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Stoichiometric Characteristics of Leaf, Litter and Soil during Vegetation Succession in Maolan National Nature Reserve, Guizhou, China

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Abstract: Carbon (C), nitrogen (N), phosphorus (P) and potassium (K) are the main nutrient elements widely found in soil, litter and leaves, and their stoichiometric ratios are important indicators of ecosystem functions. However, there is little research on the effects that nutrient cycle and vegetation succession have on leaf, litter and soil nutrients and stoichiometric ratios, especially in the fragile karst areas. To reveal the nutrient cycling characteristics and ecosystem stability mechanism during vegetation succession, leaf, litter and soil samples were collected from the herbaceous community (HC), shrub community (SC), secondary forest community (SF) and primary forest community (PF) in a typical karst area at growth and senescence phases. The results showed that the nutrient contents and stoichiometric ratios of leaf, litter and soil in the main layers of each community were significantly different at the growth and senescence phase. The utilization efficiency of N in the leaves of the main layers of each succession community first decreased and then increased at different growth stages, and the utilization efficiency of P increased but the reabsorption rates of N and P showed a continuous decreasing trend. In addition, there was a significant allometric relationship between N and P contents in plant leaves during the growth phase. More importantly, the internal stability of N content in plant leaves was higher than the P content, suggesting that vegetation succession significantly affected leaf, litter and soil nutrient contents and their stoichiometric ratios in our study region. The strength of the relationship between them reflects the inheritance and co-variation of nutrient content to a certain extent, and the differences in the strategies that different species in the community use to adapt to the fragile karst environment. This study concludes that plants in the karst region mainly improve their P utilization efficiency to adapt to low phosphorus stress in soil and ensure the normal physiological and biochemical responses in the process of vegetation succession.

Keywords: vegetation succession; leaf–litter–soil; stoichiometric characteristics; homeostasis; resorption efficiency; nutrient use efficiency; Maolan National Nature Reserve

1. Introduction

Ecological stoichiometry (ES) is the study of the balance of energy and multiple chemical elements in ecological systems [1–3], which can quantitatively reveal the soil properties, nutrient absorption efficiency, nutrient interactions such as decomposition, and energy balance processes [4–6]. ES is a helpful tool for studying the coupling of carbon (C), nitrogen (N), phosphorus (P) and other chemical elements in biogeochemical cycles and ecosystem processes [7–9]. C, as the structural element of plants, and N and P, as the limiting elements [10,11], are involved in the physiological and biochemical processes of plants and play a critical role in plants' growth and development, and even in ecosystem structure and function [10,12,13]. Potassium (K), which is second only to N in dry matter content in

plants [14], not only maintains cellular osmotic pressure and promotes protein synthesis, photosynthesis and enzyme activation [15], but is also associated with water regulation and stress resistance in plants [16,17]. From the perspective of the entire ecosystem, the chemical elemental composition in producers, consumers, decomposers and soil determine the main processes of the ecosystem, and the stoichiometric ratios of elements are very important indicators of ecosystem energy flow, substance cycling and nutrient limitation, as well as the survival strategies and adaptation mechanisms of different species [18,19].

As a major part of terrestrial ecosystems, forests have a relatively complete community structure and complex species composition [20]. In a forest ecosystem, plants, litter and soil are the most important components, with the plants absorbing water and nutrients from the soil through the root system, and the leaves assimilating and accumulating organic matter through photosynthesis, and returning nutrients to the soil in the form of litter [2,21]. The litter and its decomposition form the hub of substance–energy exchanges between the plants and the soil, and are also an important form of nutrient storage for forest ecosystems [22]. They interact with each other and are closely linked, forming a plant leaf–litter–soil nutrient cycle continuum [23]. The stoichiometric characteristics of plant leaves can reflect the supply of soil nutrients and identify their dynamic equilibrium thresholds [2]. C:N and C:P ratios can, to a certain extent, indicate plants' growth rate, C-fixation capacity and N- and P-use efficiency [24,25]; the N:P ratio is a key indicator that determines the structure and function of communities and affects the stability of ecosystems [26], and the ratio can also indicate the limiting elements in plant growth [27,28]. Studies on soil stoichiometry help to understand the nutrient regulation mechanisms of plant–soil interactions [29], and the difference in plant leaf–litter–soil C:N:P ratios can explain changes in ecosystem structure [18]. However, studies of the nutrient content of the leaf–litter–soil continuum are made more complex by the differences and interactions between the soil nutrient supply, the nutrient content returned during litter decomposition, the plant's nutrient demands and the self-regulation of nutrient demands [21,30,31]. Therefore, studying the stoichiometric characteristics of C, N and P in the plant–litter–soil continuum and the interrelationship between successional communities is of great research significance, as this can systematically reveal the nutrient–cycling patterns of forest ecosystems and the nutrient balance characteristics of the components [13,20], as well as helping to further understand plants' growth strategies and their adaptability to environmental changes and stresses [2].

Karst refers to the geological process that is largely carried out by the chemical dissolution of water on water-soluble rocks, such as limestone, gypsum and rock salt, and supplemented by the mechanical actions of erosion or latent erosion of flowing water and rock avalanche. This is a general term for the phenomena that arise from these actions [32]. Southwestern China, the Mediterranean coast of Europe, and the Eastern United States are the three major regions worldwide, with extensively distributed continuous karst landscapes [33]. China has approximately 3.44 million km² of karst area, which accounts for about 15.6% of all karst areas in the world [34], while Guizhou, as the center of southwest China's karst landform, has a total area of approximately 540,000 km² [32]. Karst forests are found on topography formed from the dissolution of soluble rocks, e.g., limestone [35]. Different vegetation types, such as grassland, shrub, secondary forest and primary forest, coexist due changes in intense human activities, the influence of drought and fire [36], the ecosystem and the environment [37–39].

Locally reputed as the “emerald on the girdle of the Earth”, the Maolan Karst Forest comprises azonal vegetation, with its main vegetation type being the native evergreen deciduous broad-leaved mixed forest developed on the karst landscape, in addition to a small population of vine shrub and shrubby grassland [40]. Ecological degradation varies by location [41], as the fragility of the environment in the karst area makes it highly susceptible to vegetation degradation disturbances, with a slow and difficult natural recovery [40]. On the other hand, vegetation restoration is a key factor and an effective way to curb ecosystem degradation [42]. Vegetation restoration plays an effective role in controlling

soil erosion, promoting plant–soil nutrient cycling and improving soil properties [42,43]; at the same time, it also drives species turnover, changing community structure and species diversity, and forming a diverse ecosystem with more distinct community stratification and a more complete community structure [44]. This will change the distribution of the content of each chemical element among the leaf, litter and soil [45]. The distribution of nutrients among successional communities may also considerably vary according to the vegetation restoration and succession [42]. Therefore, it is necessary to study the changes in the stoichiometric characteristics of the plant–litter–soil continuum with vegetation succession in the karst area.

However, studies on karstic stoichiometry to date have mostly focused on a single component of the ecosystem (leaves [46,47], litter [48,49] or soil [4,50,51]) or on two components (leaves–litter [52], leaves–soil [16,53] or litter–soil [54,55]), or on a single organ of a tree species (leaf or fine root [14]). Relatively fewer studies have been conducted on the synergistic changes between plant–litter–soil as a continuum with vegetation succession (and those that have pay more attention to the general type of landform [9,13,20–23,42,56]), limiting the understanding of nutrient cycling in forest ecosystems in the karstic area of Maolan. Moreover, some researchers have made progress in understanding the karst forest vegetation in the rest of the tropical or subtropical zone [57–60]. In this study, four different successional communities (i.e., herbaceous communities (HC), shrub community (SC), secondary forest community (SF) and primary forest community (PF, evergreen deciduous broad-leaved mixed forest)) were selected as the subjects according to the natural succession process of vegetation communities, using a spatial instead of temporal approach. The goals of the study are to answer the following questions: (1) how does the C, N, P and K content distribute in leaf–litter–soil in successional communities in terms of time and space, and how different are the stoichiometric characteristics in these distributions? (2) How does vegetation succession impact the C, N, P and K content in leaf–litter–soil, in addition to their stoichiometric characteristics and homeostasis? (3) How do the C, N, P and K content in leaf–litter–soil and the stoichiometric characteristics interact, and what is their coupling relationship like? (4) How do the different successional communities' respond to the environmental changes following vegetation succession, and what are their nutrient use strategies? Studies on these questions will help us understand the nutrient cycling characteristics and system stability mechanisms of the ecosystem during vegetation succession in karstic Maolan, and provide a scientific basis for the restoration, reconstruction, conservation and management of vegetation in the degraded karst ecosystems.

2. Materials and Methods

2.1. Overview of the Study Area

The study area was located in the Maolan National Nature Reserve (107°52'10"–108°5'40" E, 25°09'20"–25°20'50" N), Guizhou province, China. The average elevation ranges from 550 to 850 m above sea level. The area has a subtropical humid climate with an average annual temperature of 15.3 °C. The average annual precipitation reaches 1752.5 mm, with an average annual relative humidity of 83%. The studied area is characterized by a typical karst landscape, including a series of typical peak cluster–depression habitat types, from mountain tops and hillsides to depressions [61], with over 80% of the rock being exposed [62]. The forest land is rarely covered by a shallow layer of soil, which is mostly retained in the rock fissures. The soil is rich in calcium and organic matter, and has high degree of basification. The soil is mainly dark or brown calcareous soil developed over carbonate rocks. The forest coverage rate is 87.4%, and the main type of vegetation is evergreen and deciduous, broad-leaved, mixed forest. The area has the largest, most unique and relatively stable karst forest ecosystem remaining in the world at the same latitude [62].

