Article

The Variation in the Stoichiometric Characteristics of the Leaves and Roots of Karst Shrubs

Zhigang Zou ^{1,2}, Fuping Zeng ^{1,2}, Zhaoxia Zeng ^{1,2}, Hu Du ^{1,2} , Hui Tang ³ and Hao Zhang ^{1,2,*}

- ¹ Key Laboratory of Agro-Ecological Processes in Subtropical Region, Institute of Subtropical Agriculture, Chinese Academy of Sciences, Changsha 410125, China; zhigangzou0203@163.com (Z.Z.); fpzeng@isa.ac.cn (F.Z.); zengzhx@isa.ac.cn (Z.Z.); hudu@isa.ac.cn (H.D.)
 - ² Huanjiang Observation and Research Station for Karst Ecosystem, Chinese Academy of Sciences, Huanjiang 547100, China
 - ³ Guangxi Key Laboratory of Plant Conservation and Restoration Ecology in Karst Terrain, Guangxi Institute of Botany, Chinese Academy of Sciences, Guilin 541006, China; th@gxib.cn
- * Correspondence: zhanghao@isa.ac.cn

Abstract: Currently, vegetation restoration is being implemented in the ecologically fragile karst areas in southwest China; however, the stoichiometry of the dominant shrubs and their relationship with the environmental factors in the degraded habitats is still unclear. In this study, we investigated the stoichiometry of C, N, and P, their internal correlations, and influencing factors in 23 shrub species in the Huanjiang County in northwest Guangxi Province, China. We found that the mean contents of C, N and P in leaves were higher than those in roots. In addition, the N:P ratio in the leaves was significantly higher than that in the roots, but the opposite was observed for the C:N and C:P ratios. Except for Leaf C and Root C, significant positive or negative correlations were observed across the stoichiometry of the shrub leaves and roots. A factor analysis of variance demonstrated that the differences across species had higher explanatory power than the topography and soil nutrients in terms of the shrub leaf and root stoichiometry. Hence, our results can improve the understanding of the distribution patterns of these vital elements, as well as of the interactions and influencing factors in the different organs of the karst shrubs.

Keywords: ecological stoichiometry; factor analysis; shrub species; karst ecosystem

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1. Introduction

The elements that primarily makeup living organisms, C, N, and P, have long been researched by biologists. C, the basic skeletal element of plants, provides energy for plant metabolism, growth, development, and reproduction [1,2], and is used as an indicator for measuring the organic material reserves of an ecosystem [3]. The concentrations of N and P, elements that are required for plant life cycle activities, reflect functional traits in plants and play key roles in ecosystem dynamics [4,5]. Moreover, the stoichiometry of C, N, and P is related to organism growth and development, population growth, community biodiversity, structure, and dynamics, as well as ecosystem functions and processes [6–11].

The concentrations of N and P can limit plant growth and development in terrestrial ecosystems and are easily influenced by abiotic factors. N and P concentrations in the vegetative organs of plants are primarily determined by the climate and nutrients in the soil, and when these environmental constraints change, the plants adapt by adjusting the allocation of the restricted resources to maximize growth [4,5,8,12]. In addition, changes in light and CO₂ concentration can affect plant stoichiometry by changing the distribution of photosynthetic products, and thus, alter the production and decomposition processes of natural ecosystems, ultimately affecting the entire N and P cycles [13,14]. Plant N and P stoichiometry may also be influenced by a variety of environmental factors, such as temperature and rainfall, both on a global and regional scale [15]. Moreover, biological

factors can also affect plant N and P stoichiometry [16]. Previous research has shown that there are significant differences in the stoichiometric characteristics of plants at different growth stages, where leaf N concentration decreases as plant age increases [2]. In addition, there are significant differences in N and P stoichiometry across different organs within the same plant, but the N and P concentrations in the leaves, stems, roots, and reproductive organs are still related [17]. Due to the difficulty in measuring root biomass and identifying living roots, there are relatively few studies on the underground biomass and ecological characteristics of plant roots.

Additionally, significant differences in N and P stoichiometry have been observed across different species [18], while plants of the same species tend to share a set of key plant functional traits to achieve a similar adaptation approach to the changes in environmental conditions [19,20]. Many studies have examined the geographical variation in plant stoichiometry [21,22] and found that due to the influence of different factors, the stoichiometry of plant N and P varied. However, most of these studies have not determined the stoichiometry of the different functional types in a degraded environment. Therefore, examining the stoichiometry of dominant plants and their relationship with environmental factors would deepen the understanding of the plant nutrient cycling and adaptation strategies in degraded habitats.

