56.90% of the total AGB (Figure 4b).

The linear regression analysis showed a statistically significant positive connection ($F = 4.521$, $p < 0.05$) between the important value of species and AGB. This suggests that species with higher importance levels generally have greater AGB values. These findings indicate that dominating species play a substantial role in the accumulation of AGB (Figure 5).

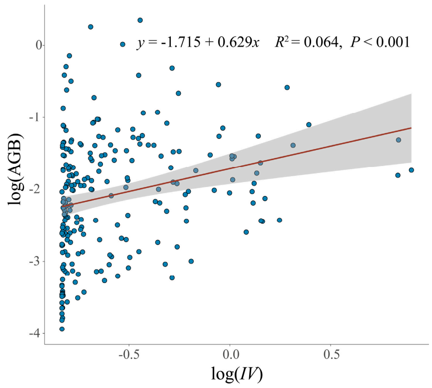

Figure 5. Correlation between importance value (IV) and aboveground biomass (AGB). The darkened regions indicate a 95% confidence interval for the models that have been fitted.

3.3. The Relative Importance of Individual Ecological Factors in Influencing Aboveground Biomass

The Nonggang plot exhibits complex topography, with marked variations in habitat-specific topographic characteristics and soil physicochemical properties. Elevation positively correlates with slope and convexity. C, N, and SOC peak at the summit, while P, K, Ca, Mg, and SWC maximize in the valley, and pH is highest on slopes (Table A1).

The variance decomposition of individual ecological factors revealed that among the 10 ecological factors, only convexity had no significant impact on AGB, while the remaining 9 factors, including structural diversity, individual interactions, and abundance, had a highly significant influence on AGB ($p < 0.01$). Among them, the biotic factors (structural diversity, richness, abundance, individual interactions) collectively explained 63.53% of the total variation in AGB, with structural diversity having the highest individual effect of 34.31%. The topographic factors (elevation, slope, convexity, aspect) accounted for 8.38% of the total variation in AGB, with convexity having no significant individual effect. The soil physicochemical properties (soil PC1, soil PC2) only explained 4.24% of the total variation in AGB (Figure 6).

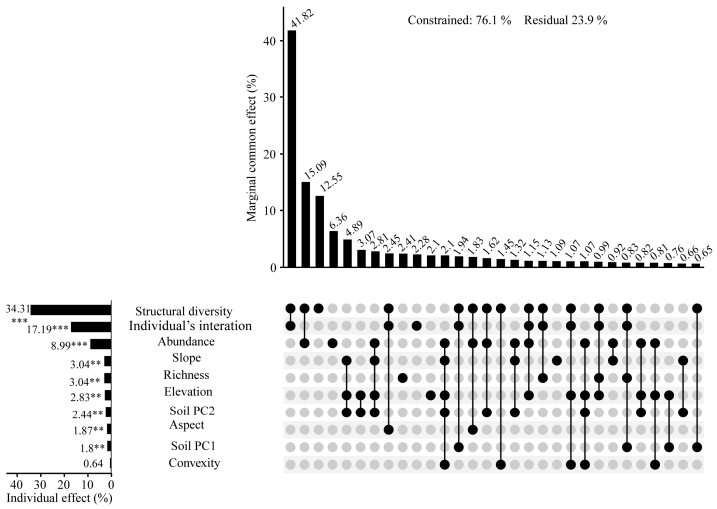

Figure 6. Matrix displaying the precise significance of each ecological element on aboveground biomass. Every row in the dot matrix figure on the right is an environmental component. The single black dot in each column represents the marginal impact of each environmental component. The shared effects between these corresponding environmental elements are indicated by the lines that connect several dots. The variation partitioning process yields the percentage of variance explained by each component, which is shown in the top column graphic. Each environmental element's individual impact, as determined via hierarchical partitioning, is displayed in the column diagram on the left. Each factor's value is determined by adding its average shared common effect with other factors to its marginal effect. The notation used for statistical significance is as follows: **, $p < 0.01$; ***, $p < 0.001$.

