

STOICHIOMETRIC CHARACTERISTICS AND DRIVING MECHANISMS OF PLANTS IN KARST AREAS OF ROCKY DESERTIFICATION OF SOUTHERN CHINA

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Abstract. In this study, we selected karst areas of rocky desertification in southern China as a subject analyze the nutrient transport patterns of the plant–litter–soil continuum and the effect of soil environmental factors on plant stoichiometry in two areas: potential-mild and moderate-severe rocky desertification. The results show that (1) the carbon (C), nitrogen (N), and phosphorus (P) contents of plant leaves in karst areas are higher than those of litter or soil; (2) the plant leaves have a high C storage capacity, P sufficiency, and N deficiency; and (3) the Monte Carlo test of eight soil environmental factors showed that the influences of soil environmental factors on plant stoichiometry vary with the level of rocky desertification. In the area of potential-mild rocky desertification, soil pH, TP, C:P, and SOC were the main driving factors. In the area of moderate-severe rocky desertification, soil TP, TP, C:N, and SWC were the primary driving factors. The comprehensive analysis can provide a theoretical basis for nutrient transport and soil environmental factor regulation in areas with different levels of rocky desertification. It is necessary to target the primary factors for fertilization management and nutrient transport protection in future rock desertification control.

Keywords: *ecosystem, rocky desertification degree, nutrient cycling, environmental factor*

Introduction

The karst region in southern China, centered in Guizhou, is one of the three continuous karst distribution centers in the world and one of China's four ecologically fragile areas, making it the nation's key ecological development hinterland and poverty alleviation core area (LeGrand, 1973; Sheng et al., 2015; Wang et al., 2016a; Wang et al., 2016b). The karst rocky desertification ecosystem has low environmental capacity and poor anti-interference ability and is thus vulnerable to disruptions in ecological security and regional economic and social development (Xiong et al., 2016). Since the 1990s, a large number of vegetation restoration projects have been carried out in the region to promote the comprehensive management of rocky desertification, but the artificial vegetation ecosystem constructed is monotonous in structure and poor in stability, making it ill equipped to mitigate the ecological problems caused by the ecological environment with its shallow and noncontinuous soil layer and poor water conservation capacity (Zeng et al., 2015). Under intensive interference by human activities, natural secondary forests dominated by viny and thorny shrubs and scrub-grassland were formed (Zhong et al., 2018). Therefore, vegetation restoration and reconstruction are a necessary measure for the control of karst rock desertification.

Ecological stoichiometry is a discipline that studies the balance between important elements, such as carbon (C), nitrogen (N), and phosphorus (P), in ecosystem interactions (Zhao et al., 2019). Plant stoichiometric characteristics can characterize the plant's ability

to maintain internal stoichiometric stability while reflecting its adaptability to environmental changes (Sterner and Elser, 2002; Elser et al., 2010). In this way, they can provide the basis for the equilibriums of energy and chemical elements of the ecosystem as well as the structure and function of the ecosystem and soil nutritional diagnosis (Elser et al., 2000; Zhao et al., 2016). In the past, the characterization of stoichiometric characteristics has been focused on individual components of the ecosystem (e.g., soil, vegetation, or litter) or plant organs (plant leaves or fine roots, etc.) (Pena-Claros, 2003; Wu et al., 2010; Wang et al., 2011). Some other studies only examined the differences in stoichiometric characteristics and their intraspecies variation in different succession stages and during seasonal changes. These studies demonstrated that the stoichiometric characteristics of C, N, and P of plant leaves vary with vegetation type, functional group, and species (Sterner and Elser, 2002; Agren, 2004; Reich, 2003), but they rarely addressed the comprehensive situation of the community composed of trees, shrubs, and grasses and thus failed to integrate ecosystem components or comprehensively characterize the stoichiometric characteristics by taking into account environmental factors (Hu et al., 2014; Cao et al., 2015).

Soil is an important factor of terrestrial ecosystems (Gusewell, 2004). To examine the variation characteristics of nutrient elements, it is necessary to thoroughly investigate the conversions between the nutrient return from litter decomposition, soil nutrient supply, and plant nutrient demand in different environments (Xiang et al., 2015). Soil environmental factors not only provide plant nutrients but also catalyze and regulate the process of litter decomposition, thereby sensitively reflecting the direction and intensity of the driving mechanism of nutrients in different karst areas of rocky desertification. Currently, the nutrient element transfer and its regulation mechanism in karst areas with different levels of rocky desertification have rarely been addressed, and there has been no study on the soil environmental factors that drive the plant stoichiometry (including leaf stoichiometry and litter stoichiometry), making it difficult to systematically reveal the coupling mechanism between plants and the environment. Therefore, it is necessary to conduct an in-depth stoichiometric study that takes plants and soil as a whole (Du et al., 2016, 2017).

In this study, our aims were to: (1) examined vegetation, litter, and soil as a whole system and investigated the stoichiometric characteristics of karst areas. (2) Describe the elemental circulation and balance mechanism of the soil–litter–vegetation continuum in environments with different levels of rocky desertification. (3) Revealed the synergistic driving effect of soil environmental factors on the stoichiometric characteristics of plant leaves and litter. Our findings are conducive to strengthening the management and protection of the ecological environment in areas of rocky desertification and provide a theoretical basis for the management of vegetation restoration and reconstruction in karst areas of rocky desertification.

Materials and methods

Overview of the study area

The Salaxi Rocky Desertification Comprehensive Management Demonstration Area of Bijie and the Guanling-Zhenfenghuajiang Rocky Desertification Comprehensive Management Demonstration Area (*Fig. 1*) are the two most representative areas of rocky desertification in Guizhou Province of southwest China, with diverse rocky desertification levels and typical rocky desertification status. These were selected as the

study area. Both demonstration areas have been used as special study cases for the comprehensive control of rocky desertification of Guizhou Province from 1995 to 2019.