The southwest karst area covers 540,000 km² and is one of China's four main ecologically and environmentally fragile areas [23,24]. The unique geological background and structure (such as high rock exposure rate and rich rock pores) have caused soil erosion and soil quality degradation in this region; additionally, the regional ecological environment quality has also deteriorated, leading to declines in ecological services [25,26]. Since the implementation of the Grain for Green Program in 1999, the human disturbance has been gradually reduced, and vegetation has been slowly restored in the karst areas in southwest China [27]. However, owing to severe soil and water loss, insufficient soil nutrients, and seasonal drought, shrubs are the main type of vegetation in the karst areas, and there is a risk of reverse succession [28]. In the case of the karst shrub community, once the C, N, and P relationships in the abiotic environment are out of balance, the element cycling pathway may change, affecting the competition between the species in the community and changing the community structure [23]. In individual shrubs, element imbalance may change the growth and metabolism processes, potentially leading to death. Moreover, because the roots of karst shrubs grow in gaps between the soil and rocks, it is still unclear whether their nutrient absorption is completely dependent on the soil nutrients [29].

Although the differences and the internal correlation between the concentrations of C, N, and P in karst forests have been studied, little attention has been paid to the stoichiometry of different organs of the karst shrubs and their influencing factors. Hence, in the present study, shrub communities in the karst areas of the northwest Guangxi Province were selected to study the stoichiometry of C, N, and P in the leaves, roots, and soil, and to identify the influencing factors.

2. Materials and Methods

2.1. Research Site

The research site was situated in the Huanjiang County (24.44°–25.33° N, 107.51°–108.43° E), northwest Guangxi Province, which is part of the karst region in southwest China (Figure 1). According to observation data from the Meteorological Bureau of Huanjiang County from 1986 to 2019, the average annual sunshine is 1451 h, the average annual temperature is 19.3 °C, the average annual effective accumulated temperature is 6260 °C (≥10 °C), the average annual frost-free period is 310 d, and the average annual precipitation is 1529 mm. The karst peak cluster depressions are concentrated in the southwest of the county, where the soil has developed from carbonate rocks and is mainly brown calcareous earths. The soil layer is shallow, and the slope is steep. There is a trend of desertification as the soil erosion is severe, and rock is exposed. The research area contained grasses, shrubs, and primary and secondary forests.

Figure 1. Map showing the field site (★) where we collected shrubs.

2.2. Field Survey

A total of 30 10×10 m quadrats were established in the middle and lower slopes with different slope directions, positions, levels, and altitudes. A high-precision Global Positioning System (E640, Mobile Mapper, Spectra Geospatial, Trimble Inc., Sunnyvale, CA, USA) was used to record the longitude, latitude, and altitude at the centre of the quadrat. We also recorded the slope direction, slope position, slope level, rock exposure rate, and soil layer thickness (Table A2). Each quadrat was subdivided into four small quadrats of 5×5 m that were used as the basic unit to investigate each individual with a diameter at a breast height (DBH) ≥ 1 cm, and the shrub species name, ground diameter (at 10 cm high above the ground), DBH, shrub height, crown width, and growth status were recorded.

In addition, sampling was conducted at five points across the soil surface (0–20 cm) according to the shrub distribution, and the samples were then fully mixed to form composite samples for testing. The samples were brought back to the laboratory and air dried before being analyzed to determine the soil nutrients as per previously described methods [30]. Soil organic carbon (SOC) was measured by the dichromate oxidation method. Total nitrogen (TN) was measured with dry combustion using a C-N analyser. Total phosphorus (TP) was determined by wet digestion with sodium hydroxide. Available nitrogen (AN) was assayed by the alkaline potassium permanganate distillation method, and available phosphorus (AP) by the Olsen method [31].

2.3. Measurement of Plant C, N, and P Concentrations

In July 2019, 115 plants belonging to 23 dominant shrub species were selected in the sample quadrats. The main species we focused on were the shrubs *Bauhinia brachycarpa*, *Alchornea trewioides*, *Vitex negundo*, *Rhus chinensis*, and *Pyracantha fortuneana* (Table A1). Five plants of medium size with similar growth rates and canopy width were surveyed in each species, and leaf and root samples were collected. To reduce the damage to the plants during sampling, four branches were fixed to each plant, and five or six leaves were collected from each branch, which were then mixed and used as a repeat sample. For each individual plant, the root was excavated completely, and the biomass was weighed. These

were then categorized into three groups according to their diameter: small roots (<5 mm), medium roots (5–10 mm), and large roots (>10 mm). In order to avoid differences in the nutrient content of roots at different developmental stages or life forms, roots of different sizes are mixed in proportion and used as a sample [32]. Next, the leaf and root samples collected in the field were oven-dried to reach a constant weight at 65 °C; then, they were crushed by a planetary mill (Pulverisette 5, Fritsch, Germany) into a 0.5-mm sieve to determine the C, N, and P concentration. C and N were determined using an organic element analyzer (Flash-EA1112, Thermo Scientific, West Palm Beach, FL, USA), while P was determined by the molybdenum-antimony anti-colourimetric method [25].