3.4. Direct and Indirect Effects of Biotic and Abiotic Factors on AGB

After excluding the aspect factor and insignificant paths, the final fitted model met the criteria (F = 29.068, p > 0.05). AGB was impacted directly and indirectly by geographic and biotic variables. Regarding biotic factors, structural diversity, individual interactions, and abundance had a strong and favorable impact on AGB. Richness had a highly significant direct negative effect on AGB, but it indirectly influenced AGB through abundance, resulting in a positive effect. Structural diversity had an indirect effect on AGB through individual interactions. As for topographic factors, elevation and slope had direct and indirect effects on AGB, while convexity had an indirect effect. Among them, elevation had a significant and substantial beneficial impact on AGB (the standardized path coefficient was 0.364). In addition, the AGB was influenced by both topography and soil physicochemical properties, which had indirect impacts mediated by biotic variables (Figure 7a). The results indicated that the relative contributions of different ecological factors to AGB were as follows: biotic factors (85.52%) > topography (8.73%) > soil physicochemical properties (5.75%) (Figure 7b).

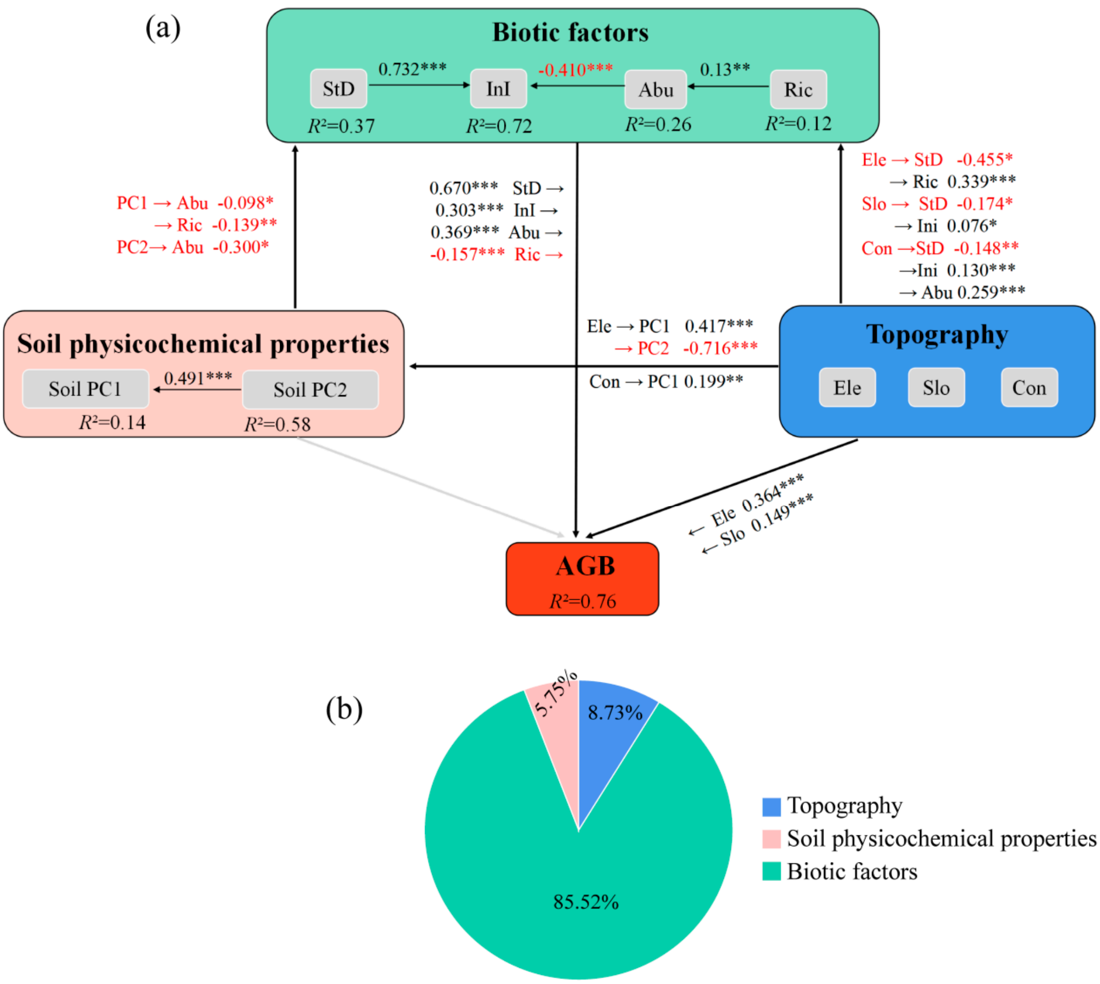

Figure 7. SEM analysis examining the impact of biotic variables, soil physicochemical parameters, and topographic factors on aboveground biomass (**a**), as well as the respective contributions of these factors on aboveground biomass (**b**). The significant effects are represented by black solid arrows (p < 0.05), whereas the non-significant effects are represented by gray solid arrows. The values adjacent to the arrows indicate the standardized coefficients. Abbreviations: StD, structural diversity; InI, individual interactions; Abu, abundance; Ric, richness; Ele, elevation; Slo, slope; Con, convexity. The notation used for statistical significance is as follows: *, p < 0.05; **, p < 0.01; ***, p < 0.001.

4. Discussion

4.1. Aboveground Biomass of Tropical Karst Forests in China

In this study, the AGB of the karst seasonal rainforest was found to be 125.7 Mg/ha. This value is significantly higher than the average AGB of forests in Guangxi, China (73.3 Mg/ha) [44] and the average AGB of a 25-ha plot in the Guangxi Mulun National Nature Reserve in a similar latitude zone (73.92 Mg/ha) [5]. These findings highlight the previously underestimated ecological value of the karst seasonal rainforest in terms of carbon storage.

Taking a broader perspective on a global scale, we find that the average AGB of the karst seasonal rainforest is lower than that of the forest in the Kimbi-Fungom National Park in Northwest Cameroon (149.2 Mg/ha) [45] and the average AGB of subtropical forests in South America (246.5 Mg/ha) [24]. Additionally, two surveys of lowland tropical rainforests in French Guiana showed a much higher AGB range of 356 to 398 Mg/ha [45], further highlighting the variation in AGB among different study areas.