2.2. Sampling Site Setting

In May 2015, we selected three primary forest communities (PF) and three secondary forest communities (SF) after surveying and examining the sampling sites used to conduct studies in the station area. Using a space-for-time substitution approach [63], the sampling sites were selected based on the natural successional process of vegetation communities [64], the degree of recovery, distribution of community types and the species composition, taking topographic and landscape homogeneity, representativeness of sampling sites and accessibility into consideration. In addition, three shrub communities (SC) and three herbaceous communities (HC) were added, making a total of 12 sampling sites, which represented the very late, late, mid and early stages of succession, respectively. The locations of these sampling sites are shown in Figure 1.

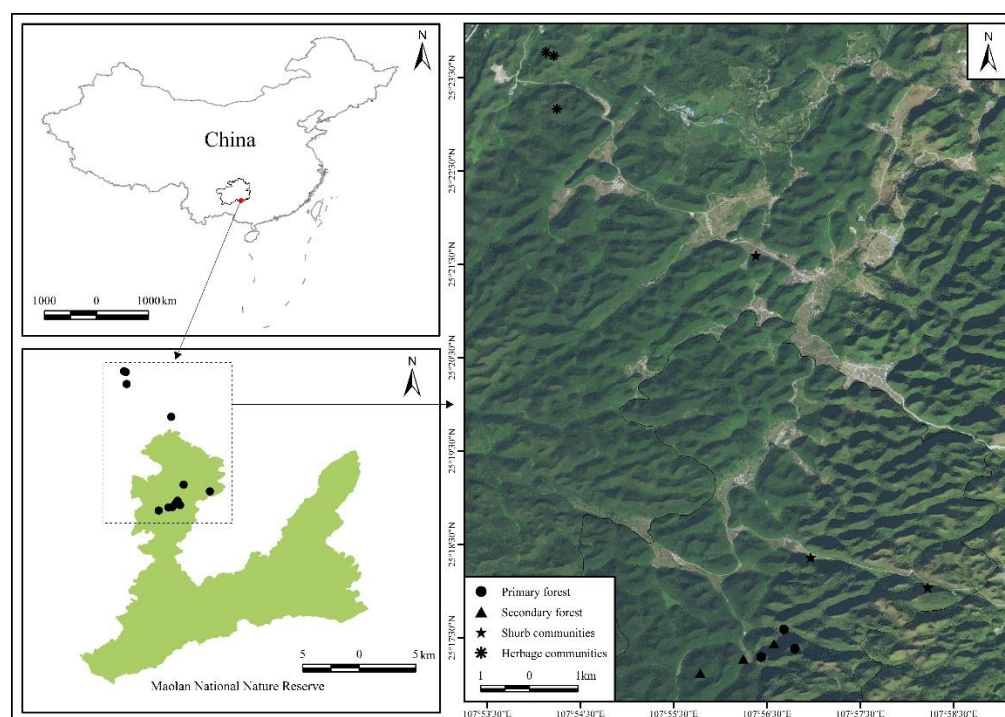


Figure 1. Studied Sampling Sites in Karstic Maolan Area.

2.3. Sampling Site Survey

A hand-held Global Positioning System (GPS) and compass were used to measure and record the latitude, longitude, elevation and slope of each sampling site. The shrub coverage was measured by the diagonal method. Other habitat factors, including the slope position, herb coverage, and bedrock outcrop rate, were measured by the same single observer through visual observation [65]. For PF and SF, the tree layer, shrub layer and herbaceous layer were surveyed separately; for SC, the layers of shrub and herbaceous plants were surveyed; for HC, the herbaceous layer only was surveyed. When surveying the tree layer, each sampling site was divided into 9 quadrats (10 m × 10 m), and each tree species with a diameter at breast height (DBH) of 5 cm or more was surveyed for each tree species in each quadrat, with its species name, DBH, tree height and crown width recorded. When surveying the layers of shrub and herbaceous communities, each sampling site was first randomly divided into three quadrats of shrub layer (5 m × 5 m) and three quadrats of herbaceous layer (1 m × 1 m), with each layer randomly laid in the upper, middle and lower parts of the plot. The species name, number of plants (clumps), basal diameter, height (length) and coverage were recorded [46,65]. The surveyed data of each sampling site are detailed in Table 1.

Table 1. Basic Data of the Sampling Sites.

Successional Community	Sample Area	Altitude /(m)	Slope /(°)	Location	Bedrock Outcrop Rate	Community Characteristics	Dominant Species
Herbaceous communities	10 m × 10 m	620–710	20–30	Middle slope	55–75%	Only one layer of herb layer with a height of 1.0–1.5 m and coverage of more than 80%. Very few pioneer tree species with a height of generally 2.0–3.0 m in specific plots. Litter abundant.	<i>Digitaria sanguinalis</i> <i>Imperata cylindrica</i> <i>Pteridium aquilinum</i> <i>Miscanthus floridulus</i>
Shrub communities	20 m × 20 m	770–790	20–30	Middle slope	80–85%	The dominant species are mostly shrubs with a height of 3.0–5.0 m and a coverage of >80% and the vertical structure is relatively simple, with few trees. Interlayer plants are common spiny vines. Litter layer 2.0–4.0 cm.	<i>Alangium platanifolium</i> <i>Pyracantha fortuneana</i> <i>Nandina domestica</i> <i>Lindera communis</i> <i>Tirpitzia sinensis</i>
Secondary forest	30 m × 30 m	760–800	20–25	Lower-middle slope	70–80%	The hierarchical structure showed obvious differentiation, with relatively developed trees and shrubs. Average height of tree layer 8.0–12.0 m. Shrub height 3.0–5.0 m with a coverage of 10–20%. The forest floor was covered by a small amount of lianas, thorny vines, ferns, lichen, and moss. Litter layer 2.0–3.0 cm.	<i>Pittosporum lenticellatum</i> <i>Platycarya longipes</i> <i>Machilus litseifolia</i> <i>Cornus wilsoniana</i> <i>Lindera communis</i> <i>Daphniphyllum calycinum</i>
Primary forest	30 m × 30 m	740–780	15–35	Lower-middle slope	75–85%	The community level differentiation is clear and the structure is complete. It is mainly composed of tall trees with a height of 12–20 m and a coverage of more than 80%. Average height of shrubs 3–8 m with a coverage of 5–10%. Litter layer 2.0–3.0 cm.	<i>Cyclobalanopsis multinervis</i> <i>Carpinus pubescens</i> <i>Phoebe crassipedicella</i> <i>Cornus wilsoniana</i> <i>Castanopsis fargesii</i> <i>Acer wangchii</i>

2.4. Sample Collection

Sampling time: Plant leaves and litter were sampled twice: one time in the senescence phase (October–November 2015) and one in the growth phase (May–June 2016). Soil was sampled only once, in June 2015, as the nutrient content does not significantly vary in the short term in its natural state.

Tree layer leaf sampling: The dominant tree species were sampled according to their diameter class ($5.0 \text{ cm} \leq \text{DBH} < 7.5 \text{ cm}$, $7.5 \text{ cm} \leq \text{DBH} < 22.5 \text{ cm}$, and $\text{DBH} \geq 22.5 \text{ cm}$), based on the calculation results of the importance value (>5.0). A long-arm pruner was used to cut branches in the upper, middle, and lower parts of the canopy from the east, south, west, and north directions. Leaves, which must be fully extended, disease-free, and complete (without petioles), were collected from the branches. The leaf samples were thoroughly mixed and then divided by quartering. Subsamples (total samples ≥ 30 leaves) were sealed in plastic bags and kept in a portable refrigerator. An individual tree was taken as one replicate sample for a tree species [65].

Shrub layer leaf sampling: The dominant shrub species were sampled, with two to three plants per species. The sampling procedure was performed as described for the tree layer. A mixture of two to three plants was taken as one sample for each plant species.

Herb layer leaf sampling: The dominant herb species were sampled by directly cutting fresh and fully expanded leaves of herbs or ferns using scissors. The leaves from five to seven plants per cluster were mixed to provide one sample for tall herbs or ferns (≥ 80 cm), and at least 300 g of fresh leaves was taken as one sample for short herbs or ferns (< 80 cm).

Litter sampling: Four quadrats (1 m $\times$ 1 m) were set at the four corners of each sampling site. Sampling was layered (at the undecomposed layer and semi-decomposed layer) with the harvesting method. In herbaceous communities, it was hard to distinguish between the undecomposed layer and semi-decomposed layer as standing litter was abundant; thus, the sample was mixed. Before being taken to the lab, the fresh weight of the sample was scaled. All the samples were dried at 65 °C in an oven to a constant weight.

Soil sampling: In each fixed sample plot, 12 soil profiles were randomly arranged according to different micro-habitats, such as stone surface, stone gully, stone crevices, stone pit and soil surface (based on the large spatial heterogeneity of karst landform soil). The soil color, structure, texture, tightness, humidity, root amount, gravel content and other factors were recorded according to the depth of 0–10 cm and 10–20 cm soil layers, respectively. Then, the same amount of soil sample was taken from each layer, and the 12 soil samples at the same level were randomly divided into four parts. After fully mixing, the soil samples were divided into four parts and put into a soil bag (no less than 500 g). Impurities were removed and the samples were labelled. They were then transported back and underwent indoor natural air-drying for preparation [51].

