

137. Jahrgang (2020), Heft 2, S. 109-132

**Austrian Journal of  
Forest Science**

---

**Centralblatt**  
für das gesamte  
Forstwesen**Stoichiometric characteristics of ecological-economic forests in karst rocky desertification areas of southern China****Stöchiometrische Eigenschaften von verkarsteten Öko-ökonomischen Wäldern in Südchina**Yu Zhang<sup>1</sup>, Kangning Xiong<sup>\*</sup>, Yao Qin<sup>1</sup>, Yanghua Yu<sup>1</sup>, Tingling Li<sup>1</sup>

**Keywords:** *karst; plantations; afforestation, biogeochemistry; litter, soil, Eucalyptus robusta, Cupressus funebris, Eriobotrya japonica, Zanthoxylum bungeanum, Juglans regia*

**Schlüsselbegriffe:** *Karst, Aufforstungen, Wiederbewaldung, Streu, Boden, Biogeochemie; Eucalyptus robusta, Cupressus funebris, Eriobotrya japonica, Zanthoxylum bungeanum, Juglans regia*

**Abstract**

Investigating the eco-stoichiometric characteristics of carbon (C), nitrogen (N), and phosphorus (P) in plants, leaf litter, and soil of revegetated forests in areas of karst rocky desertification can improve our understanding of nutrient cycling and stability of karst ecosystems. In this paper, we selected five forest types typical for South China karst regions to study the stoichiometry of C, N, and P, and their internal correlation with the "plant leaf-litter-soil continuum". The five forest types were Chinese weeping cypress (*Cupressus funebris* Endl.) mixed with Eucalyptus (*Eucalyptus robusta* Smith), loquat (*Eriobotrya japonica* (Thunb.) Lindl.), Chinese prickly ash (*Zanthoxylum bungeanum* Maxim.), walnut (*Juglans regia* Linn.), and teak (*Tectona grandis* Linn. f.). The average C, N, and P contents in the leaves of the five species were 481.66, 14.68,

---

<sup>1</sup> School of Karst Science, Guizhou Normal University / State Engineering Technology Institute for Karst Desertification Control, Guiyang, 550001, China

<sup>\*</sup>Corresponding author: Kangning Xiong, hxcandzy@163.com

and 2.23 mg g<sup>-1</sup>, respectively; in leaf litter 434.52, 9.22, and 1.70 mg g<sup>-1</sup>, and in soil 36.74, 2.85, and 0.64 mg g<sup>-1</sup>. The vegetation of the eco-economic forest in the karst area was low in N, rich in P, and had a relatively high C storage. The order of C:N ratios was leaf litter > plant leaf > soil for all forests, except for the teak forest. No statistically significant difference was observed in soil C: N ( $P > 0.05$ ). N and P content in plant leaves was significantly positively correlated with that in leaf litter ( $P < 0.05$ ), although the reabsorption rate of N and P was relatively low. The reabsorption rate may not be an important adaptation mechanism to plant nutrient limitation, but appears to be an intrinsic characteristic of the studied species. Productivity was not correlated with C, N, or P in plant, litter, and soil and was probably influenced by other factors than nutrient supply. The grade of rocky desertification strongly affected the C storage. For our study region we estimated a potential C sequestration in litter alone of 3748 t C (in decreasing order, the potential, mild, moderate, and severe rock desertification areas contributed 1220.40 t, 1566.87 t, 556.60 t, and 403.59 t). This study contributes to our understanding of nutrient uptake and utilization of nutrients by tree species in karst areas and provide a theoretical basis for vegetation restoration and reconstruction to control karst rocky desertification.

### Zusammenfassung

Eine Untersuchung der stöchiometrischen Eigenschaften von Kohlenstoff (C), Stickstoff (N) und Phosphor (P) in Pflanzen, Streu und Böden von rekultivierten Wäldern in einem ökologisch fragilen, zum Karst verwüsteten, felsigen Gebiet ermöglicht ein besseres Verständnis deren Nährstoffkreisläufe. In dieser Studie haben wir fünf Waldtypen des südchinesischen Karst ausgewählt, Zypresse (*Cupressus funebris* Endl.) gemischt mit Eukalyptus (*Eucalyptus robusta* Smith), japanische Mispel (*Eriobotrya japonica* (Thunb.) Lindl.), Szechuan-Pfefferbaum (*Zanthoxylum bungeanum* Maxim.), Walnuss (*Juglans regia* Linn.) und Teak (*Tectona grandis* Linn. f.). Es zeigte sich, dass der durchschnittliche Gehalt von C, N und P in der Laubmasse der fünf Pflanzen 481.66, 14.68 und 2.23 mg g<sup>-1</sup> war, in der Laubstreu 434.52, 9.22, und 1.70 mg g<sup>-1</sup> und im Boden 36.74, 2.85 und 0.64 mg g<sup>-1</sup>. Die Vegetation dieser Wälder war somit arm in N, reich an P und zeigte eine relativ hohe Kapazität für C-Speicherung. Das C:N Verhältnis war in der Reihenfolge Laubstreu > Pflanzenblatt > Boden, außer für den Teak Wald. Wir fanden keine statistische Signifikanz in den C:N-Verhältnissen in den Böden ( $P > 0.05$ ). Der Gehalt von N und P in den Blättern war signifikant positiv korreliert mit C und N in der Laubstreu ( $P < 0.05$ ). Die Reabsorptionsrate von N und P war relativ gering und offensichtlich ist die Reabsorptionsrate in einem Karst-Milieu kein wichtiger Mechanismus zur Anpassung an den Nährstoffbedarf von Pflanzen. Die Reabsorptionsrate scheint hingegen ein inhärentes Merkmal der untersuchten Baumarten zu sein. Produktivität hatte keinen Zusammenhang mit C-, N- und P-Gehalt und steht offensichtlich unter dem Einfluss anderer Faktoren. Die Kohlenstoffspeicherung wirdentscheidend vom Grad der Verkarstung beeinflusst. Schätzungen der potenziellen Kohlenstoffreserven in der Streu sind 3748 t für das Untersuchungsgebiet (in absteigender Reihenfolge potenzielle, milde, mäßige und schwere Verkarstung 1220.40

t, 1566.87 t, 556.60 t und 403.59 t). Diese Studie kann zu einem Verständnis von Nährstoffaufnahme in Aufforstungen in Karstgebieten beitragen. Außerdem liefert sie eine theoretische Basis für die Restoration und Rekonstruktion von Vegetationen zur Kontrolle von Verkarstungen.

## 1. Introduction

Ecological stoichiometry studies the interaction of various elements in ecosystems, mainly how the balance and interaction of carbon (C), nitrogen (N), and phosphorus (P), and other elements affect ecosystems and ecological processes (Sternner and Elser 2002). C, N, and P are essential elements for all living matter. Soil nutrient supply, plant nutrient requirements, self-regulation of nutrient requirement by plants, and nutrient return by litterfall and litter decomposition are accomplished through transformation of C, N, and P. Therefore, ecological stoichiometry is an important method for the study of chemical cycles in biological systems (Agren and Bosatta 1998; Shen et al. 2019).

There are differences in the stoichiometric characteristics of different climatic regions. Studies have shown that the productivity of temperate and boreal forests is mainly limited by N, while the productivity of tropical rainforests and subtropical evergreen forests is generally limited by P (Aerts and Chapin 2000; Aerts et al. 2003). These findings have been confirmed at a global scale; however, there is a sparsity of research on the stoichiometric characteristics of vegetation at a regional level and within various landform types. Currently, much research is conducted on the coupling of stoichiometric characteristics and environmental factors, mostly focusing on three ecosystems: forests, wetlands, and grasslands (Kerkhoof et al. 2006; Yan et al. 2010; Zhang et al. 2017; Ye et al. 2016; Zhao et al. 2016). Previous research focused more on stoichiometric characteristics of different successional stages, seasonal changes, vegetation types, different plant organs, and spatial variability such as latitude and longitude (Liu et al. 2010; Zhou et al. 2010; Wardle et al. 2004; Sun et al. 2018; Zhao et al. 2018; Wang et al. 2018). Stoichiometry studies have often focused on single components (soil or vegetation) or single plant organs (plant leaves or fine roots). Consequently, there are still many research gaps in the study of stoichiometry in terms of vegetation, litter, and soil as a whole system, particularly at a regional scale.