Moreover, certain researchers have observed that the AGB in karst regions is considerably less than in regions without karst formations [44], and the average AGB of the tropical karst seasonal rainforest in this study area is indeed significantly lower than that of non-karst lowland tropical rainforests in French Guiana. The low biomass vegetation, harsh habitat conditions, shallow soil layers, and limited water availability in karst greatly restrict plant growth and reduce assimilation efficiency, leading to low biomass accumulation. However, the AGB in karst regions is significantly higher than the average biomass of forests in the same region of south China.

These findings highlight that tropical karst forests can also store relatively high aboveground biomass, contrary to the previous belief that karst forests have lower aboveground biomass. This has significant implications for future assessments of forest carbon stocks, as the enormous variability in aboveground biomass across different forest types needs to be fully considered to obtain relatively accurate assessment results.

4.2. Effects of DBH Classes and Dominant Tree Species on Aboveground Biomass

Our study reveals significant disparities in AGB across DBH classes and species, aligning with prior research indicating that enormous trees accrue AGB at much faster rates than small ones [7,46]. Notably, we emphasize that medium-sized trees (10 cm $\leq$ DBH < 30 cm) constitute 56.23% of the total AGB, while trees with DBH $\geq$ 10 cm account for 83.94%, highlighting the pivotal role of mature trees in AGB accumulation. This dominance reflects the mid-to-late successional stages of the study area's forests, characterized by harsh conditions, slow growth, and low canopy density [47], potentially leading to higher AGB among medium-sized trees. The high proportion of these trees suggests significant productivity potential in the karst seasonal rainforest.

Furthermore, species composition significantly impacts AGB distribution, with dominant tree species exhibiting higher AGB values. Species like *Saraca dives*, *Erythrina stricta*, *Excentrodendron tonkinense*, and *Diplodiscus trichosperma*, despite not being abundant, contribute to elevated AGB due to their tall stature and efficient light utilization. Dominant tree species with high abundances, such as *Vitex kwangsiensis*, also exhibit higher AGB values due to widespread occurrence and vigorous growth. This is consistent with the "biomass ratio hypothesis" proposed by Grime [48], which highlights that the functional features of dominant tree species are the main drivers of ecosystem function.

In summary, our main discoveries demonstrate the significance of trees with large to medium diameters and dominating species in the accumulation of biomass and the functioning of ecosystems. These findings emphasize the need of taking into account the dimensions and types of trees when evaluating and overseeing forest ecosystems. Our findings have both theoretical and practical implications, enhancing understanding of biomass dynamics and informing conservation strategies in karst regions.