2.5. Sample Processing and Measurement

Samples of plants (litter included) and soil were prepared with reference to LY/T 1267–1999 and LY/T 1210–1999; C content was determined by potassium dichromate heating of oxidation–volumetric with reference to LY/T 1237–1999; total N was determined by Kjeldahl method with reference to LY/T 1269–1999; total phosphorus (TP) was determined using the Olsen method (LY/T 1270–1999, and LY/T 1234–1999); soil alkali-hydrolysable nitrogen (AHN) was quantified by the alkali-hydrolyzed reduction diffusing method with reference to LY/T 1229–1999; and soil-available phosphorus was determined with reference to LY/T 1233–1999 [66].

2.6. Data Processing and Analysis

1. When acquiring the data for the nutrient contents in plant leaf, a weighted average of the importance value index (IV) of the dominant species at the different layers of each community (tree, shrub and herbaceous layers) was adopted as a weighting factor within each sampling site. The formula is as follows:

$$Z_i = \frac{\sum_j C_{ij} \times IV_{ij}}{\sum_j IV_{ij}} \quad (1)$$

where Z_i is C, N, P and K contents in leaf in Layer i at the sampling sites ($i = 1 - 3$, corresponding to the tree, shrub and herb layers, respectively); C_{ij} represents the average value ($\text{g} \cdot \text{kg}^{-1}$) of C, N, P and K contents in Species j in Layer i (j is the number of dominant species in each layer with $IV > 5.0$).

2. When acquiring the data for the nutrient contents in litter, a weighted average of the biomass density of the undecomposed and semi-decomposed layers of the litter in each sampling sites was adopted as a weighting factor. The formula is as follows:

$$W = \frac{\sum_i C_i \times BD_i}{\sum_i BD_i} \quad (2)$$

where W means the average value ($\text{g} \cdot \text{kg}^{-1}$) of C, N, P and K contents in the litter at the sampling sites; C_i is C, N, P and K contents in the litter in Layer i ($i = 1 - 2$, representing the undecomposed and semi-decomposed layers, respectively) at the sampling sites; BD_i is the biomass density ($\text{g} \cdot \text{m}^{-2}$) of the litter in Layer i .

3. The nutrient contents of the soil are the average value of the topsoil (0–10 cm) for each profile at the sampling sites.
4. The allometric relationship [67], estimated using Package SMATR in R4.1.2 for standardized major axis estimation (SMA), reflects the variations between two attributes (e.g., C, N, P, K contents) within the organism during plant growth [56]. The most commonly used formula is as follows:

$$y = ax^b \quad (3)$$

where x and y mean the biological properties, while a and b are constants. However, in practical studies, the equations are often presented in logarithmic form, as follows:

$$\log(y) = b \log(x) + \log(a) \quad (4)$$

where the allometric scaling exponent b is the slope; $\log(a)$ is the intercept of a straight line.

5. The nutrient–use efficiency (NUE) reflects how well the plant use the nutrients from the soil and the plant’s adaptability [68]. This study adopts Chapin’s unit to calculate NUE . The formula is as follows:

$$NUE = \frac{M}{A} = \frac{M}{M \times Z} = \frac{1}{Z} \quad (5)$$

where NUE refers to the nutrient–use efficiency; M means the vegetation biomass; A represents the plant’s nutrient restoration ($\text{kg} \cdot \text{hm}^{-2}$); and Z is N, P contents in the leaf of the layers of the main communities (HC, SC, SF and PF) at the sampling sites ($\text{g} \cdot \text{kg}^{-1}$).

6. The nutrient resorption efficiency (NRE) is the efficiency with which nutrients are transferred from the senescing leaves to the new plant tissues or organs. Plant’s N, P resorption efficiency is calculated with the following equation [69]:

$$NRE = \frac{Z - W}{Z} \times 100 \quad (6)$$

where NRE refers to nutrient resorption efficiency (%); Z is N, P contents in leaf of the layers of the main communities at the sampling sites ($\text{g} \cdot \text{kg}^{-1}$); and W is the average N, P contents in litter at each sampling sites ($\text{g} \cdot \text{kg}^{-1}$).

7. Stoichiometric homeostasis refers to an organism’s ability [70] to maintain a given elemental composition in the body despite the variation in the elemental composition of its environment or diet. Homeostasis is expressed by the index H . Sterner and Elser proposed a model of stoichiometric homeostasis based on their theoretical derivation and studies, and this model is as follows [8]:

$$y = cx^{\frac{1}{H}} \quad (7)$$

where x is the content of the soil alkali–hydrolysable nitrogen or available P ($\text{mg} \cdot \text{kg}^{-1}$) in the topsoil at each sampling site, or N:P ratio; y means the contents ($\text{g} \cdot \text{kg}^{-1}$) of the total nitrogen (TN), total phosphorus (TP) in the plant leaf of the layers of the main communities at the sampling sites, or N:P ratio; c is the constant; and H is the plant’s homeostasis index. The significance test for the linear regression analysis is a one–sided test with $\alpha = 0.1$. It is defined as “absolute homeostasis” in $p > 0.1$; when p values are less than or equal to 0.1, the homeostasis is divided into four types, in accordance with the level of the homeostasis index H , i.e., “homeostatic” ($H > 4$), “weak homeostatic” ($2 < H < 4$), “weak sensitive” ($\frac{4}{3} < H < 2$) and “sensitive” ($H < \frac{4}{3}$) [71].

8. In this study, the C, N, P and K contents in plant leaf, litter and soil are expressed as mass contents and the stoichiometric ratios between the elements are used as mass

ratios. Excel 2013 and SPSS 22.0 were used for data processing and statistical analysis; Origin 2021 software was used for graphing. The data were tested for normality using the Kolmogorov–Smirnov test (K–S); the data were first log-transformed (i.e., $\ln(x + 1)$) in correlation analysis to be in line with the ANOVA assumption and normal distribution. The data were subjected to homogeneity of variance test when ANOVA test was performed, using the LSD method for normally distributed data with equal variances, or Tamhane’s T2 method for normally distributed data with unequal variances [72].

3. Results

3.1. C, N, P and K Contents in Leaf, Litter and Soil of Different Successional Communities

As shown in Table 2, the C and N contents of different community compositions in the growth and senescence phases are ordered as follows: plant layer (i.e., the leaves of HC, SC, SF and PF layers) > litter layer > soil layer, and there is a significant difference between the plant layer and the soil layer. The C content in communities of SF and PF decreases in the following order: shrub layer > tree layer > herbaceous layer, and the N content is measured the most in herbaceous layer and the least in tree layer, with an insignificant difference throughout. The P contents of different community compositions in HC and SC decrease in the following order: plant layer > litter layer > soil layer in their growth phase, but plant layer > soil layer > litter layer in the senescence phase, and the P content is highest in the herbaceous layer in SF and PF at all stages, followed by shrub layer, tree layer, soil layer and litter layer, in decreasing order. The K contents of different community compositions in HC and SC in all stages decrease in the following order: plant layer > soil layer > litter layer, and K content. This was the highest in the herbaceous layer and the lowest in the litter layer in SF and PF communities.

Table 2. Contents of carbon, nitrogen, phosphorus and potassium at different successional communities.

Content	Components	Successional Communities							
		Herbaceous Communities		Shrub Communities		Secondary Forest		Primary Forest	
		Growth Phase	Senescence Phase	Growth Phase	Senescence Phase	Growth Phase	Senescence Phase	Growth Phase	Senescence Phase
C (g/kg)	Tree layer	/	/	/	/	459.02 ± 7.69 aB	424.00 ± 9.83 aA	458.05 ± 11.92 aB	432.54 ± 8.05 aA
	Shrub layer	/	/	448.33 ± 26.38 a	458.07 ± 28.12 a	472.21 ± 17.07 a	449.72 ± 9.25 a	461.03 ± 5.03 a	432.42 ± 21.50 a
	Herb layer	467.94 ± 5.17 a	471.31 ± 5.4 aA	429.62 ± 47.16 a	423.92 ± 33.91 aAB	410.76 ± 28.75 a	388.66 ± 23.26 abAB	417.47 ± 10.21 aB	380.92 ± 4.58 bBA
	Litter layers	375.91 ± 7.80 bA	368.02 ± 20.68 aA	451.42 ± 7.29 aBB	344.62 ± 22.22 bABA	404.44 ± 23.68 aAB	316.32 ± 11.48 bBA	380.44 ± 19.45 aAB	317.78 ± 17.15 cBA
	Topsoil	50.39 ± 4.26 cA	50.39 ± 4.26 bA	62.25 ± 5.35 bB	62.25 ± 5.35 cB	68.46 ± 9.83 bBC	68.46 ± 9.83 cBC	77.36 ± 6.31 bC	77.36 ± 6.31 dC
N (g/kg)	Tree layer	/	/	/	/	17.28 ± 2.74 ac	15.79 ± 0.58 a	16.26 ± 1.31 ab	16.03 ± 1.24 ab
	Shrub layer	/	/	18.80 ± 1.43 a	19.14 ± 3.16 a	19.99 ± 0.85 a	20.52 ± 0.83 b	21.85 ± 1.46 a	20.76 ± 0.61 a
	Herb layer	16.25 ± 0.71 a	14.75 ± 0.72 aA	19.68 ± 5.49 a	17.49 ± 2.84 aAB	26.02 ± 3.62 b	23.64 ± 2.27 cB	24.27 ± 4.82 ab	22.37 ± 0.69 aB

Table 2. Cont.