Karst rocky desertification is a process of land degradation caused by dissolution of soluble rocks such as limestone and dolomite. Human activities can promote karst rocky desertification by vegetation damage and soil erosion, which increase the speed by which rock is exposed, eventually leading to a decline in land productivity. Finally, the soil surface becomes dominated by bare rocks which is visually similar to a desert landscape (Yuan 1997). Karst landforms are frequent worldwide, particularly in Mediterranean Europe, south Australia, the Russian Ural mountains, Kentucky and Indiana in the United States, South China, and Cuba (Gao et al. 2003).

Consequently, many countries have paid attention to the effect of karst on soil formation and vegetation. In China, karst landforms are particularly widespread, covering an area of 1.24 million ha (approx. 13% of the total land mass of China). China's karst rocky desertification is mainly present in the southwest centered on the Guizhou Plateau, and it represents one of three major ecological problems in China (Xiong et al. 2012; Yuan and Zhang 2008; Yue et al. 2011). The main challenges caused by karst rocky desertification are its ecological fragility, low ecological carrying capacity, and slow recovery, which impairs the economic and social sustainable development of karst-affected regions. Unsuitable land use is the dominant reason for rocky karst desertification in the southwest karst region (Yuan 1997). Karst rocky desertification restricts plant growth, the establishment of secondary forests leading to stunted tree growth, and it is problematic both for regional socio-economic development and the healthy ecological functioning of ecosystems (Gra and Hetherington 2004). Therefore, to control karst rock desertification, the ecological and economic functions of ecosystems have to be balanced to ameliorate environmental conditions and improve ecosystem health. Studies have shown that afforestation of woody plants with high calcium and drought tolerance, and conservation of soil and water, are important for sustainable land management in karst regions (Zhang et al. 2019). Afforestation, which considers local conditions, may be an effective way to ecologically restore and control karst rocky desertification.

The ecosystems in southwest China karst are fragile and sensitive to environmental stress and disturbances (Xiong et al. 2016; Xiong et al. 2017). Since the 1990s, a large number of vegetation restoration projects have been carried out to control karst rocky desertification, and large-scale eco-economic forests have been planted. The ecological status of karst has been significantly improved since the development of these projects. To date, China has planted 5.5 million hectares of Chinese weeping cypress (*Cupressus funebris* Endl.), 4.5 million hectares of Eucalyptus (*Eucalyptus robusta* Smith), 13,000 hectares of loquat (*Eriobotrya japonica* (Thunb.) Lindl.), 833,300 hectares of Chinese prickly ash (*Zanthoxylum bungeanum* Maxim.), 440,000 hectares of walnut (*Juglans regia* Linn.) and 4,000 hectares of teak (*Tectona grandis* Linn. f.) (Xiong et al. 2002). However, studies on vegetation restoration in the control of karst rocky desertification have largely focused on grassland productivity and establishing economic forests (Xiong et al. 2002). There has been limited research on the mechanisms of degradation and the effect of adaptive rehabilitation technology such as afforestation. The interactions between plants, litter, and soil in these ecosystems are still unclear, which may potentially lead to continued degradation, and a decrease in productivity or failure of restoration projects.

The aims of this study were to investigate the stoichiometry of C, N, and P of leaf-litter-soil in eco-economic forests in karst rocky desertification areas. The objectives were:

1. to quantify nutrient cycling and nutrient absorption of five important ecoecono-

- mic forest types in SE China karst regions, and explore the relationship between nutrient cycling and productivity, and
2. to provide a theoretical basis for the restoration, reconstruction, and management of eco-economic forests in karst rocky desertification regions.

## **2. Material and Methods**

### **2.1 Study region**

South West China has eight provinces with karst formations, and our study region is located in Guizhou province (Fig. 1). The demonstration area of Guanling-Zhenfeng Huajiang for studying comprehensive treatments for karst rocky desertification is located in the southwest part of the Guizhou province (105°36'30"–105°46'30"E, 25°39'13"–25°41'00"N). Huajiang canyon of the Beipanjiang river is a typical karst valley area on the Guizhou Plateau. It has a subtropical monsoon climate (Fig. 1) with an annual average temperature of 18.4 °C, an annual average rainfall of 1100 mm, and the elevation ranges from 450 to 1450 m. The experimental plots used in this study are located at elevations from 526 to 1133 m, representing a wide elevation gradient, which may also cause differences in soil fertility and nutrients between the sites. The karst area accounts for 87.92% of the total demonstration area of 51.62 km<sup>2</sup>, and the area of karst rocky desertification is 13.52 km<sup>2</sup> with potential, mild, moderate, and severe karst rocky desertification contributing to 3.32 km<sup>2</sup> (24.54%), 5.47 km<sup>2</sup> (40.48%), 2.42 km<sup>2</sup> (17.93%), and 2.31 km<sup>2</sup> (17.06%) of the area, respectively (Fig. 2). The dominant soil types are calcisols with discontinuous distribution and poor water-holding capacity, which are inadequate for agriculture or as pasture due to the shallow soil.

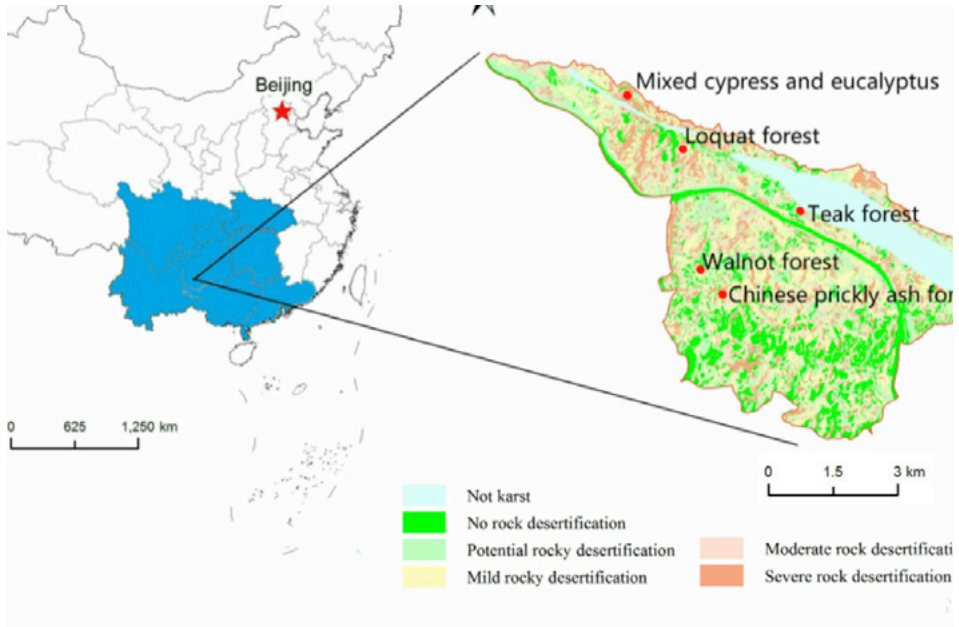


Figure 1: Location of study area for karst rocky desertification control in Guizhou in southeast China and the grades of desertification.

Abbildung 1: Lage des Untersuchungsgebietes in Guizhou, Südostchina, und die unterschiedliche Intensität der Verkarstung.

We studied five tree species, which are favoured for karst rocky desertification control: cypress (*Cupressus funebris* Endl.) mixed with eucalyptus (*Eucalyptus robusta* Smith), loquat (*Eriobotrya japonica* (Thunb.) Lindl.), Chinese prickly ash (*Zanthoxylum bungeanum* Maxim.), walnut (*Juglans regia* Linn.), and teak (*Tectona grandis* Linn. f.). The management of the forests is conducted under the guidance of the provincial government. The selected stands are about 20 years old. For the duration of the research, the stands received the same fertilizer treatment with a compound fertilizer applied in April and August at 45 kg per hectare. Trunk diameter was measured at 50 cm height in Chinese prickly ash, and at 1.3 m for other tree species. 5 m × 5 m subplots were established in three 30 m × 30 m plots, and the number of plants and their trunk diameters were measured in each plot. The number of plants and their diameters (basal area) per hectare were estimated by averaging the number of trees and diameter in the three plots. The basic characteristics are summarized in Table 1.

Table 1: Stand characteristics of the studied forests. KRD is kart rocky desertification.

Tabelle 1: Zusammenfassung der Bestandeseigenschaften der untersuchten Wälder. KRD ist der Verkarstungsgrad.