2.4. Statistical Analysis

All statistical analyses were performed using the Statistical Package for the Social Sciences (SPSS v17.0, Chicago, IL, USA) by implementing a two-way analysis of variance and Fisher's least significant difference tests for the stoichiometry data. The significant differences across different organs were considered at the 0.05 significance level. A Pearson correlation analysis was used to test the correlation between the plant stoichiometry traits, and after log-transforming the data, a principal component analysis (PCA) was used to analyze the main manifestation of the differences in the stoichiometry of the shrub leaves and roots. In addition, a generalized linear model was used to analyze the topography, soil nutrients, and species in terms of the variation in the stoichiometry in the leaves and roots [20].

3. Results

3.1. Summary of the Stoichiometry Data of the Shrub and the Soil

As a structural element, C showed little variation among shrub species (<8%), but N and P contents in leaves and roots differed significantly (>35%) (Table 1). Furthermore, the leaves and roots also showed different stoichiometry levels across different organs (Table 2). The N:P ratio in the leaves was significantly higher than that of the roots, but the opposite was observed in terms of C:N and C:P.

Table 1. The content and distribution characteristics of carbon, nitrogen and phosphorus in leaves and roots of shrubs.

Parameter (mg/g)	Leaf			Root		
	Mean $\pm$ S.D. ¹	Range	C.V. ²	Mean $\pm$ S.D.	Range	C.V.
Carbon	445.66 $\pm$ 33.54 a ³	386.99–514.38	7.53	436.03 $\pm$ 32.57 a	268.71–480.04	7.47
Nitrogen	20.94 $\pm$ 8.17 a	9.20–41.09	39.04	8.41 $\pm$ 4.73 b	2.59–22.28	56.28
Phosphorus	1.25 $\pm$ 0.65 a	0.44–3.54	51.60	0.67 $\pm$ 0.34 b	0.23–1.71	50.55

¹ S.D means standard deviation. ² C.V means coefficient of variation (%). ³ Different letters in the same row indicate significant differences ($p < 0.01$).

Table 2. The stoichiometric distribution characteristics of shrub leaves and roots.

Parameter (mg/g)	Leaf			Root		
	Mean $\pm$ S.D. ¹	Range	C.V. ²	Mean $\pm$ S.D.	Range	C.V.
C:N	24.92 $\pm$ 10.61 a ³	9.63–49.49	42.59	69.56 $\pm$ 38.22 b	18.86–173.14	54.94
C:P	445.48 $\pm$ 222.77 a	118.70–1148.39	50.01	830.79 $\pm$ 448.15 b	257.39–2029.93	53.94
N:P	17.91 $\pm$ 4.57 a	8.73–31.76	25.49	13.73 $\pm$ 6.91 b	2.98–36.60	50.34

¹ S.D means standard deviation. ² C.V means coefficient of variation (%). ³ Different letters in the same row indicate significant differences between leaf and root ($p < 0.05$).

In the soil, the mean values of C, N, P were 47.46 mg/g, 0.40 mg/g, and 0.15 mg/g, respectively, with more than 35% variation (Table 3). Correspondingly, C:N, C:P and N:P also showed strong variation, with values of 29.89%, 39.51% and 40.53%, respectively.

Table 3. The content and stoichiometry characteristics of carbon, nitrogen and phosphorus in soil.

Parameter	Mean $\pm$ S.D. ¹	Range	C.V. ² (%)
Carbon (C, mg/g)	47.46 $\pm$ 17.27	12.93–74.24	36.39
Nitrogen (N, mg/g)	0.40 $\pm$ 0.16	0.16–0.74	40.32
Phosphorus (P, mg/g)	0.15 $\pm$ 0.05	0.06–0.29	35.23
C:N	124.63 $\pm$ 37.25	77.14–351.32	29.89
C:P	344.29 $\pm$ 136.02	89.27–808.83	39.51
N:P	2.84 $\pm$ 1.15	0.74–6.11	40.53

¹ S.D means standard deviation. ² C.V means coefficient of variation (%).

3.2. The Correlations in the Stoichiometry of the Shrub Leaves and Roots

The leaf N concentration was significantly positively correlated with the leaf P, root N concentration, and root N:P, while being significantly negatively correlated with leaf C:N, leaf C:P, and root C:N ($p < 0.01$; Figure 2; Table 4). In addition, leaf P concentration was significantly negatively correlated with leaf C:N, leaf C:P, leaf N:P, and root C:N. However, no significant correlations were detected between the leaf C concentration and the other stoichiometry traits (Table 4). Furthermore, root C concentration was only positively correlated with root C:P ($p < 0.05$). The root N concentration was significantly correlated with the ratio of C, N, and P in the leaves and roots. Except for leaf N:P, the root P concentration was also significantly negatively correlated with the ratio of C, N, and P in leaves and roots. The leaf C:N was significantly positively correlated with leaf C:P, root C:N, and root C:P. Finally, both leaf N:P and root C:N were significantly negatively correlated with root N:P (Table 4).