Content	Components	Successional Communities							
		Herbaceous Communities		Shrub Communities		Secondary Forest		Primary Forest	
		Growth Phase	Senescence Phase	Growth Phase	Senescence Phase	Growth Phase	Senescence Phase	Growth Phase	Senescence Phase
P /(g/kg)	Litter layers	6.32 ± 1.38 bA	6.58 ± 1.71 bA	13.18 ± 3.86 aB	11.38 ± 2.76 bB	14.32 ± 2.01 cB	13.42 ± 1.08 dB	14.19 ± 0.96 bB	13.45 ± 0.90 bcB
	Topsoil	3.85 ± 0.24 cA	3.85 ± 0.24 cA	4.66 ± 0.36 bA	4.66 ± 0.36 cA	6.64 ± 0.70 dB	6.64 ± 0.70 eB	6.69 ± 0.99 cB	6.69 ± 0.99 cB
	Tree layer	/	/	/	/	1.48 ± 0.22 aB	1.00 ± 0.04 aA	1.50 ± 0.25 aB	1.02 ± 0.16 adA
	Shrub layer	/	/	1.97 ± 1.03	1.70 ± 0.84	1.57± 0.09 aB	1.18± 0.13 abA	1.55± 0.18 a	1.24± 0.12 a
	Herb layer	1.72 ± 0.23 a	1.55 ± 0.24 a	2.69 ± 1.79	2.41 ± 1.54	1.85 ± 0.44 a	1.70 ± 0.43 ab	2.02 ± 0.28 b	1.70 ± 0.26 b
	Litter layers	0.49 ± 0.07 b	0.37 ± 0.08 b	0.95 ± 0.47	0.63 ± 0.27	0.73 ± 0.02 bB	0.47 ± 0.01 bA	0.66 ± 0.06 c	0.49 ± 0.09 c
	Topsoil	0.45 ± 0.05 bA	0.45 ± 0.05 bA	0.72 ± 0.04 B	0.72 ± 0.04 B	0.94 ± 0.07 bC	0.94 ± 0.07 abC	0.97 ± 0.09 dC	0.97 ± 0.09 dC
	Tree layer	/	/	/	/	9.61 ± 1.96 a	7.51 ± 1.90 a	9.67 ± 1.24 a	7.67 ± 0.88 a
	Shrub layer	/	/	10.66 ± 3.25 a	8.09 ± 2.87 a	11.07 ± 1.02 a	8.51 ± 1.26 ab	13.18 ± 1.97 b	10.49 ± 1.60 b
	Herb layer	14.75 ± 1.19 aA	11.80 ± 1.83 aA	18.63 ± 3.46 bAB	16.83 ± 2.32 bB	21.16 ± 3.36 bB	20.72 ± 4.10 cB	22.93 ± 1.57 cB	21.90 ± 2.74 cB
K /(g/kg)	Litter layers	1.18 ± 0.06 bA	0.95 ± 0.14 bAC	1.37 ± 0.33 cAB	0.90 ± 0.28 cA	2.64 ± 0.42 cABB	1.81 ± 0.16 dBA	1.69 ± 0.11 dB	1.44 ± 0.37 dBC
	Topsoil	7.35 ± 1.57 a	7.35 ± 1.57 c	8.04 ± 0.71 a	8.04 ± 0.71 a	10.22 ± 0.73 a	10.22 ± 0.73 b	8.30 ± 0.72 a	8.30 ± 0.72 ab

Note: The use of different small letters denotes a significant difference between different compositions of the same community in the same growth stage; different capital letters denote a significant difference between different communities with the same composition and in the same growth stage; different capital letters in italics denote a significant difference between different growth stages in the same community and with the same composition ($p < 0.05$).

Along with the vegetation succession (from HC to PF), the C and K contents in the leaves of the main layers (HC herbaceous layer, SC shrub layer, SF and PF tree layer) in each plant community show a declining trend in the growth and senescence phases, while the N and P contents first show a rising trend and then a declining trend. The C content in the litter layer first rises and then declines in the growth phase, with a significant difference between HC and SC, and decreases in the senescence phase. The N content shows a rising trend in all stages, with a significant difference between HC and other successional communities. The P and K contents first rise and then decline in all stages, and P is highest in SC while K is highest in SF. The C, N and P contents in the soil layer of the communities decrease in the following order: PF > SF > SC > HC, with a significant difference between HC and other successional communities. K content decreases in the following order: SF > PF > SC > HC, with an insignificant difference throughout.

Basically, the C, N, P and K contents in the tree, shrub, herbaceous and litter layers of the communities at all phases are higher in the growth phase than in the senescence phase, with a significant difference in the C and P contents in the tree layer of SF and PF, in the C

content in the litter layer of SC, SF and PF, the P content in the shrub layer and the P and K contents in the litter layer of SF, at all phases.

3.2. Stoichiometric Characteristics of C, N, P and K in Leaf, Litter and Soil of Successional Communities

The C:N, C:P, C:K, N:P and N:K ratios in different compositions of each community decrease in the following order at both growth and senescence phases: litter layer > plant layer > soil layer (the C:N ratio is the highest in the tree layer except that in SF and PF), with a significant difference in-between. The C:P and C:K ratios at different community compositions for SF and PF are notably higher in the tree layer and the shrub layer than in the herbaceous layer at all growth stages, while the N:P and N:K ratios are the highest in the shrub layer (Figure 2a–e). The K:P ratio in different compositions of the communities HC and SC decrease in the following order at all growth stages: soil layer > plant layer > litter layer, with a significant difference between the soil layer and the litter layer; both the plant layer and the soil layer have a higher K:P ratio than the other layers in the SF community. The K:P ratio in community PF decreases in the following order at all the growth stages: plant layer > soil layer > shrub layer > tree layer > litter layer (Figure 2f).

As vegetation succession proceeds, the C:N, C:P and K:P ratios in the plant leaves of the main layers in each community vary in a “V” pattern, the C:K and N:K ratios vary in a reversed “V” pattern, and the N:P ratio rises at all growth stages. In the litter layer of different communities, the C:N ratio declines at all growth stages, but the C:P ratio first declines and then increases without a significant difference. However, the C:K and N:K ratios show an “N”-pattern variation, with a significant difference between SC and both SF and PF, and the N:P ratio rises without a significant difference in-between. Interestingly, the K:P ratio varies in a reverse “N” pattern, with a significant difference between SC and other communities. In the soil layer of different communities, the C:N ratio is higher in HC and SC than in SF; the HC community has a higher C:P ratio than other communities. Moreover, the HC and SF communities have a much lower C:K ratio than PF. As vegetation succession proceeds, the N:P ratio first decreases and then increases, and then decreases with an insignificant difference among communities. The N:K ratio and the K:P ratio display the opposite trend, suggesting a significant difference between PF and other communities.

In terms of different growth stages, the C:N ratio in the different compositions (herbaceous layer excluded) of each community shows a higher result in the growth phase than in the senescence phase, yet the C:P, C:K, N:P, N:K and K:P ratios (N:K ratio in the plant layer and K:P ratio in the shrub layer excluded) show the opposite trend.

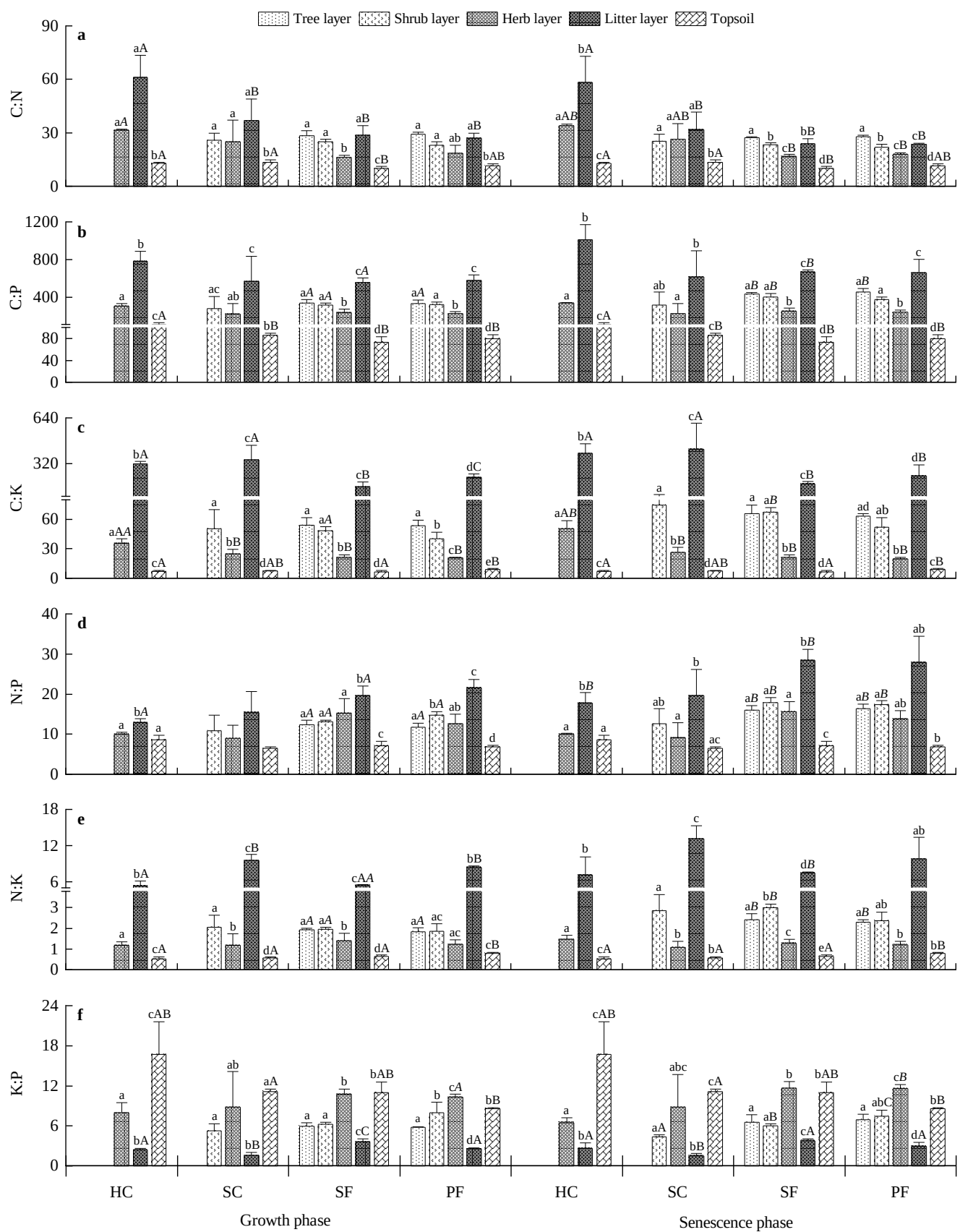


Figure 2. Stoichiometric Characteristics of Carbon, Nitrogen, Phosphorus and Potassium at Different Successional Communities. The abbreviations HC, SC, SF and PF represent herbaceous communities,

