RESPONSE OF NUTRIENT RESORPTION CHARACTERISTICS OF LEAVES AND RHIZOSPHERE SOILS TO VEGETATION SUCCESSION ALONG THE EARLY VEGETATION PRIMARY SUCCESSION STAGES IN THE HAILUOGOU GLACIER FOREHEAD IN THE SOUTHEAST OF THE TIBETAN PLATEAU, CHINA

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Abstract. – Understanding patterns and drivers of leaf (C, N, P) nutrient resorption, its stoichiometry and efficiency in the early vegetation primary succession in the Hailuogou Glacier Forehead of China is important to understand plant adaptation and competition strategy of vegetation succession in high-altitude and nutrient-poor environment. The results showed that the trends of total nitrogen concentration of green and senescent leaves were: 4 years < 8 years < 16 years. The correlation between C:N ratio and N:P ratio did not reach significance level ($p > 0.05$), but positive significance was showed between C:P ratio and C:N ratio ($p < 0.05$). The ranks of the NuRE values showed: the four-year > the eight-year > the sixteen-year. And the value of nutrient resorption efficiency decreased in the following order: PRE > NRE > CRE. 4 years of vegetation succession showed growth competition strategy with low value of N:P ratio and high value of C:N ratio. Consequently, as the vegetation primary succession compelled, the eight-year and the sixteen-year vegetation succession, with high value of N:P ratio and low value of C:N ratio which had competitive advantages, replaced the species of the four-year vegetation succession in this glacier forehead alpine region with high altitude and poor nutrients.
Keywords: *high-altitude and nutrients-poor environment, vegetation primary succession, green and senescence leaves, the rhizosphere soils, stoichiometry, nutrients resorption efficiency*

Introduction

Carbon (C), Nitrogen (N) and phosphorus (P) are important nutrients in plant metabolic processes. They are also primary nutrients that restrict plant growth in many natural environments (Aerts and Chapin, 2000; Koerselman and Meuleman, 1996). The stoichiometrics of C, N, P and nutrient resorption play key roles in terrestrial biogeochemical cycling. Nutrient resorption is the process by which nutrients are retranslocated from senescence leaves to storage organs or growing tissues (Killingbeck, 1996). The characteristics of nutrient resorption are important plant nutrient conservation mechanisms for plants and reduce the dependence of plants on soil nutrients (Hayes et al., 2014). Nutrient conservation strategy of plant is closely related to plant nutrient status and recyclings (Tully et al., 2013). Therefore, understanding nutrient resorption strategies and their response factors are critical to explore the adaptive capacity of plants and nutrient cyclings. It is also a key nutrient

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conservation strategy in perennial plants and is frequently studied to understand the internal cycling of nutrients in plants (Brant and Chen, 2015). It contributes to nutrient cycling, growth, reproduction, and competition of plants and plays an important role in modulating the feedback of plant and soil and maintaining the balance of plant stoichiometry (You et al., 2018; Drenovsky et al., 2019).

Nutrient resorption is usually quantified as nutrient resorption efficiency (NuRE), which is defined as the ratio between the amount of nutrients reabsorbed prior to leaf shedding and leaf nutrient content before the onset of leaf senescence (Huang et al., 2007). Differences in NuRE values are associated with leaf life span, leaf nutrient content, soil nutrient availability and so on (Tsujii et al., 2017; Van Heerwaarden et al., 2003). For instance, NuRE is higher in deciduous species and graminoids than in evergreen species and forbs (Aerts, 1996). However, the relationship between NuRE and soil nutrient availability and leaf nutrient status is not clear. Some studies have suggested that plants would resorb more nutrients in nutrient poor environments (Tully et al., 2013). While as, there exist some opposite opinions (See et al., 2015). In addition, the existence and mechanism of nutrient resorption regulation by plant nutrient status across different functional types and forest ecosystems remains unresolved (Vergutz et al., 2012). So far, most studies on species leaf nutrient resorption were mainly concentrated on species of the temperate regions (Killingbeck, 1996; Kobe et al., 2005). Although some widely accepted theories have been developed for the explanation of the relationship between plant stoichiometry and the environment, the underlying mechanisms are still not clarified. Especially, whether nutrient resorption can indicate plant adaptation to nutrient-poor environment remains a controversial problem. On one hand, less studies exist about the nutrient resorption characteristics of species living in high-cold and high-altitude regions, especially in the Qinghai-Tibetan Plateau. On the other hand, the comprehensive effects from taxonomy of the multi-species studies showed the relationships between plant stoichiometry and environment, such as plant itself physiological characteristics, plant distribution and community composition (Yang et al., 2016; Tian et al., 2019). Furthermore, relatively few studies have examined the characteristics of nutrient resorption in different vegetation types at the early vegetation succession stage in glacier forehead. Moreover, less research had discussed the reciprocal effects of NuRE and nutrient availability of soil and leaf nutrients in this region. Therefore, we quantified nutrient resorption efficiency along the early vegetation primary succession stage in glacier forehead in the east of the Qinghai-Tibetan Plateau. Our results offer insights into nutrient management and ecosystem restoration in nutrient-poor environment and delivers information and data supports for upcoming meta-studies and model simulation of global leaf nutrient resorption of the inhabitants of high elevation and nutrient-poor environments.