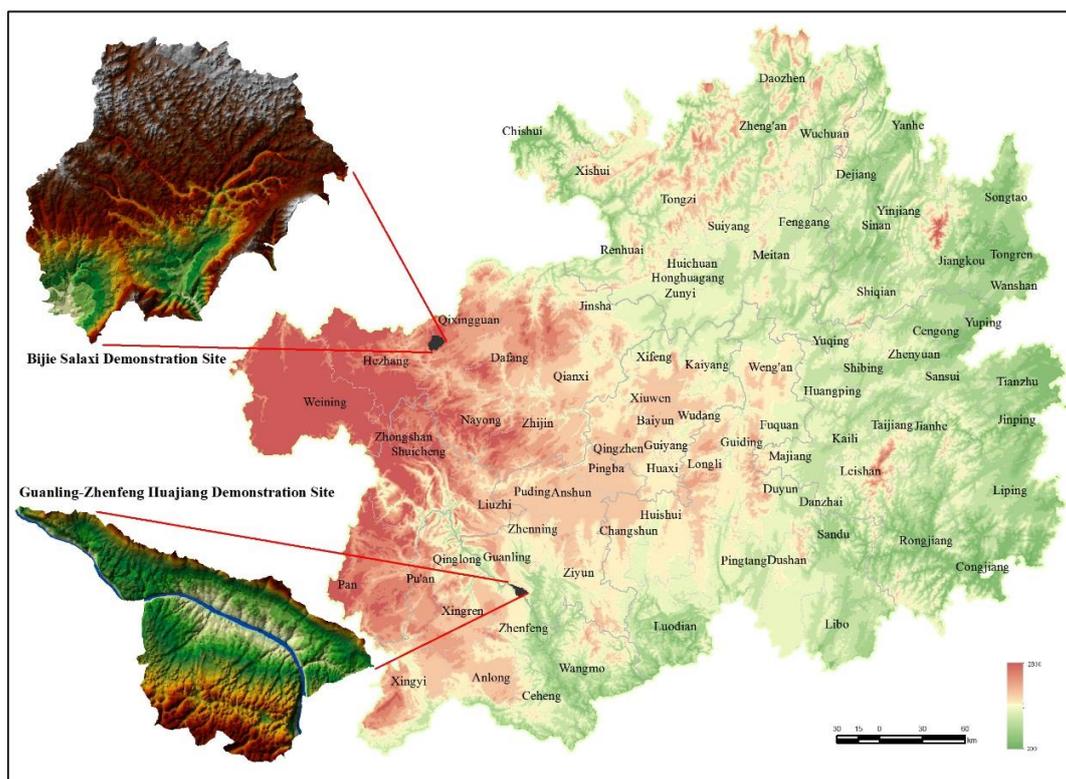


Figure 1. The location of the two demonstration areas in Guizhou Province

The Salaxi Rocky Desertification Comprehensive Management Demonstration Area of Bijie (Fig. 2), located in the northwest of Guizhou Province ($105^{\circ}01'10''$ - $105^{\circ}08'39''$ E, $27^{\circ}11'08''$ - $27^{\circ}17'30''$ N) and the southwest of Bijie city, is within the tributary area of the Liuchong River Basin. It has a north subtropical humid monsoon climate (annual average temperature: 12°C ; annual average precipitation: 984.40 mm) and an altitude of 1,495-2,200 m (relative height difference: 705 m). The total size of the demonstration area is 86.27 km^2 , of which the karst area accounts for 73.94%. The areas of potential, mild, moderate, and severe rock desertification account for 30.91%, 22.26%, 8.57%, and 3.09% of the karst area, respectively. The soil is dominated by zonal yellow soil, with a small proportion of yellow-brown soil and weathered calcareous soil. The native vegetation was mostly destroyed and is now dominated by secondary forests, in which *Pinus armandii*, *Pinus yunnanensis*, *Betula luminifera*, *Populus alba*, and *Quercus variabilis* dominate the arborous layer; *Pyracantha fortuneana*, *Rosa roxburghii*, *Cotoneaster franchetii*, *Hypericum chinense* L., *Rhododendron simsii*, and *Corylus heterophylla* var. *sutchuenensis* dominate the shrub layer; and *Trifolium repens*, *Lolium perenne*, *Dactylis glomerata* L., *Bromus catharticus*, and *Imperata cylindrica* dominate the grassland.

The Guanling-Zhenfenghuajiang Desertification Comprehensive Management Demonstration Zone of Bijie (Fig. 3) is in the southwestern part of Guizhou Province ($105^{\circ}36'30''$ - $105^{\circ}46'30''$ E, $25^{\circ}39'13''$ - $25^{\circ}41'00''$ N) and the river banks of the Huajiang Valley of the Beipan River, which is to the south of Guanling County and the north of Zhenfeng County. It has a north subtropical monsoon climate (annual average

temperature: 18.4 °C; annual average precipitation: 1,100 mm) and an altitude of 450-1,450 m (relative height difference: 1,000 m). The total area of the demonstration area is 51.62 km², of which the karst area accounts for 87.92%, and the areas of potential, mild, moderate, and severe rock desertification account for 24.54%, 40.48%, 17.93%, and 17.06% of the total karst area, respectively. The soil is dominated by yellow soil and yellow calcareous soil. The natural vegetation in the area includes *Cupressus funebris*, *Eucalyptus* spp., *Tectona grandis*, *Koelreuteria paniculata*, and *Cladrastis platycarpa* (Maxim.) Makino in the arborous layer; *Broussonetia papyrifera*, *Viburnum foetidum* var. *ceanothoides*, *Alchornea trewioides*, and *Rhus chinensis* Mill. in the shrub layer; and *Pennisetum hybridum*, *Lonicera japonica*, *Miscanthus sinensis*, *Arthraxon hispidus*, and *Imperata cylindrica* in the grassland.

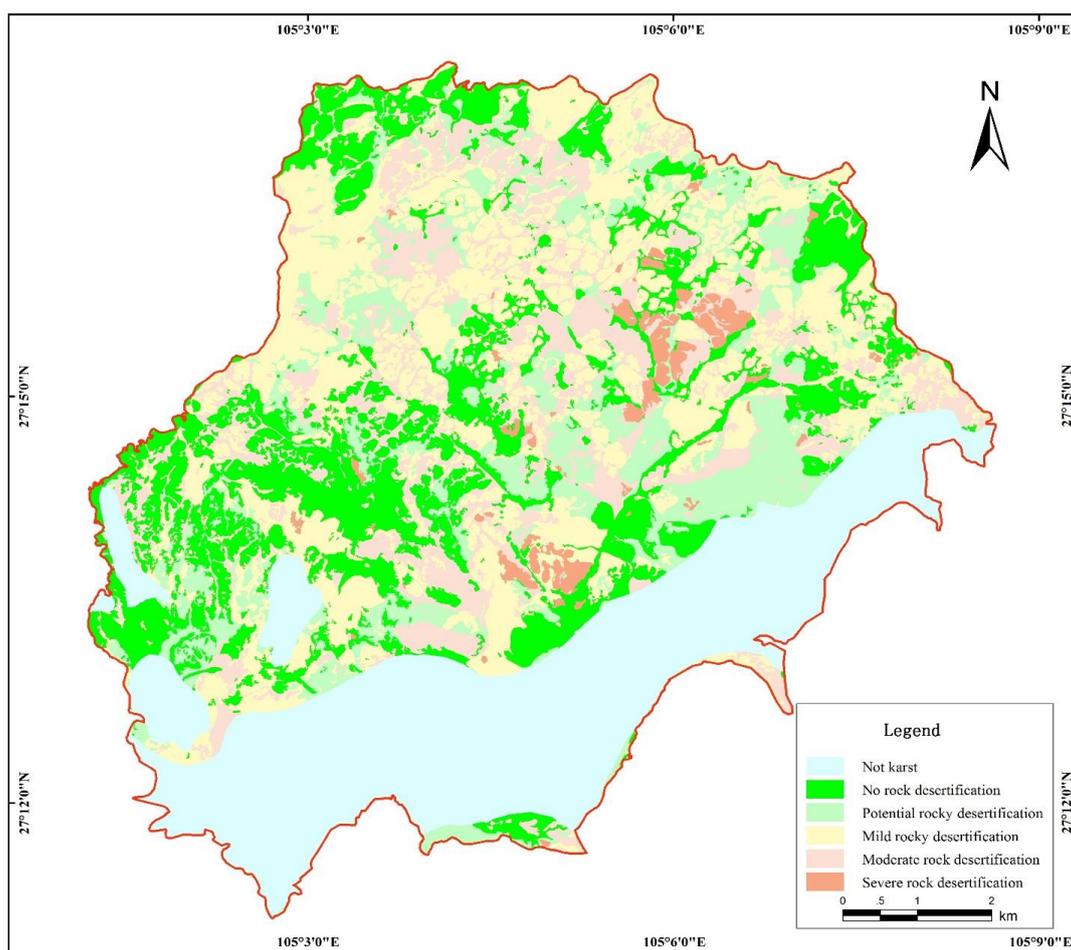


Figure 2. The Salaxi Rocky Desertification Comprehensive Management Demonstration Zone of Bijie