shrub communities, secondary forest communities and primary forest communities, respectively. (a–f) represent C:N, C:P, C:K, N:P, N:K and K:P, respectively. By the different small letters, it means there is significant difference between different compositions of the same community and in the same growth stage; by different capital letters, it means there is significant difference between different communities but the same composition and in the same growth stage; and by different capital letters in italics, it means there is significant difference between different growth stages but in the same community and in the same composition ($p < 0.05$).

3.3. Correlation of C, N, P and K Contents in Leaf, Litter and Soil and Their Stoichiometric Characteristics

According to Figure 3, the correlation between the main element content and the stoichiometric characteristics of the plant leaf–litter–soil continuum at the main levels of each succession community varies with the growth stage. The C content, C:N, N:P, N:K and K:P between plant leaves and litters showed significant or extremely significant ($p < 0.01$) positive correlations in the senescence phase; the P content and C:P and N:P also showed a significant or extremely significant ($p < 0.01$) positive correlation in the growth phase. There was no significant correlation between the N and K content and C:K at different growth stages. The P content between plant leaves and soil showed a significant negative correlation in the senescence phase, while there was a significant or extremely significant ($p < 0.01$) positive correlation between the leaf N:P and soil N and P contents in the senescence phase. However, there was a significant or extremely significant negative correlation between plant leaf K content and soil P content at different growth stages. The N and K contents of litter were positively associated with the N and K contents of soil at different growth stages ($p < 0.01$), while there was a significant or extremely significant ($p < 0.01$) negative correlation between C:N in litter and C, N, P in soil at different growth stages. Interestingly, there was no significant correlation of P content between litter and soil at different growth stages.

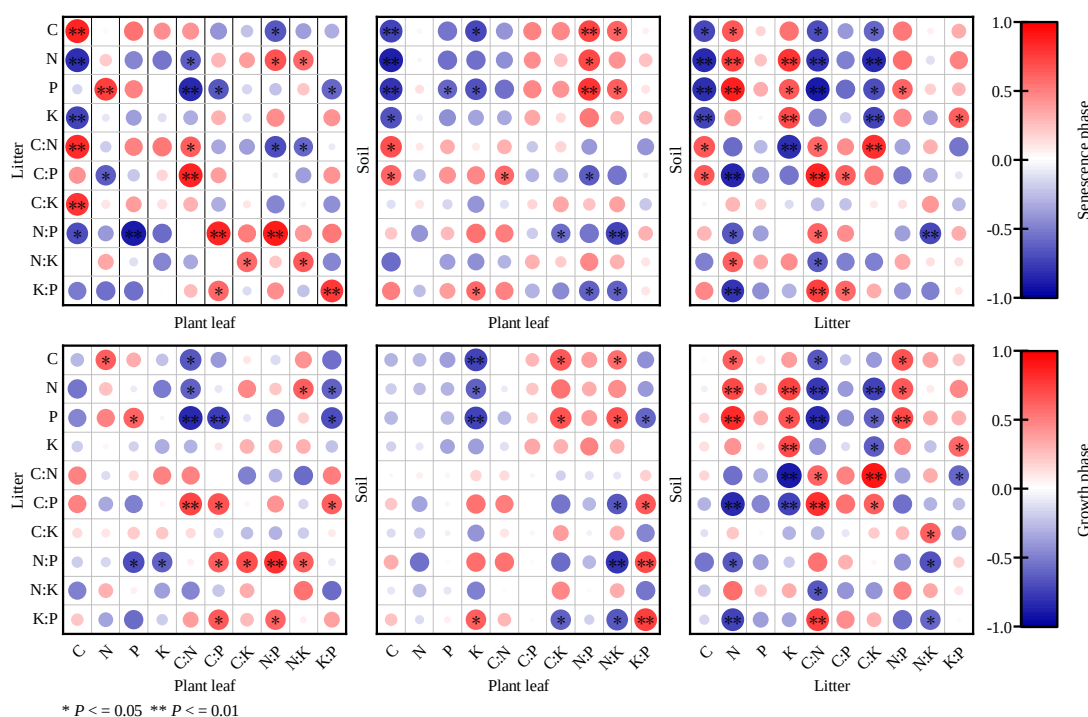


Figure 3. Correlation of C, N, P and K contents in plant leaf, litter and soil and their stoichiometric characteristics during vegetation succession. The scale on the right represents the size of the correlation coefficient, while red represents a positive correlation, and blue represents a negative correlation; the larger the circle, the stronger the correlation.

3.4. N and P Use Efficiency and Nutrient Resorption Efficiency of Plants in Successional Communities

As vegetation succession proceeds, the nitrogen (N) use efficiency in plant leaves of the main layers in each community declines first and then increases at growth and senescence phases, with a significant difference between HC, SF and SC in the senescence phase (Figure 4). The phosphorus (P) use efficiency shows an increasing trend but there is no significant difference. At different growth stages, the N- and P-use efficiency of each community in the senescence phase is higher than that in the growth phase, and SF and PF communities show a significant difference in P-use efficiency at different growth stages. Furthermore, the P-use efficiency of each community at the same growth stage is significantly higher than the N-use efficiency.

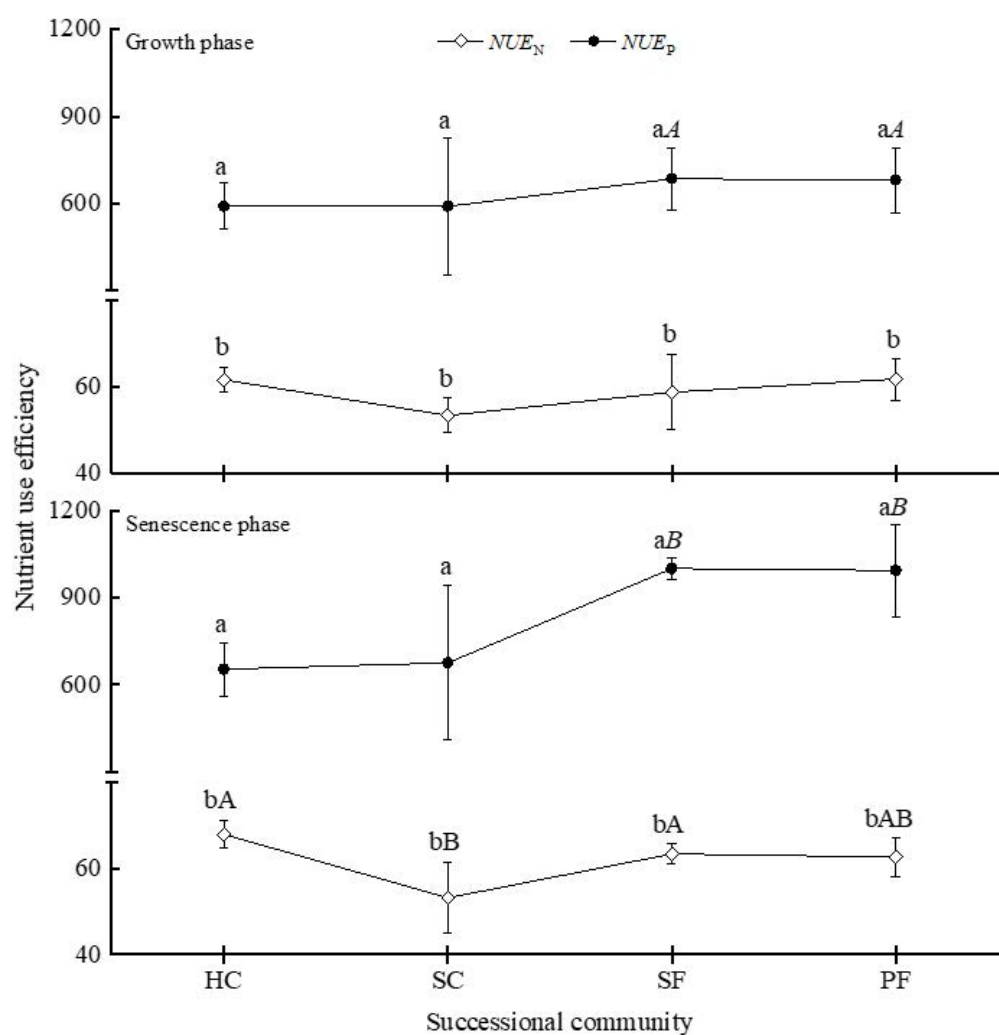


Figure 4. The N- and P-use efficiency of different successional communities. The abbreviations HC, SC, SF and PF represent herbaceous communities, shrub communities, secondary forest communities and primary forest communities, respectively. The subscript “N” in NUE_N refers to the nitrogen (N)-use efficiency, and the subscript “P” in NUE_P refers to the phosphorus (P)-use efficiency. The different small letters denote a significant difference between N- and P-use efficiency of the same community and in the same growth stage; different capital letters denote a significant difference between different communities with same nutrient elements and at the same growth stage; different capital letters in italics denote a significant difference between different growth stages with the same nutrient element and in the same community ($p < 0.05$).