4.3. Influence of Biotic Factors on the Spatial Distribution of Aboveground Biomass

The SEM model results revealed that biological factors account for 85.52% of the relative contribution to AGB, highlighting their pivotal role in driving the spatial distribution of AGB (Figure 7b). Structural diversity emerged as the primary biological factor influencing the spatial distribution of forest biomass, demonstrating a robust and positive direct effect, as evidenced by a significant standardized path coefficient of 0.670. This underscores the importance of complex structural diversity in favoring biomass accumulation. Previous studies have demonstrated that complex structures enhance tree capture and make use of light, water, and soil nutrients, hence facilitating the buildup of biomass in forest ecosystems [6,13]. However, complex community structures may also intensify competition among neighboring trees for key resources, driving tree optimization and community succession [6].

Contrary to some previous findings indicating a favorable relationship between richness and AGB [17], our study discovered a significant direct negative effect of richness on AGB (standardized path coefficient: −0.157). This unexpected result may be attributed to habitat fragmentation, where increased fragmentation leads to decreased richness and subsequently lower AGB values. Our study area, a karst seasonal rainforest in the middle to late stages of succession, represents a mature forest with well-preserved species. Here, the negative correlation between richness and AGB could be influenced by canopy gaps, which reduce AGB when large trees fall [49] but promote species diversity by increasing environmental heterogeneity [50]. This could ultimately result in an adverse association between richness and AGB across the forest [16].

Notably, species abundance positively influenced AGB but negatively influenced individual interactions, which in turn positively influenced AGB. This aligns with previous studies indicating that species abundance positively affects AGB [15], potentially due to niche differentiation [51] and differences in resource utilization efficiency [52]. Niche differentiation minimizes resource competition, enhancing ecosystem stability. In our study area, long-term natural selection and adaptation have likely led to a stable state of abundance. Higher abundance at different plot levels may refine resource partitioning and utilization, with different tree individuals occupying distinct ecological niches and exhibiting resource utilization strategies to avoid excessive competition. This could reduce competition among neighboring trees, improving overall resource utilization efficiency and promoting AGB accumulation. Maintaining relatively stable and high abundance in the forest environment may further enhance the forest community's stability in the face of environmental fluctuations, facilitating AGB accumulation through the cumulative effects of different species' environmental adaptability. Our results underscore the significance of incorporating structural diversity and species interactions into understanding and managing forest biomass dynamics.

4.4. Impact of Abiotic Factors on the Spatial Distribution of Aboveground Biomass

Our study has yielded valuable insights into the significant impact of topography on the spatial distribution of forest biomass. Our findings indicate that slope and elevation both exhibit direct positive influences on AGB, aligning with findings from prior investigations [4,5,10,53]. The highest AGB was observed in sloping habitats, indicating the importance of terrain complexity in promoting biomass accumulation. The influence of elevation on AGB can be due to water availability [54]. Higher elevations may limit photosynthesis, respiration, and nutrient use efficiency, resulting in decreased biomass [55,56]. In contrast, hillsides offer diverse microclimatic conditions, creating ecological niches for plant survival [28,57]. Superior soil layers and moisture on hillsides promote tree growth, potentially leading to the highest AGB values. These findings emphasize the role of terrain complexity and water availability in shaping biomass distribution, providing insights for forest management and conservation.

The indirect effects of topography on AGB distribution are mediated through biotic factors and soil physicochemical properties. Tree density, diameter diversity, and abundance are influenced by elevation, slope, and ruggedness, ultimately impacting AGB distribution [5,58]. Moreover, topography affects soil conditions such as nutrient availability, moisture content, and microorganism activity, which directly influence plant growth and indirectly affect AGB accumulation [53].

The significant impact of soil physicochemical parameters on the accumulation and distribution of AGB has been demonstrated [11,59], and our study confirms these findings. Soil PC1, representing C, N, and SOC content, was highest in the mountain top habitat (Figure A1b), indicating potentially greater nutrient availability. However, harsh environmental conditions in this habitat may limit nutrient uptake and directly impact plant growth, resulting in lower AGB values. Conversely, soil PC2, including P, K, and SWC, was highest in the valley bottom habitat (Figure A1b), suggesting favorable nutrient and water availability. Nevertheless, waterlogging and shading caused by topography may hinder nutrient absorption and utilization, leading to lower AGB values. These findings underscore the significance of soil physicochemical properties in shaping AGB distribution, highlighting the complex ecological processes involved.