Sample collection

In the study area, the communities of trees, shrubs, and herbs with neat forests, uniform forest distribution, and similar average forest age were selected as subjects. In each demonstration area, 40 experimental plots were designed (80 in total in the two demonstration areas), including 27, 27, and 26 plots for trees, shrubs, and herbs,

respectively, in which typical quadrats of 20 m × 20 m were designed. The samples were collected in late August 2018, when plants were in the fast growth season. When collecting plant leaves, five to six healthy individual plants of the dominant species with similar vigor were randomly chosen from each quadrant, and healthy and mature leaves were collected from each of these plants facing four directions, i.e., east, west, south, and north, which were then mixed well and placed in a brown paper bag to be transferred to the laboratory. In each quadrant, approximately 350 g of each of dry, undecomposed, and semi-decomposed litter was collected from multiple spots. At each sampling site, soil samples were collected from the 0-20 cm soil depth (due to the shallow topsoil depth, in places with a topsoil depth shallower than 20 cm, the samples were collected from the actual soil depth) in 3-4 root zones in an S-shaped sampling line and mixed, from which 1 kg was taken using the quartering method and brought back to the laboratory. Plant leaves and litter were baked in an oven at 65 °C to constant weight and then pulverized to powder 0.1 mm in size. The soil samples were air-dried, removed of impurities such as animal and plant residues and gravels, and then ground using an agate mortar and sieved through a 100-mm sieve. The sieved soil sample was placed in a plastic bag for analysis of soil chemical properties.

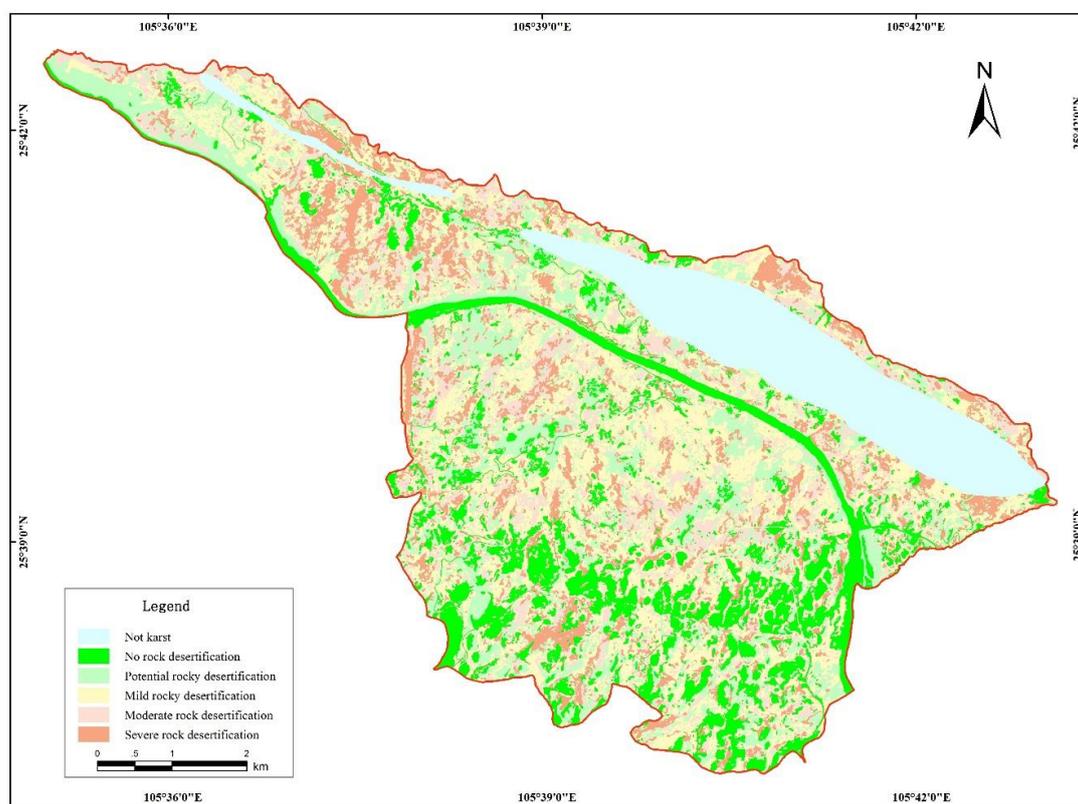


Figure 3. The Guanling-Zhenfenghuajiang Desertification Comprehensive Management Demonstration Zone

Sample analysis

The organic carbon (OC) contents of the leaf, litter, and soil were determined by oxidation with potassium dichromate under external heating, the total nitrogen (TN)

contents using the semi-micro Kjeldahl method after heating in perchloric acid-sulphate acid, and the total phosphorus (TP) contents using Mo-Sb colorimetry–UV spectrophotometry after heating in perchloric acid and sulfuric acid. Soil pH was determined using a potentiometer in the soil solution (water: soil ratio 2.5:1). Soil water content (SWC) was determined using the cutting ring method.

Data processing and statistical analysis

The nutrient content data of plant leaf, litter, and root-zone soil were performed with one-way analysis of variance and regression analysis. The result of a data distribution test showed that the contents of C, N, and P of plant leaf, litter, and soil samples mostly assumed nonnormal distributions but were normally distributed after logarithmic transformation, so their log-transformed values were described with geometric means. The significance test of multiple comparisons was performed using the least significant difference method, and $P < 0.05$ indicated that the difference was significant. The C:N:P comparison results were plotted using 3D Scatter software. The above-described statistical analyses of the data were performed within Origin 8.6 for Windows.

The soil C, N, and P contents of different sampling sites and their respective stoichiometric variation strengths were categorized into three levels (Eq. 1): low [coefficient of variation (CV) < 10%], moderate (10% < CV < 100%), and high (CV > 100%) (Zheng et al., 2004). According to the method of Xiong et al. (2011) (Table 1), the 80 experimental plots were categorized into two types: potential-mild rocky desertification and moderate-severe rocky desertification.

$$CV = \frac{SD}{MN} \times 100\% \quad (\text{Eq.1})$$

SD is the standard deviation; MN is the mean.