The stoichiometry and nutrient resorption have been evaluated at global, regional and smaller spatial scales (Han et al., 2005; Ren et al., 2018), and vary with factors such as vegetation composition (Bui and Henderson, 2013; Marty et al., 2017; Yang et al., 2018), nutrient addition (Kou et al., 2017; Yang et al., 2019), different inhabitation environment and regional climate change (Brant and Chen, 2015; Ren et al., 2018), which can help to provide theoretical supports for ecological restoration and conservation. Variations in carbon (C), nitrogen (N) and phosphorus (P) stoichiometry and nutrient resorption of the glacier forehead development are essential indicators for assessing vegetation succession process. Yet, their patterns along a chronosequence have been inconsistent. The plant community in glacier forehead is composed by

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Epilobium hirsutum, Astragalus mahoschanicus, Hippophae rhamnoides Linn, Leontopodium longifolium, Rubia schumanniana Pritzel, Artemisia moorcroftiana, Rhizoma Cacaliae Davidii, Sanicula lamelligera Hance et al. at the early stage of the vegetation succession. Especially, *Epilobium hirsutum, Astragalus mahoschanicus* and *Hippophae rhamnoides* are the dominant species along the early stage of vegetation primary succession and accounted for more than 70% of total aboveground biomass on the Hailuogou glacier forehead. Also different succession stages in the glacier forehead may cause changes in nutrient resorption efficiency due to variations in soil nutrient availability and plant nutrient status among different succession stages. So, three study sites of different vegetation succession ages that were formed in the sixteen-year of vegetation primary succession chronosequence of the Hailuogou glacier forehead were chosen in this study and to examine whether the Plant nutrient resorption prior to leaf senescence is an important nutrient conservation mechanism for plant succession in the high altitude environment and nutrient poor regions. Meanwhile, studied on whether the phylogenetic and environmental factors influencing this trait. Therefore, The primary objectives of this study were: (1) to investigate the patterns of C:N:P stoichiometry and nutrient resorption efficiency along the early stages of vegetation primary succession. (2) to study feedbacks between NuRE and nutrient availability to reveal the possible vegetation primary succession mechanism. Our results contribute to a better understanding of plant adaptation strategies to nutrient availability, and nutrient cycling during the vegetation primary succession processes. The results also could provide novel insights to better understand the inner driving force on the vegetation primary succession process in the glacier forehead region in view of nutrient limitations. Quantifying plant nutrient resorption in this region not only enriched the global nutrient resorption data base, but also contributed to understand plant adaptation to a severe nutrient deficient and high altitude environment.

Materials and Methods

Sites description

Our study was conducted in the glacier forehead of Hailuo Gully in Gongga Mountain in the Qinghai-Tibetan Plateau, China. The Hailuogou Glacier in the Gongga mountain (29°34′21″N, 102°59′42″E, *Fig. 1*) has been retreating since the Little Ice Age (~1830), and at an accelerated rate since the 1930s due to global warming (Wang et al., 2019). The deglaciated area, which was located at the elevation of 2950-3000 m, forms 2 km of complete vegetation succession chronosequence, from annual herbaceous to perennial herbaceous, shrub community, and arbor community. This region was mainly impacted by the Southwest monsoon in the summer season, also with heavy precipitation, while it was dry and cold in the winter season. The average annual temperature is 3.8 °C, with -4.38 °C as the lowest temperature and 11.9 °C as the highest temperature. The average annual precipitation was 1960 mm, with 90% of relative humidity. This region had good hydrothermal conditions and vegetation at the early succession stages in the glacier forehead, which was dominated by *Epilobium hirsutum, Astragalus mahoschanicus* and *Hippophae rhamnoides,* which belonged to 4 years, 8 years and 16 years of vegetation restoration succession, respectively, at the early succession stages in the glacier forehead and accounted for more than 70% of total aboveground biomass in these areas.