Figure 2. Trait dimensions from the first four principal components (PCs) of the principal component analysis.

Table 4. Correlations and correlation probability between C, N, and P stoichiometry traits in karst shrubs.

Variables	Leaf C	Leaf N	Leaf P	Root C	Root N	Root P	Leaf C:N	Leaf C:P	Leaf N:P	Root C:N	Root C:P
Leaf N	−0.022										
Leaf P	−0.075	0.712 **									
Root C	−0.165	−0.043	−0.126								
Root N	−0.143	0.646 **	0.305 *	−0.015							
Root P	−0.199	0.134	0.181	−0.131	0.426 **						
Leaf C:N	0.251	−0.895 **	−0.694 **	−0.084	−0.603 **	−0.283 *					
Leaf C:P	0.282 *	−0.748 **	−0.792 **	−0.132	−0.381 **	−0.295 *	0.890 **				
Leaf N:P	0.063	0.15	−0.508 **	−0.028	0.440 **	−0.121	−0.019	0.389 **			
Root C:N	0.05	−0.603 **	−0.383 **	0.009	−0.840 **	−0.457 **	0.655 **	0.417 **	−0.297 *		
Root C:P	0.22	−0.268	−0.256	0.302 *	−0.467 **	−0.824 **	0.402 **	0.309 *	−0.011	0.546 **	
Root N:P	0.028	0.539 **	0.17	0.132	0.628 **	−0.360 **	−0.399 **	−0.199	0.486 **	−0.480 **	0.293 *

* represents $p < 0.05$. ** represents $p < 0.01$.

The PCA data showed four independent axes representing the stoichiometry of the leaves and roots in the karst shrubs (Figure 2; Table A3). The first four principal components collectively accounted for 86.11% of the total variation, whereas the fifth principal component further accounted for 6.27%. The first PC, which was predominantly related to leaf N, leaf P, root N, leaf C:N, leaf C:P, and root C:N, accounted for 40.73% of the total variation, whereas PC 2 and 3 together accounted for 35.19% of the total trait variation, indicating that root P, leaf N:P, root C:P, and root N:P dominated these PCs. PC 4, which accounted for 8.810.19% of all the trait variation, was found to be dominated by leaf C and root C (Table A3).

3.3. Factors Affecting the Stoichiometry in the Karst Shrub

Factor analysis of variance demonstrated that the differences in species had a high explanatory power in terms of the stoichiometry of the shrub leaves and roots (Table 5). Coefficient of determination (R^2) values between the species and the stoichiometry of the shrub leaves and roots ranged between 0.07 and 0.63. Among the variables, the differences in species significantly explained the variation in terms of the stoichiometry in the leaves and roots, except in the case of leaf C and root C:P. In addition, the different soil nutrients had a small effect on the variation of the stoichiometry of the shrub leaf and root, except for the leaf N, leaf N:P, and root C:P. Then, the effect of the topography on the variation of the stoichiometry of the shrub leaf and root was smallest, except in the case of leaf N ($p < 0.05$; Table 5). Therefore, the model of combining species and soil nutrient characteristics can already reflect most stoichiometric changes, especially in leaf N and Leaf P. The full models that included the species, topography, and soil nutrients showed a greater effect on most of the stoichiometry variation than when the species, topography, and soil nutrients were considered individually (Table 5).

Table 5. Effects of species (S), topography (T), and soil nutrient (SN) on C, N, P stoichiometry traits in karst shrubs (R^2 contents of the generalized linear model).

Variables	Leaf C	Leaf N	Leaf P	Root C	Root N	Root P	Leaf C:N	Leaf C:P	Leaf N:P	Root C:N	Root C:P	Root N:P
S	0.12	0.55 **	0.63 **	0.32 *	0.18	0.13	0.44 **	0.44 **	0.2	0.22	0.09	0.33 **
T	0.04	0.17	0.03	0.18	0.31 **	0.11	0.13	0.09	0.17	0.12	0.22 *	0.19
SN	0.2	0.07	0.09	0.26 *	0.05	0.12	0.06	0.12	0.25 *	0.11	0.13	0.25 *
S × T	0.14	0.72 **	0.69 **	0.41 *	0.54 **	0.22	0.64 **	0.57 **	0.39 *	0.42 *	0.31	0.46 **
S × SN	0.29	0.61 **	0.77 **	0.49 **	0.21	0.26	0.51 **	0.58 **	0.53 **	0.29	0.21	0.42 *
T × SN	0.26	0.28	0.15	0.38 *	0.35	0.26	0.33	0.31	0.34	0.24	0.3	0.42 **
S × T × SN	0.4	0.76 **	0.79 **	0.56 *	0.58 **	0.32	0.7 **	0.68 **	0.67 **	0.46	0.38	0.58 **

* represents $p < 0.05$. ** represents $p < 0.01$.