Forest type	Location	Altitude (m)	Grade of KRD	Slope (°)	Stem number (ha <sup>-1</sup> )	Average diameter (cm)	Basal area (m <sup>2</sup> /ha)	Age (year)	Tree height (m)	Canopy cover (%)
Mixed cypress and eucalyptus	25° 42' 16" N 105° 37' 11" E	1133	Severe	18	800	11.68	9.50	24	11.28	88
Loquat	25° 41' 32" N 105° 37' 58" E	817	Moderate	7	400	11.89	4.56	18	9.34	80
Chinese prickly ash	25° 39' 23" N 105° 38' 35" E	773	Severe	15	600	5.64	1.68	20	2.03	68
Walnut	25° 39' 24" N 105° 38' 21" E	804	Mild	12	420	10.91	3.92	23	8.13	81
Teak	25° 40' 25" N 105° 39' 56" E	526	Potential	15	700	12.90	9.43	19	13.54	73

## 2.2 Field sample collection and pretreatment

Three plots of 30 m × 30 m were used for each of the five forest types. All field measurements were taken in late August 2017. Five to six plants with similar growth were randomly selected in the plots, and 1,000 g of healthy mature leaves (50% sun leaves, 50% shade leaves) from four directions of the canopy were collected, mixed, and dried in the lab at 105 °C for 15 min. Undecomposed and semi-decomposed litter was collected from multiple areas in four plots sized 1 m × 1 m, mixed and brought back to the lab. Tree branches, humus, and other debris in the litter layer were removed in order to analyze the relationship between plant leaves and leaf litter. All samples were dried at 65 °C in an oven until constant weight was reached. A subsample of the plant leaves and the leaf litter was pulverized into 0.1 mm powder with a shredder to determine the soil organic C, total N, and total P. Soil was collected from the root zones of three or four small plots along an "S" route at a depth of 0–10 cm (the actual soil depth was recorded, if the soil depth was less than 10 cm). After thorough mixing, about 1 kg of soil from each forest type was sampled by quartation and taken back to the lab. They were air-dried and separated from impurities such as animals, plant debris, and gravel. Then, the soil samples were ground with an agate pestle and mortar. After sieving through a 100-mesh nylon screen, the resulting samples were stored in plastic bags for the determination of chemical properties.



*Figure 2: Study site for mixed cypress and eucalyptus.*

Abbildung 2: Untersuchungsfläche mit Zypressen gemischt mit Eukalyptus.



*Figure 3: Study site of walnut (left) and Chinese prickly ash (right).*

Abbildung 3: Untersuchungsfläche mit Walnuss (links) und Szechuan-Pfefferbaum (rechts).



### 2.3 Elemental analysis

Organic C was measured using the modified Mebius method (Nelson et al. 1982). Total N was measured using the modified Kjeldahl wet digestion procedure (Gallaher et al. 1976) and a 2300 Kjeltex Analyzer Unit (FOSS, Sweden), and total P was measured using the molybdate-blue reaction (Bao 2000) with a UV-2450 spectrophotometer (Shimadzu Scientific Instruments, Japan). This method was used for plant leaves, litter, and soil.

### 2.4 Data processing and statistical analysis

The initial analysis and sorting of data were carried out with MS Excel 2010, and statistical analyses were performed by SPSS 20.0 (SPSS, Chicago, IL, USA) software. One-way ANOVA was employed to test the significance of the nutrient content in leaves, leaf litter, and soil, and their ratios (C:N, C:P, N:P). Least Significant Difference method was applied for multiple comparisons. Pearson correlation analysis was used to show the relationship of each component's ecological stoichiometry.

Litter and potential storage of soil carbon were calculated by carbon storage per unit area and the area of rocky desertification of different grades. Mixed cypress – eucalyptus and Chinese prickly ash both belong to severe rocky desertification areas, and their carbon storage per unit area was estimated as the average of the two. Soil depth was different in the severe karst rocky desertification compared to the other grades of desertification. The average thickness of the severe rocky desertification area was 5 cm, and 10 cm for other classes. The graphs were drawn with the program Origin8.6. The equation is as follows:

$$\text{SOC} = C \times D \times E \times \frac{1 - G}{10}$$

In the formula, SOC is the soil organic carbon storage ( $\text{t ha}^{-1}$ ), C is the soil organic carbon content ( $\text{g kg}^{-1}$ ), D is the soil bulk density ( $\text{g cm}^{-3}$ ), E is the soil thickness (cm), G is the volume proportion of gravel with diameter  $> 2 \text{ mm}$  (%).

$$\text{Potential C storage} = \text{C density} \times \text{Karst rocky desertification area}$$

Nutrient (N and P) reabsorption rate was calculated as the percentage of the difference in the nutrient content between plants and leaf litter and the nutrient content in plants, and it was calculated as previously described by Wang et al. (2011). The equation is as follows:

$$\text{N(P)Reabsorption rate(\%)} = \frac{\text{N(P)content in plants} - \text{N(P)content in litter}}{\text{N(P)content in plants}} \times 100\%$$

### 3. Results

#### 3.1 The characteristics of C, N, and P in plant leaf-litter-soil

The standing leaf litter of mixed cypress and eucalyptus was 4.53 t ha<sup>-1</sup>, for loquat 5.35 t ha<sup>-1</sup>, Chinese prickly ash 3.48 t ha<sup>-1</sup>, walnut 6.51 t ha<sup>-1</sup>, and teak forest was 8.80 t ha<sup>-1</sup>. The average contents of C, N, and P in leaves from the five plant communities were 481.66, 14.68, and 2.23 mg g<sup>-1</sup>, respectively. The content in leaf litter was 434.52, 9.22, and 1.70 mg g<sup>-1</sup>, which was 36.74, 2.85, and 0.64 mg g<sup>-1</sup> of soil, respectively. The content of C, N, and P in plant leaves was significantly different from those in soil in all five forests, and the order of the average C, N, and P content was plant leaves>litter>soil. In addition, significant differences were observed in N and P content in different plant communities (Table 2).

*Table 2: Content of C, N, and P in plant, leaf litter, and soil from five communities (mg g<sup>-1</sup>) (Mean ± standard error). Different capital letters in the same column indicate significant differences (P<0.05) between plant-litter-soil in same nutrient. Different lowercase letters in the same row indicate significant differences (P<0.05) among different species.*

Tabelle 2: Gehalt von C, N, und P in Pflanzen, Laubstreu und Böden in fünf Gemeinden (mg g<sup>-1</sup>) (Mean ± Standardfehler). Unterschiedliche Großbuchstaben in derselben Spalte zeigen signifikante Unterschiede (P<0.05) zwischen den Nährstoffen in den Pflanzen, Laubstreu und Böden an. Unterschiedliche Kleinbuchstaben in derselben Spalte weisen auf signifikante Unterschiede (P<0.05) zwischen unterschiedlichen Spezies.

Content	Item	Mixed cypress and eucalyptus	Loquat forest	Chinese prickly ash forest	Walnut forest	Teak forest
C (mg g <sup>-1</sup> )	plant	489.09±33.12 <sup>aA</sup>	483.24±18.18 <sup>aA</sup>	458.01±16.65 <sup>aA</sup>	503.80±17.57 <sup>aA</sup>	474.14±19.12 <sup>aA</sup>
	litter	441.04±6.68 <sup>aA</sup>	427.75±35.61 <sup>aA</sup>	433.76±4.99 <sup>aA</sup>	442.37±27.90 <sup>aB</sup>	427.70±0.34 <sup>aA</sup>
	soil	39.92±1.69 <sup>bB</sup>	26.02±1.91 <sup>bB</sup>	40.37±0.527 <sup>bB</sup>	9.57±0.38 <sup>cC</sup>	67.79±8.08 <sup>dB</sup>
N (mg g <sup>-1</sup> )	plant	9.89±0.08 <sup>aA</sup>	11.67±0.03 <sup>bA</sup>	22.46±0.20 <sup>eA</sup>	18.81±0.08 <sup>dA</sup>	10.59±0.15 <sup>cA</sup>
	litter	5.89±0.38 <sup>aB</sup>	8.81±0.36 <sup>bB</sup>	11.68±0.08 <sup>eB</sup>	13.20±0.47 <sup>dB</sup>	6.50±0.34 <sup>aB</sup>
	soil	3.92±0.75 <sup>aC</sup>	2.55±0.18 <sup>bC</sup>	3.82±0.15 <sup>cC</sup>	2.46±0.02 <sup>bC</sup>	1.49±0.09 <sup>cC</sup>
P (mg g <sup>-1</sup> )	plant	1.40±0.02 <sup>aA</sup>	1.23±0.08 <sup>bA</sup>	3.81±0.01 <sup>eA</sup>	2.69±0.01 <sup>dA</sup>	2.00±0.04 <sup>cA</sup>
	leaf	1.095±0.063 <sup>aB</sup>	1.10±0.02 <sup>aAB</sup>	3.04±0.08 <sup>bB</sup>	2.17±0.09 <sup>bB</sup>	1.07±0 <sup>aB</sup>
	soil	0.94±0.05 <sup>aC</sup>	0.98±0.03 <sup>bB</sup>	0.23±0.00 <sup>cC</sup>	0.90±0.01 <sup>bC</sup>	0.16±0.01 <sup>dC</sup>