Table 1. Classification standard of karst rock desertification

| Rocky desertification level | Rock exposure rate | Vegetation + soil coverage | Reference indicator |
|---------------------------------|--------------------|----------------------------|--|
| No rock desertification | < 20 | > 80 | Nonterraced dry hillside land with a slope of $\leq 15^\circ$, dikes, construction land, etc., with good ecological environment, densely populated trees and shrubs, with no or insignificant soil erosion; suitable for agricultural, forestry, or animal husbandry production |
| Potential rocky desertification | 20–30 | 80–70 | Nonterraced dry hillside land and grassland, etc. with a slope of $> 15^\circ$, with sparsely populated arbor, shrubby and herbaceous vegetation, and good soil-forming conditions but obvious soil erosion; showing a tendency of rock exposure |
| Mild rocky desertification | 31–50 | 69–50 | Rocks begin to be exposed, with obvious soil erosion, low vegetative patch structure, and dominance of sparse shrubs or artificial dry-land vegetation |
| Moderate rock desertification | 51–70 | 49–30 | Rocky desertification is intensifying, with severe soil erosion, shallow topsoil, dominance of rocky hillside land, and sparse shrub-grass zone |
| Severe rock desertification | > 70 | < 30 | Rocky desertification is severe, with essentially no soil erosion due to the absence of topsoil, and dominant with lands difficult to use that is about to lose agricultural value |

The relationship between plant leaf and litter stoichiometry and soil environmental factors was analyzed using Canoco 4.5 for Windows. First, we performed detrended correspondence analysis on the indicators and found that when the maximum value of the gradient length was less than 3, the linear ranking method was suitable, so we adopted the redundancy analysis of the linear model as the ranking model to examine the relationship between the stoichiometry and the environmental factors. The importance of soil environmental factors was ranked through the Monte Carlo test, and the effect of individual environmental factors on plant stoichiometry was determined using the *t*-value biplot of Canoco 4.5. When interpreting the biplot, if the arrowed connection line of a certain plant stoichiometric indicator was completely within a circle, then it indicated that this indicator was significantly correlated with the soil environmental factor (in the red circle: significant positive correlation; in the blue circle: significant negative correlation; the percentage and length of the arrow that fall within the circle represent the strength of the correlation) (Leps and Smilauer, 2003).

Results and analysis

Stoichiometric characteristics of nutrients of Karst rocky desertification ecosystems

The contents of C, N, and P in plant leaves in karst rocky desertification ecosystems were higher than those in litter or soil, while the ratios of C:N, C:P, and N:P of litter were higher than those of plant leaves or soil. The CVs of stoichiometric values of different nutrients differed, and the variations were mostly moderate. Overall, the CV of stoichiometric values of soil was the highest, followed by that of litter and that of plant leaves. The CV of stoichiometric values of soil was significantly different from those of soil or litter ($P < 0.05$) (Table 2).

Table 2. *Stoichiometric characteristics of nutrients in karst areas of rocky desertification*

| | C | | N | | P | | C:N | | C:P | | N:P | |
|---------------------|--------------|--------|-------------|--------|------------|--------|-------------|--------|---------------|--------|------------|--------|
| | Mean±SE | CV (%) | Mean±SE | CV (%) | Mean±SE | CV (%) | Mean±SE | CV (%) | Mean±SE | CV (%) | Mean±SE | CV (%) |
| Plant leaves | 482.96±4.36a | 8 | 12.39±0.6a | 40 | 1.76±0.07a | 35 | 43.77±1.57a | 30 | 303.09±11.41a | 32 | 7.06±0.16a | 19 |
| Litter | 166.4±4.8a | 22 | 10.55±0.31a | 23 | 1.24±0.07b | 44 | 46.95±1.68a | 28 | 432.41±18.50b | 34 | 9.61±0.46b | 38 |
| Soil | 38.24±1.73b | 40 | 2.62±0.15b | 50 | 0.9±0.05c | 43 | 18.84±1.40b | 65 | 51.81±3.66c | 65 | 3.02±0.14c | 40 |

In the same column, the different lower-case letters represent statistically significant differences ($P < 0.05$); the data are presented as mean ± SE (standard error)

The stoichiometric characteristics of plant leaf, litter, and soil under different levels of rocky desertification

The stoichiometric characteristics differed significantly between the areas with different levels of rocky desertification (Fig. 4). The C:N:P ratios of plant leaves, litter, and soil in the area of potential-mild rocky desertification were 361:7:1, 498:12:1, and 69:3:1, respectively, and those in the area of moderate-severe rocky desertification were 224:7:1, 301:6:1, and 29:3:1, respectively. Compared with the area with a higher level of rocky desertification, the area with a lower level of rocky desertification had higher ratios of C:N and C:P in the soil and plant leaves and higher ratios of C:P and N:P in the

litter. The N:P ratio of plant leaves and litter were 7.25 and 12.58 in the area of potential-mild rocky desertification, respectively, and 6.91 and 6.64 in the area of moderate-severe rocky desertification. The results indicate that the C content and the N:P ratios of plant leaves and litter in the area of potential-mild rocky desertification are higher than in the area of moderate-severe rocky desertification.

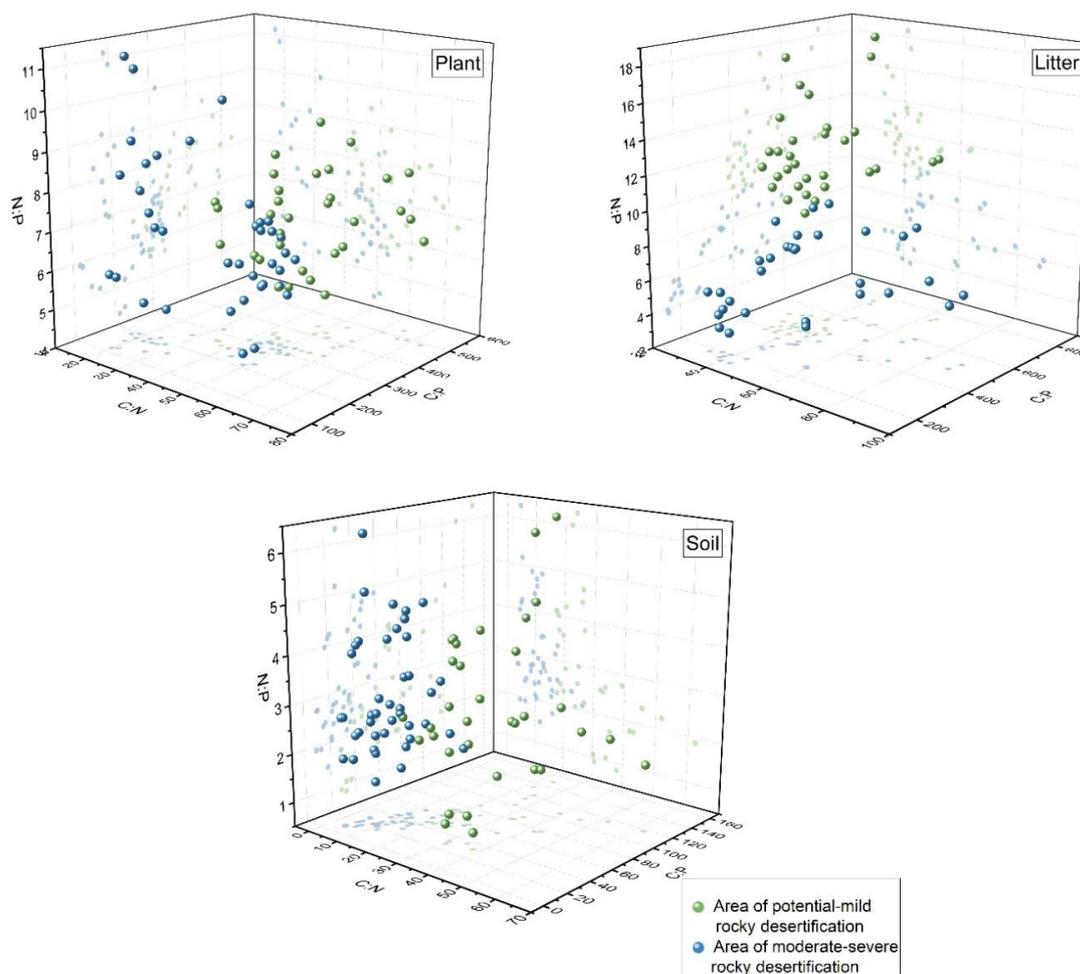


Figure 4. Stoichiometric characteristics of areas with different levels of rocky desertification