4. Discussion

4.1. Distribution Patterns and Synergies of the Phytochemical Elements

The distribution of plant resources can reflect how the plant adapts to the environment. Under drought conditions, plants tend to increase the contents of N and P in leaves and increase cell osmotic potential, so as to increase their ability to absorb and retain water. The leaves are the “drainage” (transpiration) organs of the plants, and plants, therefore, allocate less biomass to the leaves [33] to enhance water retention. However, leaves are also the main site of photosynthesis, and they are rich in photosynthesis-related enzymes, adenosine triphosphate (ATP), and other substances that have high levels of N and P; hence, the concentration of N and P in leaves is typically higher than in the roots and stems [11]. The data of this study were consistent with those of previous studies [25,28], which may be related to the seasonal drought period in karst areas.

The growth process of organisms includes regulating the accumulation and relative proportion of elements. Previous research has found a strong correlation between the C, N, and P ratio of the organism and the growth rate [34]. The rapid growth of the organism requires a large number of proteins, which in turn require a large number of ribosomal

RNAs for their synthesis. The ribosomal RNA contains large amounts of P, and proteins contain a large quantity of N. Thus, during periods of high growth, the organs typically have lower C:N, C:P, and N:P ratios [35]. This is known as the growth rate theory. In this study, the C:N and C:P ratios in the shrub leaves were significantly lower than those in the roots. This was because the samples were taken in the early middle growth stage of the shrub, during a period of high leaf metabolism. Thus, the ratios of C, N, and P across different organs were in line with the growth rate theory. However, contrary to the theory, the N:P ratio in the leaf was significantly higher than in the root, which may be related to the low soil N and P content in the karst area. In addition, N and P in plants are elements that are generally positively correlated [36]. Our study showed that N and P in the leaves and roots of the karst shrubs have an extremely significant positive correlation, which is consistent with previous research [18]. At the same time, the leaf N and root N were also significantly and positively correlated.

4.2. Stoichiometric Characteristics of the Karst Shrub Species

Differences in the C, N, and P concentration and the stoichiometry of the plants at a community level were observed, mainly owing to the differences in plant species, soil, and topography. Previous research found no significant differences in nutrient concentration in the same organ of closely related species across different habitats [21,37]. Conversely, differences were found between nutrient concentrations in distantly related species in habitats with relatively low soil nutrients, even when they lived in the same habitat. This may explain why the nutrient concentrations differed with different species in this study.

The average C concentration differed between the leaves of the karst shrubs (445.66 mg/g), the 492 global terrestrial plants (464 mg/g), the vegetation on the Loess Plateau (438 mg/g), and the monsoon evergreen broad-leaved forest of Yunnan Province (470 mg/g) [21,28]. This indicated that the C concentration of these leaves may be determined by regions, growth stage, and sampling time [25]. In addition, the N concentration of the leaves was found to be 20.94 mg/g, which was different from that of the global (20.62 mg/g) and the Chinese (20.24 mg/g) averages [21,37]. Similarly, the P concentration in the leaves and roots was also different from that of the global and the Chinese averages [37]. At the same time, our results show that there are strong variations in nutrient content and stoichiometric characteristics of soil and shrubs in karst areas. The main reasons may be as follows: First, the unique environment of karst leads to great changes in soil nutrients themselves [38], and our research results also show that there is a strong correlation between plant nutrients and soil nutrients. Secondly, the sampling is in the early middle growth period, so it can best reflect the difference of growth characteristics among species [25,39]. Meanwhile, summer is also the season with the largest difference in soil nutrients. Thirdly, because shrubs often do not occupy the dominant site in the community, which is especially obvious in the karst area, the differences caused by nutrients, illumination and other conditions on shrubs are greater than those on trees [40]. More future species-specific studies are needed to explain the exact ultimate cause of such variation of nutrient content and stoichiometric characteristics in karst shrubs.

As important physiological indicators, C:N and C:P reflect the plant growth rates [34,41]. In the present study, the C:N values of the leaves and roots were different from that of the global average (22.5), while the Loess Plateau averages 21.2 in the leaves [4,37], which was related to the relatively high N concentration in the karst shrub plants. However, the C:P values in the leaves and roots were also different from those of the evergreen broad-leaved (758.0) and evergreen coniferous (677.9) forests on Tiantong Mountain, Zhejiang, China [42]. Hence, these data indicated that the stoichiometry of these leaves may be also affected by the species across different regions, growth stages, and sampling time points [25]. In addition, as an indicator of the main elements in the photosynthetic organs, leaf N:P is commonly used to determine which element restricts the ecosystem productivity, but this relationship varies with the different external environmental conditions [8,43]. In the present study, the mean N:P ratio of the leaves in different forest communities was

17.91, which was different from those of the global (13.8) and Chinese (14.4) averages [4,37]. Previous studies have shown that plant growth is restricted by N when plant N:P < 14; when N:P > 16, it is restricted by P; and when $14 < \text{N:P} < 16$, it is restricted by both N and P [3,44]. In our study, the N:P in the leaves was >16, indicating that leaf growth was restricted by P. In contrast, the N:P in the roots was <14, indicating that root growth may have been restricted by P. However, whether the use of this ratio is suitable for the karst ecosystems needs to be investigated further by integrating other ecosystems, vegetation types, and the physical and chemical properties of the soil.