### 3.2 The ecological stoichiometric ratio of C-N-P

The C:N ratio ranged from 20.39 to 49.48 of the leaf materials from five communities with an average of 36.58. In leaf litter, its range was 33.51–83.77 with an average of 54.54. In soil, it was 3.89–45.82 with an average of 16.20. The averages of C:P of leaf, leaf litter, and soil were 257.60, 334.88, and 134.59, respectively, which indicates that the differences were significant between leaf materials from different communities. The averages of N:P were 6.96, 6.10, and 7.09 in leaf, leaf litter, and soil. Thus, various communities varied in their stoichiometric ratios, and differentiation regularities were completely consistent, showing that C:N and C:P were higher than N:P. Except for teak forest, C:N ratios of leaf-litter-soil followed the pattern of litter>leaf>soil, and no significant difference of C:N was observed among soil samples ( $P>0.05$ ) (Fig. 4).

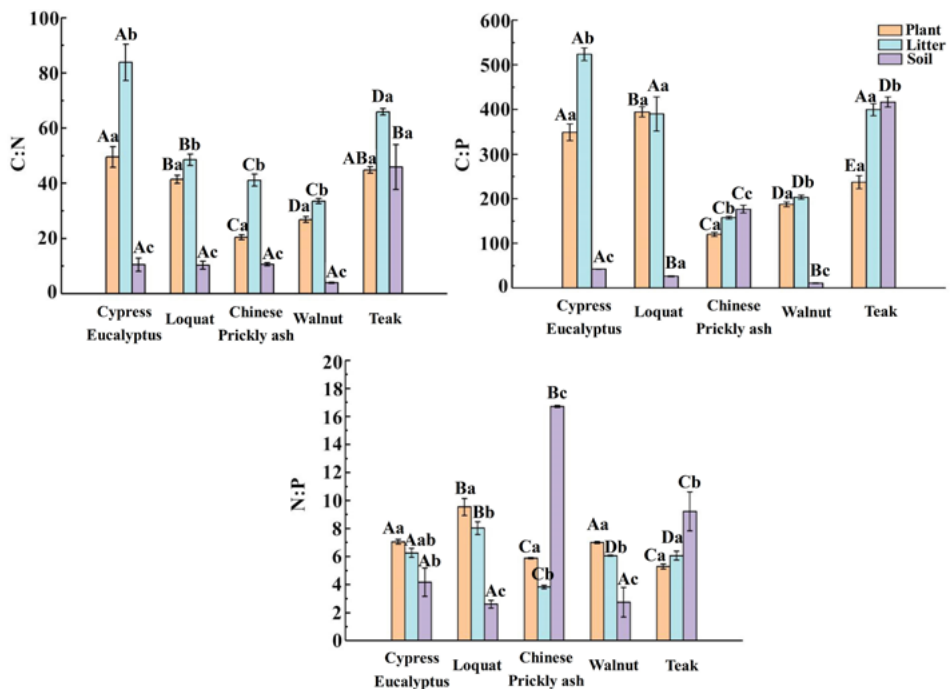


Figure 4: C:N, C:P, and N:P of leaves, leaf litter, and soil from five plant communities (Mean  $\pm$  standard error). Different capital letters indicate significant differences ( $P<0.05$ ) among different species in the same component, different lowercase letters indicate significant differences ( $P<0.05$ ) between plant - litter - soil.

Abbildung 4: C:N, C:P und N:P für Blätter, Laubstreu und Böden von fünf Pflanzengemeinschaften (Mean  $\pm$  SE). Unterschiedliche Großbuchstaben zeigen signifikante Unterschiede ( $P<0.05$ ) zwischen unterschiedlichen Spezies, unterschiedliche Kleinbuchstaben signifikante Unterschiede ( $P<0.05$ ) zwischen Pflanzen-Laubstreu-Böden.

### 3.3 Carbon and nutrient pools in afforestations in karst rocky desertification areas

Litter C storage in cypress and eucalyptus was  $199.79 \text{ g m}^{-2}$ ; loquat,  $230.05 \text{ g m}^{-2}$ ; Chinese prickly ash  $149.64 \text{ g m}^{-2}$ ; walnut  $286.44 \text{ g m}^{-2}$ , and teak  $376.37 \text{ g m}^{-2}$ . Average litter C for the entire demonstration area was  $249.15 \text{ g m}^{-2}$ . The estimated potential carbon reserves of litter in the potential, mild, moderate, and severe rock desertification areas were 1220.40 t, 1566.87 t, 556.60 t, and 403.59 t, respectively (sum 3748 t).

Carbon storage in the soil under the trees was  $6980 \text{ g m}^{-2}$  for teak,  $2694 \text{ g m}^{-2}$  for loquat,  $973 \text{ g m}^{-2}$  for walnut,  $3730 \text{ g m}^{-2}$  for Chinese prickly ash, and  $1900 \text{ g m}^{-2}$  for cypress and eucalyptus. They represent four different grades of rocky desertification areas. According to calculations, the potential carbon reserves of soil in the potential, mild, moderate, and severe rock desertification areas were 23172.47 t, 5302.64 t, 6520.00 t, and 4439.04 t, respectively (sum 39434 t). Soil carbon storage was thus 10.5 times higher than litter carbon.

Table 3: Carbon storage of litter and soil.

Tabelle 3: Kohlenstoffspeicherung von Streuschicht und Boden.

Karst rocky desertification	Area (km <sup>2</sup> )	Litter carbon density (g m <sup>-2</sup> )	Total litter carbon (t)	Soil depth (cm)	Bulk density (g cm <sup>-3</sup> )	Volume of gravel > 2 mm (%)	SOC (g m <sup>-2</sup> )	Total soil carbon (t)
Potential	3.32	376.37	1220.40	10	67.79	10	6980	23172.47
Mild	5.47	286.44	1566.87	10	26.02	14	973	5302.64
Moderate	2.42	230.05	556.60	10	9.57	12	2694	6520.00
Severe	2.31	174.72	403.59	5	40.145	15.5	2815	4439.04
All	13.52		3747.37					39434.15

### 3.4 The correlation of ecological stoichiometric characteristics

The correlation analysis of leaves, leaf litter, soil, and productivity (diameter of basal area) showed no correlation between C and tested elements. The N and P content

of plant material exhibited a significant correlation to N, P, C: N, and C:P in leaf litter ( $P < 0.05$ ). The correlation between plant N and P and the stoichiometric ratio of plant and leaf litter was relatively significant, and a very close correlation was observed between living leaf material and leaf litter. Soil N exhibited an extremely significant positive correlation to C: N and C:P with a correlation coefficient of 0.889 and 0.890, respectively. In addition, soil P was significantly correlated to C:P and N:P in both plants and soil, suggesting that the soil element dynamic balance affects the storage characteristics of nutrient stoichiometry of leaf material. Productivity (basal area) showed no correlation with the tested elements ( $P > 0.05$ ).

Table 4: The correlation between the ecological stoichiometric characteristics of plant-litter-soil. Yellow and blue indicate significant correlations at the  $p < 0.05$  and  $0.01$ , respectively.

Tabelle 4: Korrelation zwischen den ökologisch-stöchiometrischen Eigenschaften der in Pflanzen-Laubstreu-Böden. Gelb und blau weist darauf hin, dass die Korrelation signifikant sind auf der  $p < 0.05$  und  $p < 0.01$ .