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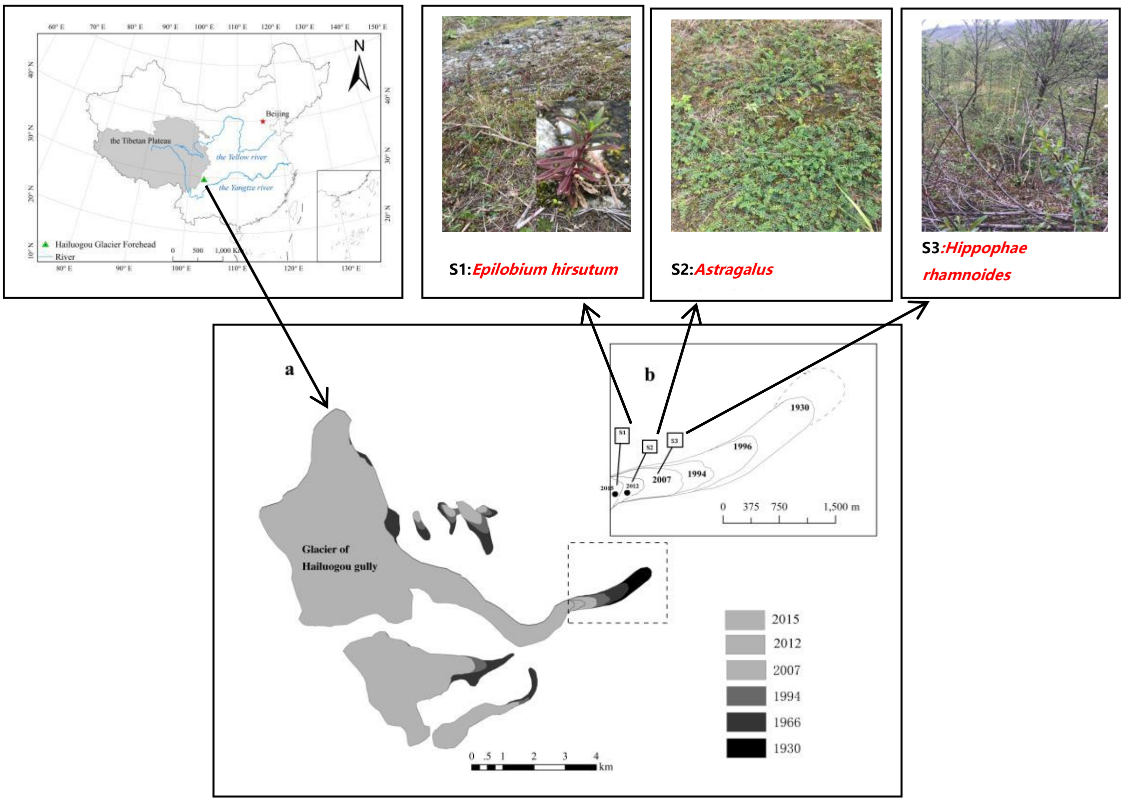

Figure 1. *The study location*

Sample collection

Different organ samples and rhizosphere soil samples were collected from the early-stage dominant plant *Epilobium hirsutum*, *Astragalus mahoschanicus* and *Hippophae rhamnoides* for the four-year (29°34′21″N,102°59′41″E), the eight-year (29°34′21″N,102°59′42″E) and the sixteen-year (29°34′20″N,102°59′42″E) chronosequence of primary vegetation succession forming on the Hailuogou glacier forehead in Gongga Mountain in the southeast of the Qinghai-Tibetan Plateau. In this study four replicate plots (4*4 m) were established. The soil and plant sampling was done in July, 2020. In each sample plot, we selected five plants with similar height and luxuriant growing to sample the green and senescent leaves. To avoid nutrient decomposition and leaching, senescent leaves were collected by gently shaking the stems or branches or waited until the end of the life span. All samples of green and senescent leaves were taken to the laboratory immediately after collection and washed with deionized water, which was subsequently dehumidified in an oven at 75 °C for 24 h to constant weight and sieved with a 0.10 mm sieve. Rhizosphere soil samples were collected (topsoil, 0–10 cm) at the same time as sampling plant leaves. Adjacent to a distances of 2.0 m, after removing the litter layer and other debris, rhizosphere soil samples were taken from 10 points in an “S” shape using a soil auger (5 cm in diameter). And the soil samples were mixed together and sealed in plastic bags, then transported to our laboratory and then air-dried at 60 °C for at least 48 h to a constant weight, gently grounded with a mortar and pestle, homogenized, and prepared to measure the soil nutrient contents. 3 duplicates of soil samples were taken from each sampling sites for the analyses. OC was determined by the $K_2Cr_2O_7$–H_2SO_4 oxidation

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method. Total N was measured by the Kjeldahl method. The TP was determined by colorimetry after digestion with H_2SO_4-H_2O_2 and H_2SO_4-$HClO_4$, respectively (Nelson and Sommers, 1982).