As vegetation succession proceeds, the resorption efficiency of nitrogen (N) and phosphorus (P) in plant leaves of the main layers in each community declines at all growth stages, with a significant difference between HC, SC and PF in the senescence phase (Figure 5). The N resorption efficiency of HC and SC communities in the growth phase is higher than that in the senescence phase, but the N resorption efficiency of SC and PF communities in the senescence phase is higher than that in the growth phase. Except PF community, other communities have a higher P resorption efficiency in their senescence phase than in their growth phase but there is no statistical difference. Further, the P resorption efficiency of each phase community in the same growth stage is significantly higher than the N resorption efficiency, and this is especially significant in PF in the growth phase and SC and PF communities when in their senescence phase.

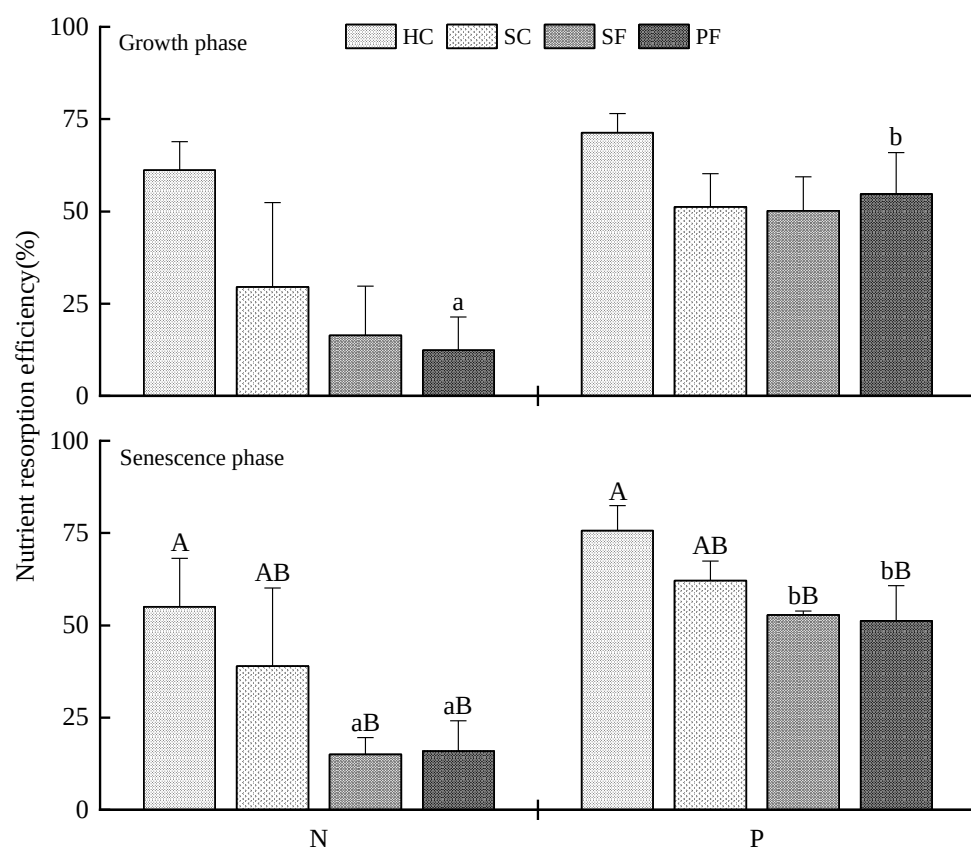


Figure 5. The N- and P-resorption efficiency of different successional communities. The abbreviations HC, SC, SF and PF represent herbaceous communities, shrub communities, secondary forest communities and primary forest communities, respectively. The different small letters denote a significant difference between the N- and P-resorption efficiency of the same community in the same growth stage; different capital letters denote a significant difference ($p < 0.05$) between different communities with the same nutrient element and in the same growth stage.

3.5. Allometric Relationships of Nutrient Contents in Plant Leaves during Vegetation Succession

The allometric relationship between the C, N, P and K contents in the plant leaves in the main layers of each successional community during vegetation succession differs to a certain extent during the growth and senescence phases, indicating the different strategies used to balance nutrient absorption and use by plants at different growth stages (Table 3). Specifically, a significant positive linear correlation was found between the C and P contents in the senescence phase and the N and P contents in the growth phase, showing a significant allometric relationship ($C-P^{0.170}$, $R^2 = 0.415$, $p = 0.024 < 0.05$; $N-P^{0.411}$, $R^2 = 0.365$, $p = 0.037 < 0.05$) as the allometric scaling exponents were below 1; however, the P and K contents show an isometric relationship at all growth stages (in the growth

phase, $P-K^{0.992}$, $R^2 = 0.397$, $p = 0.028 < 0.05$; in the senescence phase, $P-K^{1.110}$, $R^2 = 0.452$, $p = 0.017 < 0.05$). No significant allometric relationship was reached between the contents of the other nutrient elements. Further, no significant difference in the allometric scaling exponents (slope heterogeneity) was found in the pairs of C–N, C–P, C–K, N–P, N–K and P–K at different growth stages.

Table 3. Allometric relationships between leaf C, N, P, and K contents at different successional communities.

$\log y$ vs. $\log x$	Growth Stage	<i>n</i>	Slope <i>b</i> [95% Confidence Interval]	Elevation <i>a</i> [95% Confidence Interval]	Determination Coefficient (<i>R</i> ²)	<i>p</i>	Common Slope <i>b</i> [95% Confidence Interval]	Slope Hetero- geneity (<i>p</i>)
$\log C$ vs. $\log N$	Growth phase	12	−0.321 [−0.619, −0.167]	3.057 [2.778, 3.336]	0.000	0.958	0.371 [0.235, 0.585]	0.528
	Senescence phase	12	0.425 [0.224, 0.807]	2.134 [1.780, 2.488]	0.052	0.475		
$\log C$ vs. $\log P$	Growth phase	12	0.132 [0.069, 0.254]	2.634 [2.610, 2.657]	0.004	0.853	0.155 [0.103, 0.230]	0.527
	Senescence phase	12	0.170 [0.101, 0.284]	2.633 [2.617, 2.648]	0.415	0.024 *		
$\log C$ vs. $\log K$	Growth phase	12	0.131 [0.068, 0.251]	2.525 [2.430, 2.621]	0.022	0.646	0.161 [0.104, 0.247]	0.405
	Senescence phase	12	0.188 [0.105, 0.337]	2.475 [2.366, 2.583]	0.237	0.108		
$\log N$ vs. $\log P$	Growth phase	12	0.411 [0.241, 0.703]	1.147 [1.092, 1.201]	0.365	0.037 *	0.406 [0.279, 0.590]	0.930
	Senescence phase	12	0.400 [0.229, 0.696]	1.173 [1.133, 1.213]	0.313	0.058		
$\log N$ vs. $\log K$	Growth phase	12	0.408 [0.214, 0.777]	0.810 [0.516, 1.103]	0.041	0.526	0.425 [0.270, 0.669]	0.849
	Senescence phase	12	0.443 [0.230, 0.855]	0.801 [0.508, 1.095]	0.000	0.952		
$\log P$ vs. $\log K$	Growth phase	12	0.992 [0.588, 1.674]	−0.820 [−1.385, −0.254]	0.397	0.028 *	1.052 [0.739, 1.497]	0.743
	Senescence phase	12	1.110 [0.673, 1.830]	−0.931 [−1.472, −0.390]	0.452	0.017 *		

*: $p < 0.05$.

3.6. Characteristics of Homeostasis of Leaf N and P Contents and N:P Ratio in Vegetation Succession

According to the threshold [71] determined by Jonas Persson et al. for the homeostasis index (*H*), with the variation in the available N and P contents and N:P ratio in soil during the vegetation succession, no significant linear correlation was found using the homeostasis model ($p > 0.1$, Figure 6) between the N content in leaf at all growth stages, N:P ratio in the growth phase and the P content in the senescence phase. The homeostasis index (*H*) was “absolute homeostatic”. However, a significant linear correlation ($p < 0.1$) was found between the P content in leaf in the growth phase and N:P ratio in the senescence phase. The homeostasis index *H* was 1.622 for the leaf P content in the growth phase, falling into the type of “weak sensitive”; the homeostasis index *H* was 2.660 for N:P ratio in the senescence phase, falling into the type of “weak homeostatic”. In terms of the different nutrient elements, homeostasis between the N content and N:P ratio in leaf in the growth phase was much more significant than the P content, while the homeostasis of the N and P contents in leaf in the senescence phase was more significant than that of N:P ratio. In terms of the different growth stages, the homeostasis of the N and P contents in leaf in the

senescence phase was more significant than that in the growth phase, while the opposite was found in the case of the N:P ratio.