5. Conclusions

The spatial distribution of AGB and its affecting factors in the Nonggang karst seasonal rainforest in South China were thoroughly explored in this study. Our study reveals a substantial and heterogeneous distribution of AGB within the tropical karst seasonal rainforest, with notably higher AGB in hillside habitats. Biotic factors, particularly structural diversity, exert a dominant influence on AGB, while abiotic factors such as altitude and slope contribute both directly and indirectly, highlighting the complex interplay between biotic and abiotic elements in determining AGB patterns. Studying the distribution of AGB and its influencing factors in karst seasonal rainforests is crucial for understanding and conserving the fragile ecosystems in karst regions and assessing their role in global carbon cycling.

The distribution of AGB and its influencing factors may not only be related to biotic factors, topography, and soil physicochemical properties but also to woody climbers, soil microorganisms, and other factors. Moreover, current research has not fully considered the effects of forest type and age on AGB. Further research should explore these features in greater detail to obtain a more holistic comprehension of carbon storage and carbon sequestration capacity in the karst seasonal rainforest environment.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

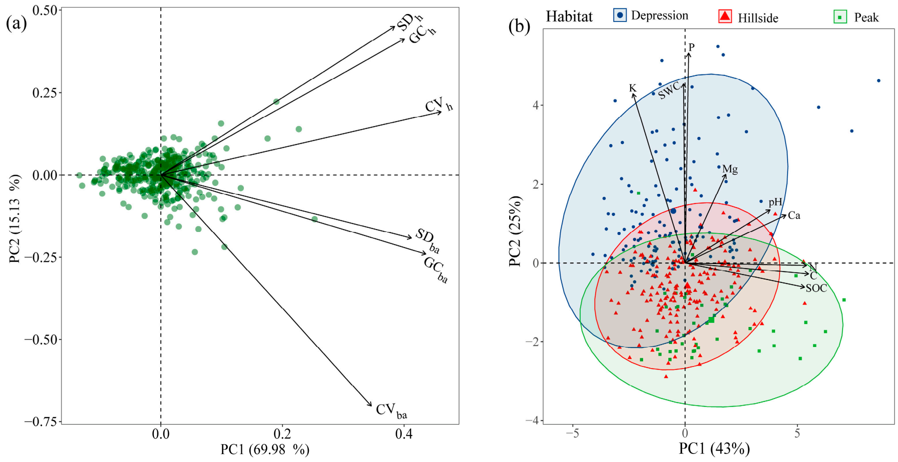

Figure A1. Principal Component Analysis (PCA) used to analyze the indices of structural diversity (**a**) and soil physicochemical property indices (**b**).

Table A1. Summary of topographic factors and physicochemical properties of soils in three different habitats.

Ecological Factors	Valley	Hillside	Mountain Top
Elevation (m)	198.80 ± 1.54	259.00 ± 1.93	335.83 ± 1.61
Slope (°)	22.34 ± 1.10	42.75 ± 0.43	48.67 ± 1.38
Aspect	0.59 ± 0.05	0.47 ± 0.02	0.53 ± 0.04
Convexity (°)	−2.12 ± 0.12	−1.08 ± 0.08	4.16 ± 0.64
Total carbon (C, g/kg)	57.39 ± 3.76	53.25 ± 0.63	64.20 ± 2.26
Total nitrogen (N, g/kg)	6.48 ± 0.37	6.19 ± 0.07	6.96 ± 0.23
Total phosphorus (P, g/kg)	2.46 ± 0.09	1.16 ± 0.02	0.78 ± 0.05
Total potassium (K, g/kg)	9.66 ± 0.15	7.74 ± 0.07	6.37 ± 0.14
Calcium (Ca, g/kg)	9.73 ± 1.43	8.17 ± 0.24	8.75 ± 0.56
Magnesium (Mg, g/kg)	8.02 ± 0.34	7.75 ± 0.09	6.88 ± 0.21
pH	7.10 ± 0.04	7.11 ± 0.02	7.07 ± 0.05
Soil organic carbon content (SOC, g/kg)	91.34 ± 5.81	87.13 ± 1.01	104.65 ± 3.47
Soil water content (SWC, g/g)	51.15 ± 1.73	34.19 ± 0.45	30.21 ± 0.67

The data ± se in the table represents mean ± standard error.

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