4.3. Stoichiometry of the Karst Plant and its Soil Characteristics

Soil nutrients are very important factors that affect plant growth. Plant photosynthesis, mineral metabolism, and other ecological processes are also closely related to soil nutrient supply. Plant nutrients are mainly sourced from the soil, and their concentration is closely related to the concentration of nutrients in the soil. Some studies have shown that leaf N and P concentration is closely related to soil N and P concentration [3,45,46]. In the present study, the different soil nutrient concentrations had little effect on the variation in the stoichiometry of the shrub leaves and roots, except in the case of the root N and leaf N:P and root N:P (Table A4). This may be due to the special plant–soil environment in the karst area. Although the karst topsoil has a high nutrient concentration, the soil is thin, and the total nutrients available are insufficient. Karst shrubs also need to maintain highly efficient photosynthetic rates and enzyme activities in a limited growth cycle, with rich N and P contents in the leaves and roots to maintain normal metabolic activities in the plant [4]. The concentrations of N and P in the plant leaves in the karst areas are relatively high, which is also consistent with a previous study [28]. Shrubs in the karst region have deeper roots that tend to penetrate deeply into the rock gaps to take advantage of the water and the nutrients in these gaps [23,24]. Thus, the karst soil had only small and insignificant effects on the shrub nutrients (Table A4). In contrast, the concentrations of N and P in the karst grass leaves were significantly correlated with the concentration of N and P in the soil, indicating that the concentration of the soil nutrients played an important role in the grass growth. This may be since karst grasses have shallow roots and are mostly distributed in the soil. It has also been found that the karst plant species, growth stage, community composition, structure, soil characteristics, and other factors directly or indirectly affect the concentration of the elements [47]. However, our current studies based on stoichiometry do not fully understand the adaptation mechanism of species to the soil environment, so more studies combining physiological processes should be carried out.

4.4. Plant Stoichiometry and Karst Vegetation Restoration

Soil depletion and nutrient restriction in the karst ecosystems are problems that require an in-depth study of vegetation restoration. In the process of restoring rocky areas that have experienced desertification, the scarce mineral nutrients in the soil will be sustained by the increased biomass of the restored community [25]. Mineral nutrients are likely to be a major factor that can limit the vegetation restoration in the rocky desertified areas (stony geochemical habitats). Additionally, owing to the differences in climate and the geographical conditions of water and heat supply, the N and P concentration and the measurement characteristics of C:N:P ratios of the plant leaves vary over large scales and are highly differentiated across the different habitats and tree species [4], which also reflects the adaptation of the plants to local nutritional conditions. Hence, our data showed that there were significant positive and negative correlations among the stoichiometry of leaves and roots, which reflected the adaptation of the shrub plants to the karst habitats. However, the present study was limited as the C, N, and P stoichiometry in the litter was not considered, which could affect the process of reabsorption and the reusing of nutrients in the karst plants. Thus, further research needs to be conducted on the C, N, and P stoichiometry in the plant–litter–soil continuum for more forest species. This could reflect

the forest ecosystem's nutrient circulation rate and nutrient use efficiency, and provide a scientific basis for the restoration of vegetation in the karst region.

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Conflicts of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Appendix A

Table A1. The plant catalogue of the sample survey.