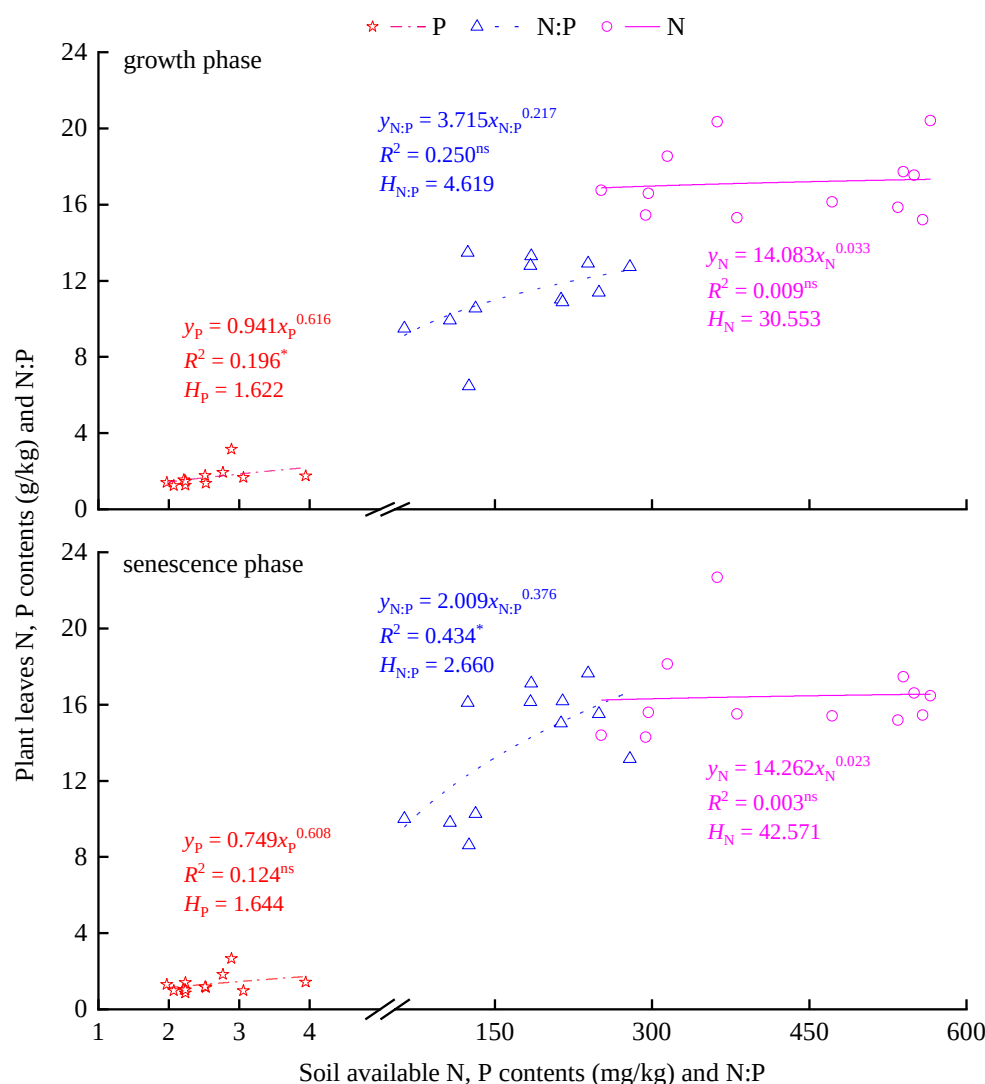


Figure 6. Relationship between available N and P contents and N:P ratio in soil and that in plant leaves. *: $p \leq 0.1$, ns: $p > 0.1$.

4. Discussions

4.1. Vegetation Succession Influence on C, N, P and K Contents in Leaf, Litter and Soil

Due to differences in genetic factors and habitats, plants can autonomously regulate their demand for specific nutrient elements [73], resulting in the selective absorption of nutrients by different phylogenetic plants. The competition and turnover of species within the community determines the direction of vegetation succession [74]; as succession proceeds, the dominant species in the plant community gradually shifts from grass to shrub and tree, and the community structure tends to be more complex, with clearer hierarchical classification and more complete ecosystem functions [44], which also leads to differences in the quantity and quality of the litter and its decomposition process. This affects the quality of the soil environment [56]. In this study, the C, N, P and K contents of plant leaves at different layers of the successional communities varied with succession, mainly because different plant communities have different mechanisms of adaptation to the environment, resulting in different nutrient demand strategies [42]. The C content in the leaves of both tree and shrub layers in the same successional community is higher than

that of the herbaceous layer, mainly because woody plants' can synthesize and accumulate more organic matter than herbs, resulting in a higher C content in the body [75].

Except for the SC shrub layer, the N content of plant leaves in the main layers of the successional communities basically tended to increase with succession at all growth stages, while the P content was the opposite (Table 2), which is basically consistent with the results of the Changbai Mountains [76] and the Loess Plateau [42]. This may be because, with vegetation succession, the biomass of the community gradually increases, prompting plants to require more N-rich substances to participate in their metabolic activities and resulting in an increase in their N absorption and, thus, a higher N content [56]. This may also be related to the gradual increase in N content in soil with the progress of succession (Tables 2 and 4). In contrast, compared to the diverse sources of N in soil [77], element P in soil comes mainly from the weathering and leaching of rocks, which is difficult for the plants to use [78]. In addition, element P is more difficult to mineralize and release than N [27]; as succession proceeds, the P content available for the plant to use gradually decreases (this is also evidenced in Table 4), making the P content in leaves decrease. The K content in the leaves of plants in the main layers of the different successional communities tends to decrease with the succession at all growth stages, which may be related to the plants' drought resistance [16,17].

Table 4. Soil-available N, P content and N:P.

Successional Community	Soil-Available Nitrogen/(mg/kg)	Soil-Available Phosphorus/(mg/kg)	AN:AP
Herbaceous communities	280.68 ± 25.40 A	2.98 ± 0.87	100.86 ± 34.41
Shrub communities	409.00 ± 124.67 AB	2.46 ± 0.46	176.22 ± 88.96
Secondary forest	472.96 ± 92.30 B	2.45 ± 0.54	193.96 ± 16.64
Primary forest	544.24 ± 12.36 B	2.33 ± 0.16	234.36 ± 17.84

Note: Capital letters indicate significant differences between different successional communities ($p < 0.05$).

The nutrients of litter originate directly from the leaves and their concentration is influenced by the dominant plants in the community and the litter composition [56]. Variation in vegetation types can significantly affect the stoichiometric characteristics of the litter [79]. In this study, the N content tends to increase at different growth stages, while the P content shows an increase followed by a decrease (Table 2). This is not only related to the different compositions of the litter in the successional communities [56], but is also influenced by the N and P nutrient resorption efficiency: a lower N and P nutrient resorption efficiency for SF and PF results in higher N and P contents in litter than in HC. The distribution of plant roots also shows that trees and shrubs usually have deeper roots and a stronger capacity to absorb nutrients from different sources in the environment, while herbaceous plants have shallower roots and rely more on their own nutrient recycling [42]. Some other researchers also suggested that the litter follows the plants' characteristics to maintain the variation in the N and P contents in the plants [21,30,52,80].

In this study, the C content of the plant leaves at different layers of the successional communities is higher than that of the litter (Table 2), which may be related to the litter decomposition [81]. The N, P and K contents are also higher in the plant leaves than in the litter, which is mainly related to the nutrient resorption characteristics [9,10,20,42]. This is a nutrient-use strategy for plants to improve nutrient utilization and adaptation to the environment. Additionally, the plant leaves consume a large amount of N in the process of photosynthesis, and transferring a high proportion of N also reduces the N content in the litter [82]. After falling to the soil, the litter is transformed into soil organic matter through microbial decomposition, during which a large amount of C, N and P in the organic state is mineralized and decomposed, resulting in lower C, N and P contents in soil than in plant leaves and litter [83].

4.2. Vegetation Succession Influence on Stoichiometric Characteristics of C, N, P and K in Leaf, Litter and Soil

The C:N and C:P ratios of leaves reflect the plants' growth rate and their nutrient use efficiency [24,25]. Lower C:N and C:P ratios mean a higher growth rate and lower N- and P-nutrient use efficiency [84]. To some extent, these ratios can also reflect the availability of N and P elements in the soil [30]. In this study, with the exception of the SC shrub layer, the C:N ratio of the plant leaves at all major layers of the successional community basically tend to decrease with succession at all growth stages, while the C:P ratio tends to increase, indicating that the nitrogen-use efficiency decreases and phosphorus-use efficiency increases with succession (also shown in Figure 4). In contrast, Bowman's study concluded that plants tend to have high nutrient-use efficiency when nutrients are in short supply, which is a survival strategy helping the plants to adapt to the fragile environments [85], while their nutrient-use efficiency is lower when nutrients are in sufficient supply. This also suggests that nitrogen in the area is relatively abundant, while phosphorus (especially the available P) is insufficient. The higher N and P contents and lower C:N and C:P ratios in the leaves of the SC shrub layer are a nutrient-use strategy in response to the changes in species composition and community structure throughout the community succession process, and are also a reflection of the "growth rate" theory.