Item		plant			litter			soil			plant			litter			soil			productivity basal area	
		C	N	P	C	N	P	C	N	P	C:N	C:P	N:P	C:N	C:P	N:P	C:N	C:P	N:P		
plant	C	1																			
	N	-0.191	1																		
	P	-0.318	-0.931	1																	
litter	C	0.23	0.104	0.49	1																
	N	0.116	0.889	0.702	0.193	1															
	P	-0.239	0.985	0.956	0.129	0.808	1														
soil	C	-0.013	0.306	0.243	0.258	0.097	0.406	1													
	N	-0.477	-0.399	-0.059	-0.267	-0.693	-0.299	-0.249	1												
	P	0.53	-0.289	-0.587	0.142	0.027	-0.357	0.201	-0.721	1											
plant	C:N	0.257	-0.984	-0.898	-0.066	-0.958	-0.947	-0.178	0.411	0.279	1										
	C:P	0.288	-0.832	-0.959	-0.024	-0.627	-0.849	-0.027	-0.05	0.658	0.813	1									
	N:P	0.227	-0.251	-0.575	0.053	0.038	-0.3341	0.079	-0.599	0.798	0.198	0.727	1								
litter	C:N	-0.049	-0.857	-0.664	-0.019	-0.967	-0.761	-0.026	0.637	0.019	0.892	0.565	-0.118	1							
	C:P	0.106	-0.987	-0.927	-0.05	-0.879	-0.976	-0.519	0.407	0.262	0.957	0.843	0.307	0.838	1						
	N:P	0.344	-0.583	-0.77	-0.057	-0.198	-0.697	-0.529	-0.251	0.549	0.481	0.748	0.753	0.096	0.618	1					
soil	C:N	-0.315	-0.445	-0.143	-0.303	-0.568	-0.412	-0.647	0.889	-0.664	0.402	-0.052	-0.541	0.501	0.445	0.03	1				
	C:P	-0.414	-0.149	0.181	-0.228	-0.37	-0.096	-0.5	0.89	-0.886	0.132	-0.337	-0.72	0.311	0.164	-0.235	0.93	1			
	N:P	-0.581	0.557	0.769	-0.059	0.162	0.652	0.267	0.48	-0.861	-0.504	-0.699	-0.648	-0.198	-0.519	0.759	0.24	0.554	1		
productivity	basal																				
	area	0.363	0.3673	0.628	-0.194	0.067	0.624	0.572	-0.444	0.629	0.626	0.5124	-0.592	0.547	0.514	-0.345	0.519	0.487	0.624	1	

### 3.5 The reabsorption rate of N and P in five tree communities

The reabsorption rates of N in the five plant communities ranged from 19.98% to 48.75% with an average of 36.30%, and its range was 5.88%–47.56% of P with an average of 23.61%. The highest reabsorption rate of N among the five species was observed in Chinese prickly ash forest, followed by cypress and eucalyptus, teak, loquat, and walnut. Teak exhibited the highest reabsorption rate of P, followed by cypress and eucalyptus, Chinese prickly ash, walnut, and loquat. Overall, teak showed a relatively high reabsorption rate of N and P, and the reabsorption rate of N was higher than that of P in all plant communities except for teak (Fig. 5).

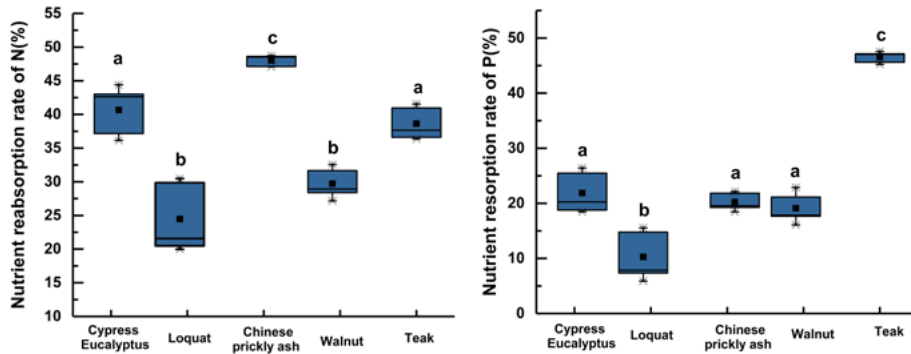


Figure 5: The reabsorption rate of C and P of five plant communities. Different lowercase letters indicate significant differences ( $P < 0.05$ ). The box represents 95th and 5th percentile; line in the box is median; ★ is maximum value; × is minimum and ■ is mean.

Abbildung 5: Die Reabsorptionsrate von C und P in fünf Pflanzengemeinschaften. Unterschiedliche Kleinbuchstaben weisen auf signifikante Unterschiede ( $P < 0.05$ ) hin. Die Box ist 95% und 5% Perzentile, die horizontale Linie in der Bok ist der Median, ★ ist der Maximalwert, × ist das Minimum, und ■ ist der Mittelwert.

## 4. Discussion

### 4.1 The content characteristics of C, N, and P of plant leaf-litter-soil

Our data demonstrated that the C, N, and P content of five economic tree species in the dry hot karst valley exhibited the order of plant leaf > litter > root soil. The C content in leaves was higher than that in leaf litter; this is because organic components such as crude fat, tannin, and soluble sugar decompose after leaf fall (Yang et al. 2007) resulting in a significant decrease in C content in leaf litter. It may also be related to the slower leaf growth rate and reduced photosynthesis prior to leaf fall. The average content of N and P in leaf litter was lower than that in leaves, the reason for which may be that partial nutrients are transferred to other components, reabsorbed, and reused. The decrease of N may also result from the utilization of N for photosynthesis, and the higher N utilization rate lowers the nitrogen level in leaf litter (Zhang et al. 2016); this result is consistent with a previous study by Bai et al. (2016), in which N and P content followed the order of leaf > litter > soil in three types of cultivated forests.

C is the structural element of plants (Xiang et al. 2006), while N and P are the main limiting elements that regulate plant growth in terrestrial ecosystems (Han et al. 2005). In this paper, the average C content in plant leaves was  $481.66 \text{ mg g}^{-1}$  higher than that reported by Wang et al. (2017) in the plants of natural secondary forest in the Loess Plateau ( $468.67 \text{ mg g}^{-1}$ ), and it was also higher than the average C content of 492 terrestrial plant leaves, which was  $464 \text{ mg g}^{-1}$  reported by Elser et al. (2000), in-

dicating a relatively strong C storage capacity in the ecoeconomic forest in the karst area. This may be determined by the sampling time that was right at the peak of the growth stage in our study, or by the availability of soil elements in sampling areas. The average N content in the leaves of the five plant communities was  $14.68 \text{ mg g}^{-1}$ , lower than that of the Loess Plateau  $21.36 \text{ mg g}^{-1}$  (Yang et al. 2014), the average of 753 terrestrial plants of China  $18.6 \text{ mg g}^{-1}$  (Han et al. 2005), and the average N content of plant leaves worldwide ( $20.09 \text{ mg g}^{-1}$ ) (Reich and Oleksyn 2004). Previous studies demonstrated that P content in terrestrial plants in China is lower than that on a global scale (Ren et al. 2007). In this paper, the average P content in the five plant communities was  $2.23 \text{ mg g}^{-1}$ , significantly higher than the global scale by  $0.43 \text{ mg g}^{-1}$  (Reich and Oleksyn 2004), and it was also higher than the average for terrestrial plants in China ( $0.77 \text{ mg g}^{-1}$ ) (Han et al. 2005). The N deficiency and P rich status of the ecoeconomic forest of karst is mainly due to the substantial bare rock, low vegetation coverage, enriched nutrition in the tree layer, lack of a symbiotic nitrogen fixation system, and low weathering of soil (Hedin 2004). In addition, high P can facilitate the metabolic rate to support the energy demand of macromolecule synthesis, and further protect vegetation against the harsh environment in karst areas (such as poor moisture retention capacity and soil nutrient loss).

Leaf litter plays an important role in forest ecosystems, which is an intrinsic component of nutrient cycling in forest ecosystems and the main source of soil organic matter. The average contents of C, N, and P in leaf litter of five plant communities were 434.52, 9.22, and  $1.70 \text{ mg g}^{-1}$ , respectively. It was lower than the global scale of N ( $10.9 \text{ mg g}^{-1}$ ), while higher than the global scale of P ( $0.90 \text{ mg g}^{-1}$ ) (Kang et al. 2010), indicating that leaf litter shows exactly the same characteristics as plants. The reason for such phenomena is that in artificial or secondary forests the dominant tree species and plant community structure are relatively simple and variation in leaves and leaf litter is limited.