Relationship between stoichiometric characteristics of plant leaves, litter, and soil environmental factors in areas of rocky desertification

Stoichiometric characteristics of the areas of rocky desertification and RDA ordination of their respective interpretation powers

The stoichiometric characteristics and the RDA ordination of their respective interpretation powers (Table 3) showed that the cumulative interpretation power of the area of potential-mild rocky desertification and that of the area of moderate-severe rocky desertification on the first and second RDA ordination axes were 72.6% and 68.4%, respectively. The correlation between the stoichiometry of the first and second axes and the soil environmental factors of the area of potential-mild rocky desertification were 0.953 and 0.969, respectively, and the correlation between the

stoichiometry of the first and second axes and the soil environmental factors of the area of moderate-severe rocky desertification were 0.916 and 0.853, respectively. Therefore, the two ordination axes were essentially vertical, indicating that the ordination results were credible. The cumulative interpretation power on the relationship between the stoichiometry and the soil environmental factors was 80% and 90.9% for the area of potential-mild rocky desertification and the area of moderate-severe rocky desertification, respectively, accounting for 81.5% and 91.8% of the total interpretation power. These data indicate that the first and second axes can well reflect the relationship between the stoichiometry and soil environmental factors.

Table 3. The stoichiometric characteristics and their RDA ordination analysis on the interpretation power

| | Ordination axis | Axis I | Axis II | Axis III | Axis IV |
|-------------------------------------|--|--------|---------|----------|---------|
| Potential-mild rock desertification | Interpretation power of stoichiometric characteristics, % | 43.4 | 29.2 | 9.5 | 6 |
| | Correlation between stoichiometric characteristics and the soil environmental factors | 0.953 | 0.969 | 0.872 | 0.95 |
| | Cumulative interpretation power of stoichiometric characteristics, % | 43.4 | 72.6 | 82.1 | 88.1 |
| | The cumulative interpretation power of stoichiometry-soil environmental factor relationship, % | 48.3 | 80.0 | 91.4 | 98.1 |
| | Canonical eigenvalue | | 89.9 | | |
| | Total eigenvalue | | 1.00 | | |
| Moderate-mild rocky desertification | Interpretation power of stoichiometric characteristics /% | 53.3 | 15.1 | 4.4 | 1.7 |
| | Correlation between stoichiometry and soil environmental factors | 0.916 | 0.853 | 0.643 | 0.781 |
| | Cumulative interpretation power of stoichiometric characteristics /% | 53.3 | 68.4 | 72.7 | 74.5 |
| | The cumulative interpretation power of stoichiometry-soil environmental factor relationship /% | 70.8 | 90.9 | 96.7 | 99.0 |
| | Canonical eigenvalue | | 0.752 | | |
| | Total eigenvalue | | 1.00 | | |

The 2-D RDA ordination results show that the lengths of arrowed connection lines of the soil environmental factors pH, TP, C:P, and SOC were the longest in *Figure 5a* and that those of C:P, TP, C:N, and SWC were the longest in *Figure 5b*, indicating that these soil environmental factors had good interpretation power for the differences in the changes in plant leaves and litter, which are consistent with the importance ordination results shown in *Table 4*. *Figure 5a* also shows that the directions of the arrows between C:P and DC:P, between pH or SOC and DC, and between TP or SWC and DP were consistent; that the angles between the lines were small; and that the factors had a positive correlation, indicating that C:P, pH, SOC, TP, and SWC had a positive effect on some plant ecological stoichiometric characteristics and were important factors affecting plant ecological stoichiometric properties in the area of

potential-mild rocky desertification. *Figure 5b* shows that the directions of the arrows between C:P and ZC:P, between TP and ZP, between C:P and ZC:P, between SOC or N:P and DN:P, and between SWC and ZN were consistent; that the angles between the lines were small; and that the factors had a positive correlation. The results indicate that C:P, TP, C:N, SWC, C:P, and N:P had a positive effect on some plant ecological stoichiometric characteristics and were important factors affecting plant ecological stoichiometric properties in the area of moderate-severe rocky desertification.

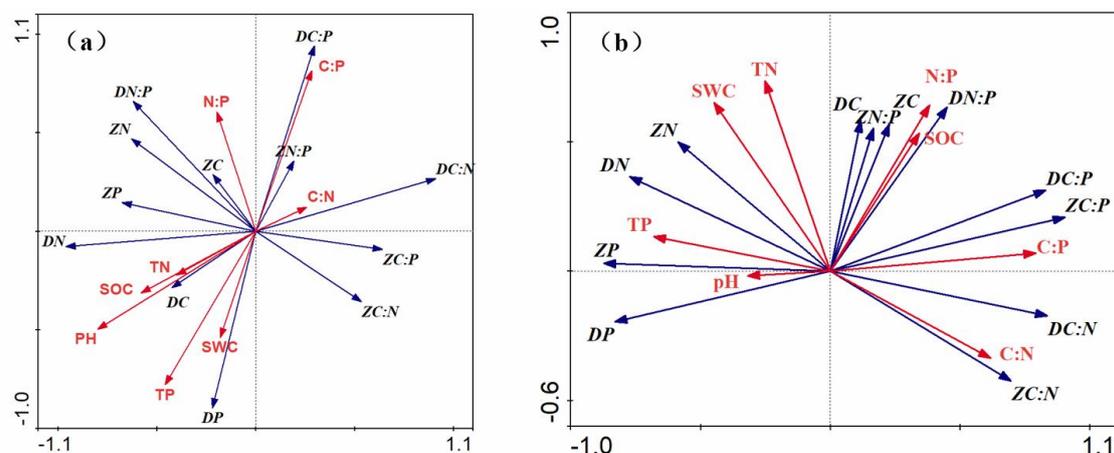


Figure 5. Redundancy analysis on plant stoichiometric characteristics and soil environmental factors. Note: pH, SOC, TN, TP, C:N, C:P, and N:P are the soil pH, soil organic carbon content, soil total nitrogen content, soil total phosphorus content, and their respective stoichiometric ratios, respectively; ZC, ZN, ZP, ZC:N, ZC:P, and ZN:P are the organic carbon content, total nitrogen content, and total phosphorus content in plant leaves and their respective stoichiometric ratios, respectively; DC, DN, DP, DC:N, DC:P, and DN:P are the organic carbon content in the litter, total nitrogen content in plant litter, total phosphorus content in plant litter, and their respective stoichiometric ratios, respectively. Part (a) shows the RDA results of plant stoichiometric characteristics and soil environmental factors in the area of potential-mild rocky desertification. Part (b) shows the RDA results of plant stoichiometric characteristics and soil environmental factors in the area of moderate-severe rocky desertification