The C:N ratio in litter is an important factor, affecting its decomposition rate and nutrient return, and a lower C:N ratio leads to a higher rate of litter decomposition [86]. In this study, with succession, the C:N ratio in litter shows a decreasing trend at different growth stages (as in Figure 2), which is consistent with Yu Yuefeng et al.'s study result [80], indicating that, during the vegetation succession process, the decomposition rate of litter in each successional community gradually accelerates, which is conducive to accelerating nutrient return to the soil and enabling the plants to obtain more nutrients from the soil. This also explains why the N- and the P-resorption efficiency of each successional community gradually decreases as succession progresses, i.e., in the middle and late stages of succession, plants may mainly rely on nutrient absorption from the soil rather than increasing their nutrient resorption to meet their own growth needs. The C:N, C:P and N:P ratios in soil are lower than those in leaf and litter, which is mainly determined by the different ecological functions they perform and is related to the fact that the plants absorb C, N and P nutrients from the soil in a selective manner [81].

4.3. Correlation of Leaf–Litter–Soil C, N, P and K Contents and Stoichiometric Ratios

The correlation between the leaf–litter–soil C, N, P and K contents and their stoichiometric characteristics can reveal the coordination between the various indicative variables of different compositions of the successional communities, and help to provide a reasonable explanation of the coupling process between nutrient elements [81]. Studies have shown that there is a strong correlation between plant leaves and soil nutrient content [13,76,87]. Some studies also suggested that there is no significant correlation between plant leaves and the N and P contents in soil [9,42,79]. In this study, no significant correlation was found between leaves and soil regarding the N content at different growth stages, nor was there any significant correlation between leaves and soil regarding the P content during the growth phase (Figure 3). This result may be related to the karst habitat, where the soil is sparse, shallow and mostly stored in rock crevices, and plant roots are directly interspersed and forced to absorb certain excessive elements from the weathered rocks, proving that there is no significant correlation between plants and soil regarding the N and P contents [88]. The long-term adaptation of plants to habitats in this area may also make them more inclined toward differences in species traits or plant functional types, while environmental factors have less influence. In this study, a significant or extremely significant ($p < 0.01$) positive correlation was found between the N:P ratio in the leaves and the N and P contents in the soil during the senescence phase. However, this correlation was found to be insignificant in the growth phase. This result is consistent with that concluded by Huang Juying et al.; i.e., the relationship between the stoichiometric characteristics of

plant leaves and soil nutrient contents may correlate with the plant's growth stage to some extent [89]. In addition, a significant or extremely significant ($p < 0.01$) negative correlation was found between the K content in leaf and the P content in soil at different growth stages, which may be because the plants in the area selectively take up more potassium to improve their resistance as a response to the deficiencies in available phosphorus in soil.

In this study, a significant or extremely significant ($p < 0.01$) positive correlation was found between the plant leaves and the litter regarding the C content, and the ratios of C:N, N:P, N:K and K:P in the senescence phase. Similarly, the positive significance was also found that P content, the ratios of C: P and N: P between the plant leaves and the litter in the growth phase. Therefore, the correlation indicate an inherited relationship between the plant leaves and the litter. However, no significant correlation was found between the plant leaves and the litter regarding the N and K contents and the C:K ratio at different growth stages, indicating that the decomposition rate of the litter in this area is faster and the degree of decomposition is higher. In addition, a significant or extremely significant ($p < 0.01$) negative linear correlation was found between the C:N ratio in the litter and the C, N and P contents in the soil, but a significant or extremely significant ($p < 0.01$) positive linear correlation was found between the C:N ratio in the litter and the C:N and C:P ratios in the soil, indicating that the soil nutrient contents are limited by the litter. There is no significant correlation between the litter and the soil regarding the P content. This is because P in the soil is not only derived from the litter, but also from the mineral compositions of the soil-forming parent material [80].

In general, the correlation presented between the leaf–litter–soil nutrient contents and stoichiometric characteristics indicates that the cycling of nutrient elements such as C, N, P and K within the ecosystem is completed by means of transporting and transforming them amidst the three pools, i.e., the plants, the litter and the soil [90]. To some extent, this cycling reflects the inheritance and co-variation among the nutrient elements [52]. The weaker coupling relation between some of the elements indicates that the nutrient conversion among the leaves, the litter and the soil has its own intensity, rather than simply being a complete inheritance [91]. This reveals the differences in the strategies that different species in the community use to adapt to the nutrient-poor environment and the plants' resilient adaptation mechanism to environmental changes [85].

4.4. Vegetation Succession Influence on Plant Leaf Homeostasis and Nutrient Use Strategies

Plants adapt to such variations in soil N and P contents by regulating their stoichiometric characteristics and nutrient-use strategies [80,92]. Studies show that the N content in plants is more stable than the P content [93], because the N content is mainly subject to biotic factors, whereas P content is subject both to biotic and abiotic factors [94]. In this study (Figure 6), the homeostasis of the N content in plant leaves at different growth stages is stronger than that of the P content, providing further evidence for the above result. Han et al. proposed the stability of the limiting elements hypothesis through an integrated analysis of the contents of 11 mineral elements in Chinese plants. As the hypothesis says, the contents of limiting elements, constrained by plant physiology and nutrient balance, are relatively stable in plants, and their response to environmental changes is also stable [95]. The homeostasis of different elements in plants at different growth stages may also reflect the nutrient element limitation at a specific phase [96]. In this study, the N content of plant leaves was tested to be of "absolute homeostasis" and the P content was "weak sensitive" during the growth phase, while the N and P contents of plant leaves were of "absolute homeostasis" during the senescence phase. This indicates that plants in this area are mainly limited by N during the growth phase, while those in the senescence phase are limited by both N and P. This conclusion is generally consistent with that of the N:P ratio threshold [97] proposed by Koerselman et al. From another perspective, this is also consistent with the ecological stoichiometry theory of "homeostasis" [96,98].

The allometric relationship among the chemical elements combining the plants' nutrient use efficiency and nutrient resorption efficiency can reflect the plants' ways of adapting

to environmental changes [56]. In this study (Figure 5), the N- and P-resorption efficiency ranged from 12.35% to 61.14% and from 50.12% to 71.31%, respectively, during the growth phase, and from 15.07% to 55.06% and from 51.19% to 75.69%, respectively, during the senescence phase. Within these ranges, successional communities other than HC have a lower N-resorption efficiency than global (50.3% [99] and 56.3% [100]) and national average levels (49.1% [101]) at different growth stages. The P-resorption efficiency tested in this study was approximately the same as the global (52.2% [99] and 56.9% [100]) and national averages (51.0% [101]). By comprehensively understanding the limiting factors for nutrients in each successional community at different growth stages [65], we found that the P resorption efficiency is much higher than the N resorption efficiency for communities limited by N at all growth stages. This result is basically consistent with the research result of Yan Enrong et al., i.e., vegetation limited by N (or P) elements does not necessarily have a higher N (or P)-resorption efficiency, and this cannot be simply deduced from the low nutrient content in a plant's leaves, the fact that its habitat is undersupplied with the relevant nutrient, or the fact that the vegetation has a higher resorption efficiency for that element [102]. This also suggests that the higher N and P resorption efficiency in the vegetation may not necessarily be an adaptive mechanism for the plants to cope with N and P nutrient stress, but may be an inherited species trait, influenced by genetic differences in plants [103].

The studies of Bridgham et al. showed that, to a certain extent, plants' nutrient-use efficiency increases as the soil nutrient effectiveness decreases [104]. On the other side, a higher nutrient-use efficiency indicates that plants can produce more biomass through lower nutrient absorption and retention. This is an important strategy, allowing for plants to adapt to the low nutrient content in soil [56]. In this study, the available P content in the soil gradually decreased as succession progresses, while the P-use efficiency of plant leaves in the main layers of each successional community tended to increase at different growth stages, indicating that plants in this area maintain a relatively stable level of this element under low phosphorus stress, and that they maintain this relative stability to ensure their normal physiological and biochemical responses by increasing the P-use efficiency of the leaves. In addition, factors such as the duration of leaf abscission (or leaf longevity), soil moisture, altered source-sink relationship, topographic conditions and the secondary metabolic processes within the plant also have a significant influence on plant nutrient-use efficiency, and plants themselves have a system of adaptation strategies, which may be the same as or different from each other, in response to environmental stress [105].

5. Conclusions

With the vegetation succession, the nutrient contents of plant leaves-litter-soil and the stoichiometric ratios of the chemical elements of the main layers of each community vary at different growth stages, i.e., the nutrient contents of the plant leaf and litter of different layers of each successional community are higher in the growth phase than in the senescence phase, while the stoichiometric ratios of the chemical elements are reversed (except for the C:N ratio). The correlation between the main element content and the stoichiometric characteristics of the plant leaf-litter-soil continuum at the main levels of each succession community varies with growth stage. Along with the vegetation succession, plant leaves in the main layers of each community show a decreasing and then increasing trend in the use-efficiency of N, an increasing trend in the use-efficiency of P, and a decreasing trend in the resorption-efficiency of N and P at different growth stages. During the process of vegetation succession, plant leaves show a significant allometric relationship between N and P at the growth phase, and the allometric indicator is 0.411. The homeostasis in the N content of plant leaf is higher than that in the P content at different growth phases, while the homeostasis in the N and P contents of plant leaf is higher at the senescence phase than at the growth phase. The opposite is true for the stoichiometric ratios of N:P. In general, vegetation succession significantly influences the nutrient contents and their stoichiometric ratios in plant leaf, litter and soil in karstic areas. Their interactive and

coupling relationships reflect, to some extent, the inheritance and covariation between nutrient contents, but the variation in this correlation indicates that the leaf, litter and soil nutrients' conversion also varies, rather than simply being inherited, which reflects the variability in different species in the plant communities' adaptation strategies to the fragile karst environment. During the process of vegetation succession, plants in the studied area mainly adapt to the low phosphorus stress in the soil by increasing the use-efficiency of P to ensure normal physiological and biochemical responses.

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