Soil nutrient composition is a key factor affecting plant growth, and it plays important roles in maintaining biological and mineral metabolism, providing nutrients and other ecological processes (Bin et al. 2014). The average C, N, and P content in the top 0–10 cm soil layer of five plant communities in the karst area was 36.74, 2.85, and  $0.64 \text{ mg g}^{-1}$ , respectively, higher than those of forest ecosystems in hilly and gully regions of the Loess Plateau (23.21, 1.91, and  $0.57 \text{ mg g}^{-1}$ ) (Zhao et al. 2017), higher than those of temperate grasslands of Inner Mongolia 0–10 cm soil layer (25.30, 1.70,  $0.10 \text{ mg g}^{-1}$ ) (Yin et al. 2010), and also higher than the 0–20 cm soil layer of north China larch plantations by 13.01, 1.51, and  $0.61 \text{ mg g}^{-1}$  (Bai et al. 2015). Although the soil layer in the karst area is thin, the nutrient content in the surface soil is very high, the reasons for which may be that the humid and hot climate conditions in the southwest karst area are favorable to the growth of soil microorganisms and small animals, leading to a stronger capacity for "self-fertilization" than other areas (Zeng et al. 2015). Alternatively, it may be attributable to the release of nutrients to soil when a large amount of tree leaf litter, root residues, and secretions decompose together, which is consistent

with the study of Zhang et al. (2012) showing that soil nutrient characteristics in the tree layer are significantly higher than shrub, grassland, and bare land in karst areas.

#### **4.2 The stoichiometric ratio of C, N, and P in plant-litter-soil-productivity and their correlation**

C:N and C:P ratios of plants usually reflect the utilization efficiency of N and P in plants, and partially reflect the supply status of N and P in soil (Zeng et al. 2015). Because different pathways control the assimilation of C in photosynthesis and absorption of plant nutrients, C content is high with little variation in most plants, and C is usually not a limiting element for plant growth (Reich and Oleksyn 2004). In this study, C:N and C:P ratios of leaves were 36.57 and 257.60, respectively, higher than those of the global average level (22.50 and 232) (Elser et al. 2004), further suggesting that C:N and C:P ratios are relatively high in the dry hot valley area of karst rocky desertification, and suggests a relatively high utilization rate of N and P. Previous studies have demonstrated that plants exhibit a higher nutrient utilization rate in nutrient deficient conditions, which is a survival strategy for plants to adapt to low nutrient levels (Bowman 1994).

The N:P critical ratio of plant leaves can be regarded as an indicator to assess the nutrient supply status of the environment to plant growth (Aerts and Chapin 2000). The growth rate hypothesis argues that organisms accumulate large amounts of P into rRNA during high-speed growth so that ribosomes can rapidly synthesize large amounts of protein to accelerate growth rate (Elser et al. 2003). The average N:P ratio of the plant leaves in this study was 6.96, which was lower than that of 753 terrestrial plants of China (16.3) (Elser et al. 2004), lower than that of forest leaves in Dinghushan mountain (25.84) (Liu et al. 2010), and lower than that of plant leaves of different life types in north Tianshan mountain (17.36) (Xie et al. 2016). Studies have shown that when the N:P ratio is greater than 16, the ecosystem is restricted by P, the ratio less than 14 indicates that the ecosystem is restricted by N, and when it is between 14 and 16, the ecosystem is simultaneously limited by N and P or nutrients are so abundant that it is not limited (Koerselman and Meuleman 1996). According to the above definition, we found that the N:P ratio of five plants in the karst dry valley is lower than 14, indicating that it is mainly restricted by N and the application of N fertilizer can increase the biomass yield of vegetation. The reason is that in the management of plantation forests in the study area, the application of compound fertilizer is the main method, and the fertilization method is relatively extensive. In addition, the shallow soil layer and the surface-subsurface binary loss exacerbate the drought stress and lack the medium for nutrient dissolution and migration, leading to a lack of synergy between water and fertilizer supply, and low efficiency of nutrient use.

The average ratios of C:N and C:P in the leaf litter were 54.54 and 334.88, respectively, which were lower than the global scale (57.30 and 1175.60), as well as Changbai Mountain, Jilin (39.43 and 552.00) (Wang et al. 2011; McGroddy et al. 2004), indicating



the limited content of N and P in leaf litter of the karst area. A significant positive correlation was observed between N and P content of plant leaves and N and P content of leaf litter. It is possible that N and P contents of plant leaves are reduced due to nutrient reuse before leaf fall, but it is insufficient to change the relationship between N and P content in leaves. Thus, the N and P content of leaf litter was similar to that of living leaves, which is consistent with the study by Zhu et al. (2017).

Soil C:N is inversely proportional to the decomposition rate of organic matter and affects the mineralization rates of N and P, so it is a sensitive index to demonstrate variations in soil quality. The average C:N ratio of five plant communities in the hot dry valley of the karst area was 16.20, higher than that of the natural secondary forests in the Ziwuling area of the Loess Plateau (11.9), that of global forest (12.40), and that of grassland (11.80) (Cleveland and Liptzin 2017) at a depth of 0–10 cm. It indicates a high-level organic matter content, a low mineralization rate of N, as well as a strong retention potential of C and N in the study area, which is consistent with the study by Ye et al. (2016). Soil C:P is generally considered as an indicator of soil P mineralization ability, and it is also a marker to indicate P release from the organic matter in microbial mineralized soil or the potential of P absorption and fixation from the environment (Pang et al. 2018). High soil C:P can cause soil microorganisms to compete with plants for soil inorganic P, which is unfavorable for plant growth. On the contrary, low C:P can facilitate microbial decomposition of organic matter to release nutrients and increase the content of available P in soil, so it can also represent high P availability in soil. The average C:P of five vegetation types in the karst rocky desertification area was 134.59, higher than global forest (81.90) and grassland (64.30) (Ye et al. 2016), indicating that soil microorganisms competed with plants for soil inorganic P, which is not favorable to plant growth. N in soil mainly originates from the leaf litter and the deposition of atmospheric nitrogen (Liu et al. 2010), and N:P in soil indicates the supply status of soil nutrients during plant growth. Our study showed that the average soil N:P of five plots was  $7.09 < 14$ , suggesting N deficiency, which impedes vegetation growth. The reason for such low N:P is that N is enriched in the surface layer of soil due to uneven topography, the severe cave, and fissures in karst, and surface water leakage; N then moves through fissures to lower layers along with water (Li et al. 2006), resulting in N deficiency in the dry hot valley area in Southwest China with ample rainfall.

Some studies have shown that soil nutrient status limits productivity (Ning et al. 2006). However, similar results have not been obtained in this study. The results showed that there was no direct relationship between plant, litter, soil, and productivity. It may be affected by the heterogeneity of the rocky desertification environment, and other factors.

### 4.3 Carbon and nutrient pools in afforestations on karst rocky desertification

Studies showed that nutritional reserves of litter C in cypress and eucalyptus were  $199.79 \text{ g m}^{-2}$ ; in loquat were  $230.05 \text{ g m}^{-2}$ ; in Chinese prickly ash were  $149.64 \text{ g m}^{-2}$ ; in walnut were  $286.44 \text{ g m}^{-2}$ ; and in teak were  $376.37 \text{ g m}^{-2}$ . The average reserves of litter C in the entire demonstration area were  $249.15 \text{ g m}^{-2}$ . Teak litter had the highest carbon storage and the teak test plot was located in a potential rocky desertification area, with thick soil, low rock exposure rate, and high carbon storage per unit area. Cypress-eucalyptus and Chinese prickly ash grow in the area of severe rocky desertification, and the carbon storage per unit area is small. Loquat and walnut grow in moderate and mild rocky desertification areas, with moderate carbon reserves. It is obvious that the grade of rocky desertification affect the carbon storage of litter. From the current rock desertification control projects in the demonstration area, these five types of eco-economic forests are mainly used. Thus we can estimated the potential carbon reserves of litter in the potential, mild, moderate, severe rock desertification areas are 1220.40 t, 1566.87 t, 556.60 t, and 403.59 t, respectively.

Studies showed that the soil organic carbon densities of the four grades of desertification were quite different, which indicates that the soil of karst rocky desertification is scattered, the thickness of the rock exposed soil layer is obviously different, and the environmental spatial heterogeneity is large. The results were consistent with those of Zhang Zhenming et al. (2017). The average carbon storage of soil in four grades of rocky desertification area was  $3.26 \text{ kg m}^{-2}$ . It was smaller than the national average level ( $9.6 \text{ kg m}^{-2}$ ) (Zhao 2005), for the Loess Plateau ( $10.92 \text{ kg m}^{-2}$ ) (Xue et al. 2015), or the Sanjiang Plain ( $9.72 \text{ kg m}^{-2}$ ) (Mao et al. 2015). Due to the special dual hydrological structure, complex topography and landform in karst areas, the rock fracture structure causes a large amount of soil organic carbon loss.