Ranking the importance of soil environmental factors to plant stoichiometric characteristics

We performed the Monte Carlo test to rank the eight soil environmental factors (Table 4) and found that the effects of soil environmental factors on plant stoichiometric characteristics differed between areas with different levels of rocky desertification. The order of importance of the soil environmental factors in the area of potential-mild rocky desertification was $pH > TP > C:P > SOC > N:P > TN > SWC > C:N$. The effects of pH, TP, C:P, and SOC on plant stoichiometric characteristics were significant ($P < 0.05$). Compared with other soil environmental factors, pH could better represent the difference in plant stoichiometric characteristics. The order of importance of the soil environmental factors in the area of moderate-severe rocky desertification was $C:P > TP > C:N > SWC > N:P > TN > SOC > pH$. The effects of C:P, TP, C:N, and

SWC were significant ($P < 0.05$), and compared with the other soil environmental factors, C:P better represented the difference in plant stoichiometric characteristics.

Table 4. Monte Carlo test ranking of eight soil environmental factors

| | Soil factor | Order of importance | Interpretation power (%) | Importance (F) | Significance (P) |
|---|-------------|---------------------|--------------------------|----------------|------------------|
| Area of potential-mild rocky desertification | pH | 1 | 35.6 | 6.625 | 0.002 |
| | TP | 2 | 27.8 | 4.625 | 0.006 |
| | C:P | 3 | 23.4 | 3.666 | 0.012 |
| | SOC | 4 | 19 | 2.809 | 0.036 |
| | N:P | 5 | 13.5 | 1.874 | 0.128 |
| | TN | 6 | 10.9 | 1.472 | 0.218 |
| | SWC | 7 | 10.0 | 1.336 | 0.264 |
| | C:N | 8 | 4.5 | 0.57 | 0.684 |
| Area of moderate-severe rocky desertification | C:P | 1 | 33.7 | 9.138 | 0.002 |
| | TP | 2 | 25.9 | 6.294 | 0.004 |
| | C:N | 3 | 22.6 | 5.252 | 0.004 |
| | SWC | 4 | 17.3 | 3.76 | 0.016 |
| | N:P | 5 | 14.7 | 3.106 | 0.066 |
| | TN | 6 | 12.3 | 2.525 | 0.076 |
| | SOC | 7 | 10.8 | 2.184 | 0.134 |
| | pH | 8 | 5.6 | 1.067 | 0.354 |

Effects of individual soil environmental factors on plant stoichiometry

We generated impact diagrams of individual soil environmental factors using the t-value biplots of the first four factors affecting plant stoichiometry in the area of potential-mild rocky desertification (Fig. 6). The Canoco biplot for pH (Fig. 6a) shows that the DP arrow falls within the red circle and that the DC:P arrow falls within the blue circle, indicating that pH had a significantly positive correlation with DP but a significantly negative correlation with DC:P. Figure 6b shows that soil TP had a significantly positive correlation with DN:P and DN and a positive correlation with plant C, N, and P. Figure 6c and d show that the plant stoichiometric indicators do not fall within the circle but mostly pass through the red circle or the blue circle, indicating that the plant stoichiometric characteristics were correlated ($P < 0.05$) with the soil environmental factors C:P and SOC, but not highly correlated ($P < 0.01$).

The t-value biplot of the area of moderate-severe rocky desertification is shown in Figure 7. Figure 7a shows that the DC:N and ZC:N arrows pass through the red circle and that the ZC:N arrow has more of its length within the red circle, indicating that C:P had a positive correlation with DC:N and ZC:N (with a stronger correlation for ZC:N). Figure 7b and c show that DC, ZC, ZN:P, DN:P, DC:P, and ZC:P pass through the blue circle and the red circle, respectively, indicating that these environmental factors were correlated negatively with TP but positively with C:N. Figure 7d shows the analysis result of SWC, indicating that SWC had a significantly positive correlation with ZP and DP, which fall into the red circle, but a significantly negative correlation with DN:P, DC:P, ZC:P, and DC:N, which fall into the blue circle.

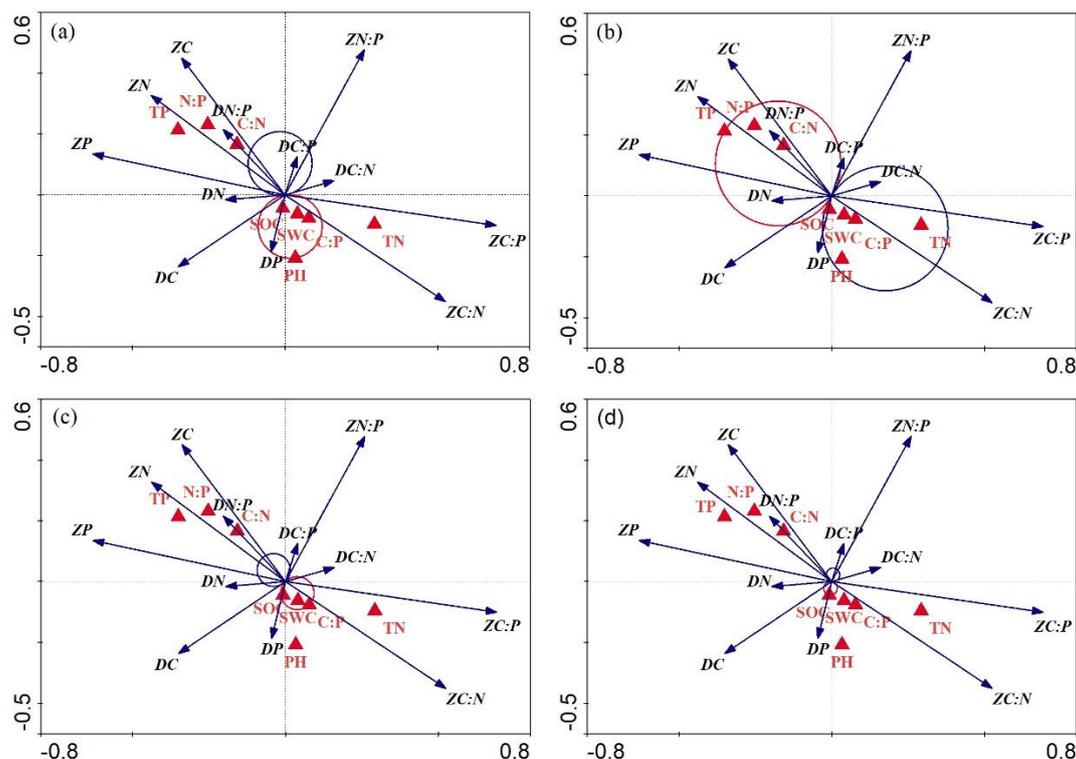


Figure 6. Effect of individual soil environmental factors on plant stoichiometry in the area of potential-mild rocky desertification. (a) pH; (b) TP; (c) C:P; (d) SOC

Discussion

Ecological stoichiometric characteristics of karst areas of rocky desertification