Species	Family	Genus	Live Form
<i>Pittosporum glabratum</i> Lindl.	Pittosporaceae	Pittosporum	Evergreen
<i>Vitex negundo</i> L.	Lamiaceae	Vitex	Deciduous
<i>Alchornea trewioides</i> (Benth.) Müll. Arg.	Euphorbiaceae	Alchornea	Deciduous
<i>Flemingia macrophylla</i> (Willd.) Kuntze ex Prain	Fabaceae	Flemingia	Evergreen
<i>Maesa perlarius</i> (Lour.) Merr.	Primulaceae	Maesa	Evergreen
<i>Zanthoxylum bungeanum</i> Maxim.	Rutaceae	Zanthoxylum	Deciduous
<i>Itea chinensis</i> Hook. & Arn.	Iteaceae	Itea	Evergreen
<i>Boehmeria nivea</i> (L.) Gaudich.	Urticaceae	Boehmeria	Evergreen
<i>Indigofera kirilowii</i> Maxim. ex Palib.	Fabaceae	Indigofera	Evergreen
<i>Cajanus cajan</i> (L.) Huth	Fabaceae	Cajanus	Evergreen
<i>Zanthoxylum dissitum</i> Hemsl.	Rutaceae	Zanthoxylum	Deciduous
<i>Alangium chinense</i> (Lour.) Harms	Cornaceae	Alangium	Deciduous
<i>Pyracantha fortuneana</i> (Maxim.) H. L. Li	Rosaceae	Pyracantha	Evergreen
<i>Maesa japonica</i> (Thunb.) Moritzi & Zoll.	Primulaceae	Maesa	Evergreen
<i>Viburnum fordiae</i> Hance	Adoxaceae	Viburnum	Evergreen
<i>Rhamnus utilis</i> Decne.	Rhamnaceae	Rhamnus	Deciduous
<i>Rubus idaeus</i> L.	Rosaceae	Rubus	Deciduous
<i>Glochidion hirsutum</i> (Roxb.) Voigt	Phyllanthaceae	Glochidion	Evergreen
<i>Euchresta japonica</i> Hook. f. ex Regel	Fabaceae	Euchresta	Evergreen
<i>Tirpitzia ovoidea</i> Chun & F. C. How ex W. L. Sha	Linaceae	Tirpitzia	Evergreen
<i>Ligustrum lucidum</i> W. T. Aiton	Oleaceae	Ligustrum	Evergreen
<i>Dodonaea viscosa</i> Jacquem.	Sapindaceae	Dodonaea	Deciduous
<i>Sophora tonkinensis</i> Gagnep	Fabaceae	Sophora	Deciduous

Table A2. Information on sampling sites.

Site No.	Elevation (m)	Slope (°)	Slope Position	Slope Direction	Soil Depth (m)	Soil pH	Soil Organic Matter (g/kg)	TN (g/kg)	TP (g/kg)	TK (g/kg)	AN (mg/kg)	AP (mg/kg)	AK (mg/kg)
1	331.3	39	M	E	0.15	7.35	66.20	0.60	0.17	1.10	461.65	0.15	0.84
2	348.6	6	M	E	0.15	7.36	73.38	0.65	0.17	2.89	429.10	0.11	0.93
3	225.4	10	L	E	0.18	7.36	73.38	0.65	0.17	2.89	429.10	0.11	0.93
4	222.5	10	L	E	0.11	7.36	31.71	0.28	0.13	1.80	272.30	0.07	1.58
5	346.5	22	M	E	0.16	7.37	72.69	0.69	0.14	1.86	540.75	0.12	0.81
6	225.4	10	L	E	0.23	7.52	55.45	0.49	0.17	3.13	367.85	0.15	0.61
7	392.3	39	L	SE	0.15	7.37	33.18	0.51	0.25	2.16	433.30	0.19	1.66
8	274.9	3	L	SE	0.25	7.01	63.82	0.53	0.23	4.11	380.10	0.15	1.58
9	366.5	22	M	SE	0.08	7.26	31.00	0.29	0.24	3.67	233.80	0.17	1.87
10	348.6	6	M	SE	0.12	7.24	56.50	0.53	0.24	1.77	397.95	0.19	1.33
11	316.1	12	M	S	0.18	7.24	56.50	0.53	0.24	1.77	397.95	0.19	1.33
12	340.6	6	M	E	0.11	6.70	33.74	0.29	0.11	0.64	242.20	0.08	0.75
13	327.6	12	L	E	0.16	7.07	70.32	0.59	0.18	2.70	412.30	0.09	2.22
14	320.2	23	L	E	0.36	7.43	58.57	0.17	0.17	2.84	122.15	0.09	2.77
15	305.7	25	L	E	0.55	6.99	33.71	0.27	0.09	3.19	235.55	0.05	2.78
16	346.5	22	M	S	0.19	7.32	42.74	0.36	0.13	2.71	342.65	0.07	1.62
17	222.5	10	L	S	0.18	7.20	43.25	0.40	0.29	1.08	355.95	0.22	0.37
18	305.7	25	L	E	0.2	7.20	43.25	0.40	0.29	1.08	355.95	0.22	0.37
19	295.5	4	L	SE	0.17	6.70	13.12	0.17	0.12	2.43	109.90	0.11	1.48
20	340.5	6	L	S	0.19	6.79	35.39	0.24	0.21	1.45	227.15	0.14	1.22
21	339.7	4	L	SE	0.23	7.30	57.74	0.41	0.19	2.56	408.45	0.11	2.09
22	280.1	3	L	W	0.2	7.47	29.38	0.26	0.27	2.92	199.15	0.19	2.76
23	316.4	19	M	S	0.27	7.43	35.17	0.28	0.20	1.12	272.30	0.13	1.03
24	340.5	18	M	SE	0.09	7.21	61.13	0.48	0.19	3.37	461.30	0.14	1.37
25	350.5	18	M	SE	0.25	7.21	61.13	0.48	0.19	3.37	461.30	0.14	1.37
26	360.5	18	M	SE	0.27	7.21	61.13	0.48	0.19	3.37	461.30	0.14	1.37
27	310.7	6	L	S	0.19	7.43	36.10	0.27	0.12	1.40	247.80	0.14	2.84
28	380.9	6	L	S	0.2	6.77	26.54	0.27	0.06	1.68	217.00	0.08	1.49
29	340.5	18	M	SE	0.27	7.19	47.95	0.49	0.16	3.45	337.75	0.07	2.79
30	316.4	19	M	S	0.29	7.19	47.95	0.49	0.16	3.45	337.75	0.07	2.79