### 4.4 The characteristics of the reabsorption rate for N and P

Nutrient reabsorption refers to the process of nutrient transfer from old tissues and organs to other fresh organs and it is an important component of the nutrient cycle, reflecting plants' ability to conserve, utilize nutrients, and to adapt to nutrient-poor environments. Our data showed that the N reabsorption ranged from 24.48% to 40.37% with an average of 36.27%, and the range of P reabsorption was 10.28%–46.52% with an average of 23.61% in the ecoeconomic forest of the hot dry valley in the karst area, which is significantly lower than those of 172 species of woody plants in East China 49.1% and 51.0%, respectively; Tang et al. (2013) and those of 199 species of woody plants worldwide (57.4% and 60.7%) respectively; Han et al. (2014). The low reabsorption rate in Han's study indicated that the contents of N and P were relatively abundant in the study area, which is inconsistent with the first result of N deficiency in our study. This is because vegetation can directly absorb and utilize effective nutrients, not total nutrients (Bai et al. 2015). In addition, microbial decomposition absorb some N and P from soil and leaf litter, thus affecting nutrient cycling.

Therefore, there can be high total N and P in root-soil with a high reabsorption rate, or low total N and P with a low re-absorption rate, indicating no correlation of the reabsorption rate of N and P with the availability of N and P in soil, which is similar to the previous study by McGroddy et al. (2004). High N and P transfer rates may be an inherent characteristic of species, but not an important adaptation mechanism of plants to N and P nutrient stress (Wang et al. 2018). Such results are consistent with Aerts et al. (2000), in which the conclusion that evergreen plants occupy more barren habitats and have higher nutrient reabsorption rates is not supported. Plants adapt to the environment mainly by absorbing nutrients from the root zone, and not by a capacity for reabsorption.

## 5. Conclusions

The vegetation of the ecoeconomic forest in the karst area was deficient in N, rich in P, and exhibited a relatively high capacity for C storage. The N and P content of leaf litter was similar to that of living leaves, so leaf litter possessed exactly the same characteristics as plants. There was no direct relationship between plant, litter, soil, and productivity. The grade of rocky desertification will affect the carbon storage of litter. Low carbon storage in karst rocky desertification areas. In general, the soil was limited by N, so appropriate application of N fertilizer could facilitate plant growth. Plants adapt to the environment mainly by absorbing nutrients from root soil, but not by reabsorption capability.

## Acknowledgments

This research was funded by the Project of the National Key Research and Development Program of China in the 13th Five-year Plan Period: Ecological Industry Model and Integrated Technology Demonstration of the Karst Plateau-Gorge Rocky Desertification Control (2016YFC0502607); The Key Project of the Science and Technology Program of Guizhou Province: Model and Technology demonstration for from the karst desertification control (No.5411 2017 Qiankehe Pingtai Rencai).

## References

- Aerts R, Chapin FS. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *J Plant Ecol* 30: 1-67.
- Aerts R, De Caluwe H, Beltman B. 2003. Is the relation between nutrient supply and biodiversity CO<sub>2</sub> limited by the type of nutrient limitation. *Oikos* 101:489-498.
- Agren GI, Bosatta E. 1998. *Theoretical Ecosystem Ecology: Understanding Element Cycles*. Cambridge University Press, Cambridge, UK. 234.
- Bai XF, Xu FL, Wang WL, Zhao YF, Wang LL, Sun PY. 2015. Ecological stoichiometry of soil carbon, nitrogen and phosphorus in a *Larix principis-rupprechtii* plantation. *Sci Soil and Water Conserv* 13: 68-75.
- Bai XJ, Zeng QC, An SS, Zhang HX, Wang BY. 2016. Ecological stoichiometry character-

- ristics of leaf-litter-soil in different plantations on the Loess Plateau, China. *Chin. J. App. Ecol* 27: 3823-3830.
- Bao SD. 2000. Soil agrochemical analysis. Beijing: China Agriculture Press.
- Bin ZJ, Wang JJ, Zhang WP, Xu DH, Cheng XH, Li KJ, Cao DH. 2014. Effect of N addition on ecological stoichiometric characteristics in six dominant plant species of alpine meadow on the Qinghai-Xizang Plateau. China. *Chin J Plan Ecolo* 38:231-237.
- Bowman WD. 1994. Accumulation and use of nitrogen and phosphorus following fertilization in two alpine tundra communities. *Oikos* 70: 261-270.
- Cleveland CC, Liptzin D. 2017. C:N:P stoichiometry in soil: Is there a "Redfield ratio" for the microbial biomass. *Biogeochemistry* 85: 235-252.
- Elser JJ, Acharya K, Kyle M, Cotner J, Makino W, Markow T, Watts T, Hobbie S, Fagan W, Schade J, Hood J, Sterner RW. 2003. Growth rate-stoichiometry couplings in diverse biota. *Ecol Lett* 6: 936-943.
- Elser JJ, Fagan WF, Denno RF, Dobberfuhl DR, Folarin A, Huberty A, Interlandi S, Kilham SS, McCauley E, Schulz KL, Siemann EH, Sterner RW. 2000. Nutritional constraints in terrestrial and freshwater food webs. *Nature* 408: 578-580.
- Gao GL, Deng ZM, Xiong KN, Su XL. 2003. The call and hope of karst. Guizhou science and technology press, Gui Yang, Chinese, 1-3.
- Gallaher RN, Weldon CO, Boswell FC. 1976. A semi-automated procedure for total nitrogen in plant and soil samples. *Soil Science Society of America Journal* 40: 887-889.
- Gra YJE, Hetherington AM. 2004. Plant development: YODA the stomatal switch. *Current Biology* 14: 488-490.
- Han WX, Fang JY, Guo DL, Zhang Y. 2005. Leaf N and P stoichiometry across 753 terrestrial plant species in China. *New Phytol* 168: 377-385.
- Han WX, Tang LY, Chen YH, Fang JY. 2014. Relationship between the relative limitation and resorption efficiency of nitrogen vs phosphorus in woody plants. *Plos One* 9. doi:10.1371/journal.pone.0083366.
- Hedin LO. 2004 Global organization of terrestrial plant-nutrient interactions. *PNAS* 101:10849-10850.
- Kang HZ, Xin ZJ, Berg B, Burgess PJ, Liu QL, Liu ZC, Li ZH, Liu CJ. 2010. Global pattern of leaf litter nitrogen and phosphorus in woody plants. *Ann Forest Sci* 67: 811-811.
- Kerkhoff AJ, Fagan WF, Elser JJ, Enquist BJ. 2006. Phylogenetic and growth and growth from variation in the scaling of nitrogen and phosphorus in the seed plants. *The American Naturalist* 168: E103-E122.
- Koerselman W, Meuleman AFM. 1996. The vegetation N:P ratio: A new tool to detect the nature of nutrient limitation. *J App Ecol* 33: 141-150.
- Li YB, Shao JA, Wang SJ, Wei CF. 2006. A Conceptual Analysis of Karst Ecosystem Fragility. *Prog Geogr* 25 :1-8.
- Liu XZ, Zhou GY, Zhang DQ, Liu SZ, Chu GW, Yan JH. 2010. N and P stoichiometry of plant and soil in lower subtropical forest successional series in southern China. *Chin J Plan Ecolo* 34: 64-71.
- McGroddy ME., Daufresne T, Hedin LO. 2004. Scaling of C:N:P Stoichiometry in forests