In this study, we examined the stoichiometric characteristics of plant leaves, litter, and soil of karst areas and found that the C, N, and P contents of plant leaves in karst areas of rocky desertification were higher than those of litter or soil. This was because the C, N, and P contents of plant leaves, an important nutrient storage organ, are much higher than in other plant organs (Minden and Kleyer, 2014). After fresh leaves fall, the organic components such as crude fat, tannins, and soluble sugars are decomposed, leading to significantly reduced C content in the litter (Yang et al., 2007). Litter had lower contents of N and P than leaves. This is because before leaves fall, the nutrients in the leaves are transferred to other components, absorbed, and utilized. The reduction in N may happen because the leaves utilizes nitrogen in photosynthesis, and high N use efficiency reduces the P content in litter (Zhao et al., 2016). Plants absorb N and P from the soil and further transfer some nutrients to plants through the nutrient reabsorption process, resulting in larger changes to the N and P contents in litter than in plant leaves, and thus the C:N and C:P contents are found in the order litter > plant > soil (Zeng et al., 2015). Soil nutrient content is an important indicator for evaluating organic matter composition and soil quality, and the soil nutrient variability in the same ecosystem is largely affected by environmental factors (Li et al., 2018). Soil nutrients in karst areas showed moderate variation but had significant fluctuations, which are caused by the changes in environmental factors derived from complicated landforms, high spatial heterogeneity, and the interference of human activities, which are consistent with the conclusions of Zhu et al. (2013) and Li et al. (2014).

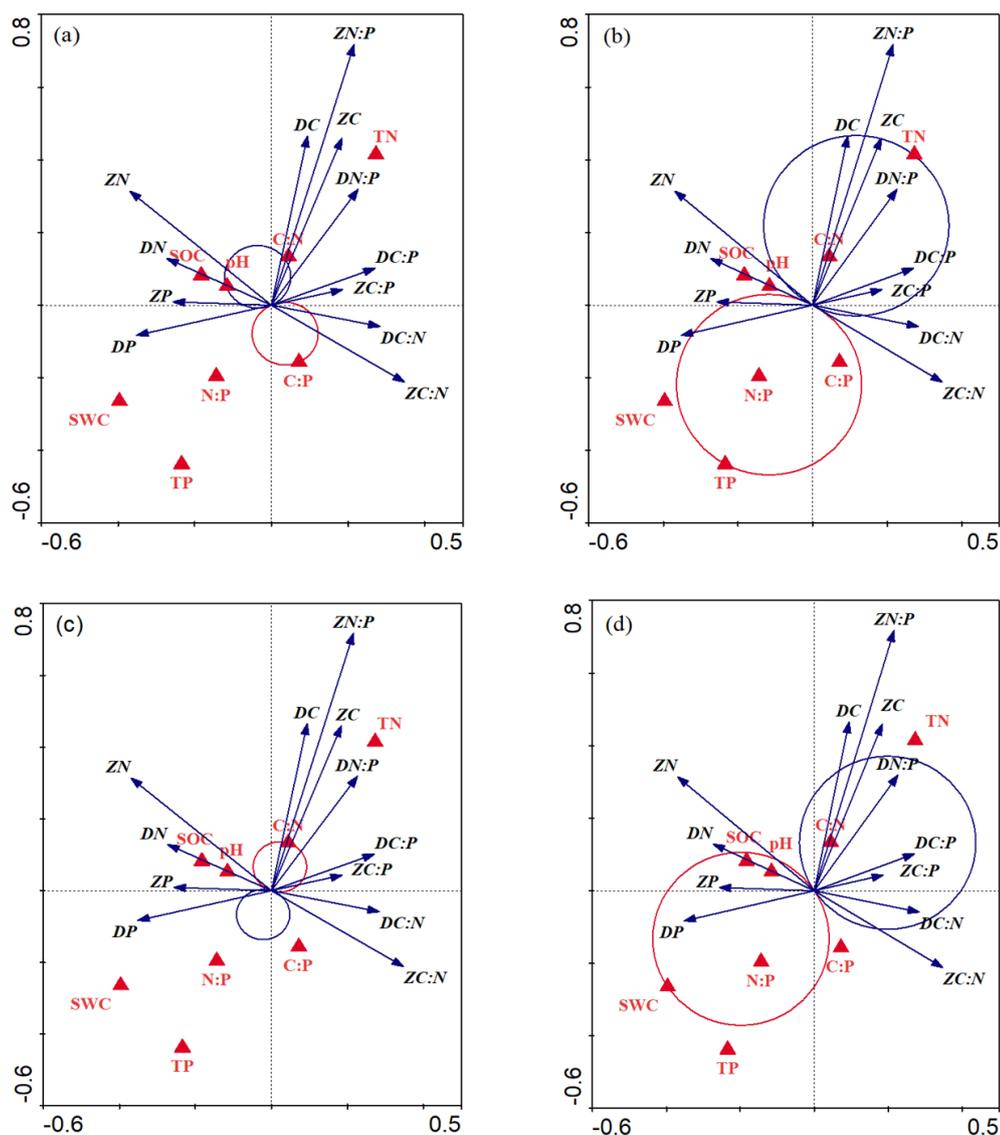


Figure 7. Effect of individual soil environmental factors on plant stoichiometry in the area of moderate-severe rocky desertification. (a) C:P; (b) TP; (c) C:N; (d) SWC

In this study, the soil P content of the areas of rocky desertification was $0.9 \text{ mg} \cdot \text{g}^{-1}$, which is lower than that of other ecosystems (Koerselman and Meuleman, 1996; Jiao et al., 2013). This was likely caused by the strong leaching effect derived from high precipitation in karst areas in southwestern China. However, compared with the average content of soil P in China (0.56 g/kg) (Tian et al., 2010), the P content of the karst areas is still higher, indicating that despite strong leaching effects in the rocky desertification environment, the P content of the karstification product from bare rocks can readily accumulate in the soil, showing a significant aggregation effect, which is consistent with the findings of Sheng et al. (2013). We also found that the average C content in plant leaves was $482.96 \text{ mg} \cdot \text{g}^{-1}$, which is higher than that ($464.00 \text{ mg} \cdot \text{g}^{-1}$) of 492 terrestrial plant species around the world reported by Elser et al. (2000) and that ($438.00 \text{ mg} \cdot \text{g}^{-1}$) of China's grassland ecosystem (He et al., 2006), indicating

that the karst area has strong C storage capacity and thus high accumulation of organic matter. The average N content in plant leaves was $12.39 \text{ mg}\cdot\text{g}^{-1}$, which is significantly lower than that ($20.09 \text{ mg}\cdot\text{g}^{-1}$) at the global scale (Reich and Oleksyn, 2004) and that of 753 species reported by Han et al. (2005), indicating N deficiency in the karst area, likely because the high precipitation in the region (over 980 mm annually) is prone to cause the leaching of available nitrogen, which has a high mobility.