Note: In slope position, L and M mean low and middle, respectively. In slope direction, E, S, W means east, south, and west, respectively. TN, total nitrogen; TP, total phosphorus; TK, total potassium; AN, available nitrogen; AP, available phosphorus; AK, available potassium.

Table A3. The characteristic value and principal component contribution rate and its loads.

PC	Eigenvalue	Percentage	Cumulative Percentage	LeafC	LeafN	LeafP	RootC	RootN	RootP	LeafC:N	LeafC:P	LeafN:P	RootC:N	RootC:P	RootN:P
1	4.89	40.73	40.73	0.23	−0.88	−0.71	0.03	−0.81	−0.47	0.93	0.81	−0.06	0.82	0.56	−0.44
2	2.30	19.14	59.87	0.23	0.20	−0.31	0.20	0.35	−0.57	−0.01	0.27	0.76	−0.20	0.50	0.83
3	1.93	16.05	75.92	0.00	0.23	0.49	0.34	−0.36	−0.57	−0.22	−0.46	−0.55	0.33	0.60	0.17
4	1.22	10.19	86.11	0.73	0.19	0.28	−0.74	−0.06	−0.12	0.06	0.09	−0.07	−0.01	−0.01	0.02
5	0.75	6.27	92.38	0.59	−0.04	−0.04	0.54	0.03	0.21	0.03	−0.01	−0.12	−0.19	0.00	−0.10
6	0.42	3.52	95.90	−0.09	−0.24	0.16	−0.05	0.21	0.05	0.25	0.11	−0.31	−0.21	0.10	0.24
7	0.20	1.68	97.58	0.03	0.07	−0.07	−0.04	0.16	0.23	0.06	−0.09	−0.01	0.27	0.14	0.07
8	0.15	1.23	98.80	−0.03	0.13	0.21	0.10	0.08	−0.03	0.11	0.18	0.05	0.11	−0.07	−0.06
9	0.09	0.77	99.57	−0.04	0.05	0.06	−0.02	−0.09	0.13	−0.02	0.07	0.06	−0.10	0.19	−0.07
10	0.03	0.23	99.80	0.00	−0.01	0.03	0.01	−0.09	0.06	−0.01	0.03	0.01	0.03	−0.05	0.10
11	0.02	0.17	99.97	0.02	−0.09	0.05	0.00	0.03	0.00	−0.07	0.01	0.04	0.03	0.01	−0.01
12	0.00	0.03	100.00	0.00	−0.01	0.02	0.00	−0.01	0.00	0.03	−0.04	0.03	−0.01	0.00	0.00

Table A4. Correlations and correlation probability between C, N, and P stoichiometry traits in karst shrubs and soil.

	Leaf C	Leaf N	Leaf P	Root C	Root N	Root P	Leaf C:N	Leaf C:P	Leaf N:P	Root C:N	Root C:P	Root N:P
SOC	−0.080	−0.161	−0.117	0.188	0.211	−0.071	0.158	0.118	0.050	−0.030	0.115	0.194
TN	−0.098	−0.302 *	−0.140	0.273 *	0.020	−0.090	0.252	0.136	−0.137	0.072	0.174	0.024
TP	−0.185	−0.035	0.177	−0.234	−0.085	0.169	−0.040	−0.167	−0.320 *	0.152	−0.232	−0.280 *
AN	−0.105	−0.288 *	−0.086	0.220	0.129	−0.014	0.240	0.170	−0.100	−0.046	0.069	0.041
AP	−0.303 *	−0.438 **	−0.269	0.210	−0.245	−0.150	0.300 *	0.268	−0.068	0.236	0.110	−0.164
Soil C:N	0.046	0.293 *	−0.028	−0.161	0.384 **	−0.026	−0.188	−0.021	0.471 **	−0.228	−0.076	0.447 **
Soil C:P	0.023	−0.083	−0.264	0.283 *	0.242	−0.235	0.147	0.210	0.346 *	−0.083	0.250	0.421 **
Soil N:P	−0.004	−0.310 *	−0.279 *	0.409 **	−0.015	−0.245	0.298 *	0.247	0.045	0.068	0.326 *	0.145

* represents $p < 0.05$. ** represents $p < 0.01$.

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