- worldwide: implication of terrestrial Redfield-type ratios. *Ecology* 85: 2390-2401.
- Mao DH, Wang ZM, Li L. 2015. Soil organic carbon in the San Jiang Plain of China: Storage distribution and controlling factors. *Biogeosciences* 12: 1635-1645.
- Nelson DW, Sommers LE. 1982. Total carbon, organic carbon, and organic matter. In *Methods of soil analysis*. Madison: American Society of Agronomy and Soil Science Society of American.
- Ning ZY, Li YL, Yang HL, Zhang ZQ, Zhang JP. 2019. Stoichiometry and effects of carbon, nitrogen, and phosphorus in soil of desertified grasslands on community productivity and species diversity. *Acta Ecol. Sin* 39: 3537-3546.
- Pang DB, Wang GZ, Li GJ, Sun YL, Liu YG, Zhou JX. 2018. Ecological stoichiometric characteristics of two typical plantations in the karst ecosystem of southwestern China. *Forests* 9: 2-14.
- Reich PB, Oleksyn J. 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. *PNAS* 101:11001-11006.
- Ren SJ, Yu GR, Tao B, Wang SQ. 2007. Leaf nitrogen and phosphorus stoichiometry across 654 terrestrial plant species in NSTEC. *Chin. J. Envir. Sci* 28: 2665-2673.
- Shen FF, Wu JP, Fan HB, Liu WF, Guo XM, Duan HL, Hu L, Lei XM, Wei XH. 2019. Soil N:P and C:P ratio regulate the responses of soil microbial community composition and enzyme activities in a long-term nitrogen loaded Chinese fir forest. *Plant Soil* 436:91-107.
- Sterner RW, Elser JJ. 2002. *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton: Princeton University Press.
- Sun SX, Yun XJ, Wu XH, Wei ZJ, Jiang C, Liu WT. 2018. Seasonal variations of ecological stoichiometry characteristics of major plant populations in desert steppe. *Ecol Environ* 27: 47-54.
- Tang LY, Han WX, Chen YH, Fang JY. 2013. Resorption proficiency and efficiency of leaf nutrients in woody plants in eastern China. *J Plant Ecol* 6: 408-417.
- Wang BR, Zeng QC, An SS, Zhang HX, Bai XJ. 2017. C:N:P stoichiometry characteristics of plants-litter-soils in two kind types of natural secondary forest on the Ziwuling region of the Loess Plateau. *Acta Ecol. Sin* 37: 5461-5473.
- Wang JY, Wang SQ, Li RL, Yan JH, Sha LQ, Han SJ. 2011. C:N:P stoichiometric characteristics of four forest types' dominant tree species in China. *Chin J Plan Ecolo* 35: 587-595.
- Wang L, Yu YH, Xing RR, Qin SY. 2018. Ecological stoichiometry characteristics of carbon, nitrogen, and potassium of different economic tree species in the karst frigid and arid area. *Acta Ecol. Sin* 38: 5393-5403.
- Wardle DA, Walker LR, Bardgett RD. 2004. Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science* 305: 509-513.
- Xiang WH, Huang ZH, Yan WD, Tian DL, Lei PF. 2006. Review on coupling of interactive functions between carbon and nitrogen cycles in forest ecosystems. *Acta Ecol. Sin* 26: 2365-2372.
- Xie J, Chang SL, Zhang YT, Wang HJ, Song CC, He P, Sun XJ. 2016. Plant and soil ecological stoichiometry with vertical zonality on the northern slope of the middle Tianshan Mountains. *Acta Ecol. Sin* 36: 4363-4372.

- Xiong KN, Li P, Zhou ZF, An YL, Lv T, Lan AJ. 2002. Study on remote sensing – GIS model of karst rocky desertification. Geological press, Beijing, Chinese, 66-68.
- Xiong KN, Chi YK, Shen XY. 2017. Research on photosynthetic leguminous forage in the karst rocky desertification regions of southwestern China. *Pol. J. Environ. Stud* 26: 2319-2329.
- Xiong KN, Li J, Long MZ. 2012. Feature of Soil and Water Loss and Key Issues in Demonstration Areas for Combating Karst Rocky Desertification. *Acta Geogr Sin* 67: 878-888.
- Xiong KN, Zhu DY, Peng T, Yu LF, Xue JF, Li P. 2016. Study on ecological industry technology and demonstration for karst rocky desertification control of the Karst Plateau-Gorge. *Acta Ecol. Sin* 36: 7109-7113.
- Xue ZJ, Ma LS, An SS, Wang WZ. 2015. Soil organic carbon density and stock at the catchment scale of a hilly region of the loess plateau. *Acta Ecol. Sin* 35:2917-2925.
- Yan ER, Wang XH, Guo M, Zhong Q, Zhou W. 2010. C:N:P stoichiometry across evergreen broad-leaved forests, evergreen coniferous forests and deciduous broad-leaved forests in the Tiantong region, Zhejiang Province, eastern China. *Chin J Plan Ecolo* 34: 48-57.
- Yang JJ, Zhang XR, Ma LS, Chen YN, Dang TH, An SS. 2014. Ecological stoichiometric relationships between components of robinia pseudoacacia forest in loess plateau. *Acta Pedol. Sin* 51:133-142.
- Yang ZJ, Zeng J, Xue DP, Li SJ, Lu J. 2007. The processes and dominant factors of forest litter decomposition: A review. *Ecol. & Environ* 16: 649-654.
- Ye C, Pu YL, Zhang SR, Wang GY, Wang AB, Wang D, Jia YX, Xu XX. 2016. Ecological stoichiometry characteristics and storage of soil carbon, nitrogen and phosphorus during the wetland degradation process. *J. Soil Water Conserv* 30: 181-192.
- Yin XR, Ling CZ, Wang LX, Wang W, Liu ZL, Liu XP. 2010. Ecological stoichiometry of plant nutrients at different restoration succession stages in typical steppe of Inner Mongolia, China. *Chin J Plan Ecolo* 34: 39-47.
- Yuan DX. 1997. Rock desertification in the subtropical karst of south China. *Z. Geomorph. N. F.* 108:81-90.
- Yuan DX, Zhang C. 2008. Karst Dynamics Theory in China and its Practice. *ACTA GEOGRAPHICA SINICA* 29: 355-365.
- Yue YM, Wang KL, Zhang B, Liu B, Chen HS, Zhang MY. 2011. Uncertainty of Remotely Sensed Extraction of Information of Karst Rocky Desertification. *Adv Earth Sci* 26: 266-274.
- Zeng ZX, Wang KL, Liu XL, Zeng FP, Song TQ, Peng WX, Zhang H, Du H. 2015. Stoichiometric characteristics of plants, litter and soils in karst plant communities of Northwest Guangxi. *Chin J Plan Ecolo* 39: 682-693.
- Zhang JP, Pan GX. 2012. Characteristics of soil nutrients and biochemical properties under different vegetation communities in karst area. *J. Soil Water Conserv* 26: 77-84.
- Zhang QF, Xie JS, Chen NS, Chen T, Lv MK, Zhang H, Yang YS. 2017. Effects of ecological restoration on stoichiometric characteristics and nutrient resorption efficiency of *Pinus massoniana* foliage. *Acta Ecol. Sin* 37: 267-276.

- Zhang WJ, Liu XD, Jin M, Zhang XL, Che ZX, Jing WM, Wang SL, Niu Y, Qi P, Li WJ. 2016. Ecological stoichiometric characteristics of carbon, nitrogen and phosphorus in leaf-litter-soil system of *Picea Grassifolia* Forest in the Qilian Mountains. *Acta Pedol. Sin* 53 : 477-489.
- Zhang Y, Xiong KN, Yu YH , Xu M, Cheng W, Tan DJ. 2019. Daily variations of soil respiration among three types of non-wood forest in karst rocky desertification areas, Southern China. *Journal of Central South University of Forestry & Technology* 39: 92-99.
- Zhao SY, Li JT, Sun XK, Zeng DH, Hu YL. 2018. Responses of soil and plant stoichiometric characteristics along rainfall gradients in Mongolian pine plantations in native and introduced regions. *Acta Ecol. Sin* 38 :1-8.
- Zhao XD, Zeng QC, An SS, Fang Y, Ma RT. 2016. Ecological stoichiometric characteristics of grassland soils and plant roots relative to enclosure history on the Loess Plateau. *Acta Pedo. Sin* 53: 1541-1551.
- Zhao YP, Cao Y, Chen YM, Peng SZ. 2017. Ecological stoichiometry in a forest ecosystem in the hilly-gully area of the Loess Plateau. *Acta Ecol. Sin* 37: 5451-5460.
- Zhou P, Geng Y, Ma WH, He JS. 2010. Linkage of functional traits among plant organs in the dominant species of the Inner Mongolia grassland. *Chin J Plan Ecolo* 34: 7-16.
- Zhu WK, Chen SX, Wang ZC, Xu YX, Zhang LL, Du AP. 2017. Ecological stoichiometric characteristics of carbon, nitrogen and phosphorus in litter and soil of *Eucalyptus urophylla* × *E. Grandis* plantation at different forest ages. *J. Trop. & Subtrop. Bot* 25:127-135.
- Zhao QG. 2005. Study on evolution of organic carbon stock in agricultural soils of China: facing the challenge of global change and food security. *Prog. Geogr* 20: 384-393.
- Zhang ZM, Zhou YC, Huang XF, Tian X. 2017. Spatial heterogeneity and distribution characteristics of soil organic carbon density and soil organic carbon storage in a small karst watershed. *J. Soil Water Conserv.* 2:184-190.