Ecological stoichiometric characteristics of areas with different levels of rocky desertification

Due to differences in geographical conditions, the N and P contents and the stoichiometric characteristics of C:N:P of plant leaves in different habitats and different tree species vary profoundly (Reich and Oleksyn, 2004; Han et al., 2005). In this study, we found that the C content in plant leaves in the area of potential-mild rocky desertification was higher than that in the area of moderate-severe rocky desertification. Because the soil is a primary environmental factor in karst areas, its stoichiometric characteristics affect the plant community characteristics of areas with different levels of rocky desertification (Zhao et al., 2019). In the area of moderate-severe rocky desertification, the rock exposure rate was high, the vegetation coverage was low, and the biomass was low, leading to the reduced stock of soil organic carbon and the accelerated decomposition of organic matter and thus a lower C content than in the area with a lower level of rocky desertification. This finding is consistent with the findings of Yang (2000) and Long et al. (2002). They found that soil C:N is inversely proportional to the decomposition rate of organic matter and that the soil with a lower C:N ratio is faster at mineralization (Zhu et al., 2013). In this study, we found that the soil C:N ratio was 28.72 in the area of potential-mild rocky desertification and was 10.85 in the area of moderate-severe rocky desertification. The soil C:N ratio in the area of moderate-severe rocky desertification was lower than the global average (14.3) (Zhao et al. 2015), indicating higher rates of decomposition and mineralization of soil organic matter. The C:N and C:P ratios in plant leaves and soil in the area of potential-mild rocky desertification were higher than those in the area of moderate-severe rocky desertification because in the area of moderate-severe rocky desertification, topsoil was shallow and had high temperature and humidity, weak nutrient retention ability, and fast nutrient turnover, leading to low nutrient use efficiency and nutrient resorption rate in plants (Cui et al., 2015). The critical values for plant N:P are 14 and 16. When $\text{N:P} < 14$, the ecosystem is N-limited, and when $\text{N:P} > 16$, it is P-limited (Koerselman and Meuleman, 1996; Tessier and Raynal, 2003). In this study, we found that the N:P ratios of the area of potential-mild rocky desertification and the area of moderate-severe rocky desertification were 6.91 and 7.25, respectively, indicating that both areas were N-limited. In the shrub and grass vegetation of the karst areas, we found that N was deficient while P was sufficient, mainly because in these areas, the rock exposure rate was high, the vegetation coverage was low, nutrients were concentrated in the arborous layer, and the symbiotic nitrogen fixation system and the slightly weathered soil were scarce (Hedin, 2004). Thus, supplementation with N fertilizer during the control process can increase the N content of the vegetation. Our results indicate that the limiting factors inhibit vegetation recovery and development and that limiting factors should be effectively regulated in forest management strategies.

Driving mechanisms of the effect of soil environmental factors on plant stoichiometry

The chemical elements of vegetation are mainly derived from the soil, and their contents are closely related to their soil contents. C, N, and P are the basic constituent elements of plants that are converted in the plant–litter–soil continuum, manifesting the nutrient cycling and use efficiency (Zeng et al., 2015). Soil pH, TP, C:P, SOC, C:N, and SWC are the main driving factors affecting plant stoichiometry. The soil environmental factors TP and C:P significantly affected the stoichiometric characteristics of the vegetation in both areas of rocky desertification, indicating that the P level in plants is closely coupled with that in soil. Soil P level is positively correlated to C, N, and P levels in plant leaves, indicating that the soil P can facilitate the absorption of C, N, and P by plant leaves. The reason that P is an important factor is that the P in soil is directly produced by rock weathering and thus is a sedimentary element. In karst areas, soil and rock are in direct contact, which is prone to cause soil erosion and slides. Therefore, the fluctuation in the content of P exerts a greater influence on the ratios of elements than other fluctuations. In the future plant nutrient recycling and utilization processes, soil P should be optimized and adjusted to achieve nutrient balance.

The soil environmental factor TP was positively correlated with DN:P and DN (Fig. 6b) but negatively correlated with DC, ZC, ZN:P, DN:P, DC:P, and ZC:P (Fig. 7b), indicating that in environments with different levels of rocky desertification, the driving effect of soil environmental factors on plant nutrient absorption varies, which is consistent with the findings of Chen et al. (2018). The soil environmental factors TP (Fig. 7b) and SWC (Fig. 7d) in the moderate-severe rocky desertification demonstration area showed similar correlations in the analysis of the effects of individual environmental factors, indicating that the driving mechanisms of the two are identical. This is mainly because the high rainfall in the karst area accelerates TP leaching, which, coupled with ground runoff, leads to the simultaneous losses of soil TP and SWC and thus a certain correlation between TP and SWC. SWC showed a significantly positive correlation with ZP and DP and a significantly negative correlation with DN:P, DC:P, ZC:P, and DC:N (Fig. 7d), indicating that the increase in SWC significantly increases P contents in plant leaves and litter while decreasing the contents of C:N, C:P, and N:P of litter, indicating that SWC can effectively increase the nutrient transfer rate of plant leaves, resulting in reduced C:N, C:P, and N:P ratios in litter.

The changes to soil nutrient supply in the environment of karst rocky desertification can affect various plant physiological and biochemical reactions to some extent. After long evolutionary adaptation, plants form relatively stable elemental stoichiometries, which also reflects plants' adaptation strategy to extreme environments. The RDA on the area of potential-mild rocky desertification showed that soil pH played the most critical role in plant stoichiometry. Past studies have shown that soil pH directly affects the decomposition, mineralization, redox reaction, and enzyme reaction rates of soil organic matter, and species richness is positively correlated with pH value (Dick et al., 2000; Xu et al., 2006; Tian et al., 2019). The species richness and the pH-driving impact of the area of potential-mild rocky desertification was higher than those of the area of moderate-severe rocky desertification. Among the soil environmental factors in area of moderate-severe rocky desertification, soil C:P showed a more profound effect and a positive correlation with DC:N and ZC:N (Fig. 7a), indicating that the increase in soil C:P can promote the C:N in plant leaves, while the C:N in litter is fully in line with the characteristics of C:N in plant leaves, consistent with the conclusions on the stoichiometric characteristics of wetland plants and litter by Wang et al. (2011).

Conclusions

Nutrient cycling and transfer occur in the plant–litter–soil continuum in karst areas of rocky desertification, which is manifested in the C, N, and P contents in plant leaves being higher than those in litter or soil.

The leaves of plants in karst areas showed N deficiency, P sufficiency, and a strong C storage capacity. Supplementation with N fertilizer during the control process can increase the vegetation biomass yield.

The decomposition and mineralization rates of soil organic matter in the area of moderate-severe rocky desertification is higher than in the area of potential-mild rocky desertification. The order of importance of soil environmental factors in the area of potential-mild rocky desertification is $\text{pH} > \text{TP} > \text{C:P} > \text{SOC}$. The soil pH has the strongest driving effect on plant stoichiometry. The order of importance of soil environmental factors in the area of moderate-severe rocky desertification is $\text{C:P} > \text{TP} > \text{C:N} > \text{SWC}$. The soil C:P has the strongest driving effect on plant stoichiometry.

It is necessary to target the primary factors for fertilization management and nutrient transport protection in future rock desertification control. In the diagnosis of plant nutrient restriction, in addition to considering the role of soil environmental nutrient factors, it is also necessary to increase the mechanism of plant photosynthesis and respiration on the maintenance of plant nutrients, as well as the decomposition and interference of underforest microenvironment, soil animals and microbial activities on litter. In the future, we should increase the systematic research of multi-disciplinary, multi-angle and multi-thinking. At the same time, the environment and livelihood problems caused by stony desertification need to be paid more attention all over the world.

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