Calculation of nutrient resorption efficiency (NuRE)

Nutrient resorption is an internal nutrient cycle of the plant that resorbs nutrients from senescing plant tissues, alleviates plant dependence on external nutrient supply, and thus plays an important role in nutrient conservation, especially in poor nutrient ecosystems. Moreover, nutrient resorption can affect litter decomposition and nutrient release through its effect on litter nutrient concentration, thus producing a positive feedback to soil nutrient availability and altering elemental cycling (Vergutz et al., 2012). Nutrient resorption efficiency (NuRE), the proportional withdrawal of nutrients during leaf senescence, was calculated using *Equation 1* (Aerts, 1996):

$$\text{NuRE} = (1 - \text{Nutrient senescence} / \text{Nutrient green}) \times \text{MLCF} \times 100\% \qquad \text{(Eq.1)}$$

where Nutrient senescence and Nutrient green are senescent and green leaf nutrient concentrations (C, N and P), respectively. MLCF was the correction coefficient of biomass loss, in this study the mean value of MLCF was 0.762 (Vergutz et al., 2012).

Statistical analysis

Contents of TC, TN, and TP for each soil and leaf samples were used to determine the C:N, C:P, and N:P ratios. C:N:P stoichiometry was calculated as a mass ratio. The differences along the chronosequence of primary vegetation succession were performed using one-way analysis of variance (ANOVA) with Tukey's multiple comparison tests at the $P < 0.05$ or $P < 0.001$ level in SPSS 23.0 (SPSS Inc., USA). Regression analysis was conducted to determine the correlations. The Pearson correlation coefficient was used to determine the correlations between (1) C, N and P contents of green leaves, senescent leaves and rhizosphere soil along the chronosequence of primary vegetation succession, (2) characteristics of NuRE (CRE, NRE, PRE) and nutrients stoichiometry in leaves and rhizosphere soils, (3) correlation between the soil stoichiometry and soil properties. The Pearson correlation coefficient and figures were performed using the corrplot package of R 3.2.5 (R Development Core Team).

Results and analysis

Characteristics of C N P concentration and its stoichiometries of the green and senescent leaves

Carbon (C), nitrogen (N) and phosphorus (P) are the most important nutrients in terrestrial ecosystems and affect the biogeochemical cyclings. In this study, three different stages of vegetation succession from the glacier forehead region exhibited divergent responses in nutrient distribution of the green and senescent leaves. The results showed that the concentration of organic carbon of the sixteen-year vegetation succession was much higher than those of 4 years and 8 years vegetation successions (*Table 1*). The main reason was that the key species of the sixteen-year vegetation succession site was a kind of shrub, while the four-year and the eight-year vegetation succession sites were mainly herbs. The accumulation ability of the organic matter of

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the shrub was much stronger. The trends of total nitrogen concentration were: the four-year < the eight-year < the sixteen-year vegetation succession sites. The key species of 8 years vegetation succession belonged to the legume species and had the ability of biological nitrogen fixation. While the key species of the sixteen-year vegetation succession site was *Hippophae rhamnoides*. The root of *Hippophae rhamnoides* and Frankia constructed a symbiotic relationship, which also could fix the nitrogen nutrients from the soil to support the absorption of the whole plant. As a result, the total nitrogen in the green leaves and senescent leaves of the eight-year and the sixteen-year vegetation succession were higher than that of the four-year vegetation succession.

Table 1. *Characteristics of carbon, nitrogen, phosphorus concentrations and its stoichiometry of the green and senescent leaves of the three different stages of vegetation succession*

Types	Index	Green leaf						Senescent leaf					
		C (mg/kg)	N (mg/kg)	P (mg/kg)	C:N ratio	N:P ratio	C:P ratio	C (mg/kg)	N (mg/kg)	P (mg/kg)	C:N ratio	N:P ratio	C:P ratio
4 years	Average	304.18a	24.83a	1.72a	10.21a	17.46a	177.55a	100.73a	11.44a	0.54a	8.81a	21.70a	190.37a
	SE	1.56	0.41	0.08	0.32	0.33	3.78	1.34	0.03	0.03	0.29	0.29	1.19
	Minimum	298.46	21.89	1.42	8.42	15.23	152.77	89.34	9.67	0.49	7.22	19.26	179.32
	Maximum	321.32	25.21	2.43	13.65	19.87	198.34	121.57	14.28	0.77	10.03	24.32	199.67
	CV (%)	3.11	2.39	6.31	3.76	2.54	10.22	6.59	3.21	1.24	2.12	3.77	8.23
8 years	Average	312.45a	30.72b	1.77a	9.85a	17.47a	172.28a	110.28b	12.54a	0.60b	8.80a	21.01a	184.99a
	SE	1.48	0.55	0.05	0.44	0.39	5.32	2.21	0.08	0.05	0.43	0.31	2.86
	Minimum	309.34	22.36	1.35	7.39	13.67	156.45	79.37	9.36	0.32	6.32	17.39	165.67
	Maximum	316.49	37.12	2.31	11.26	21.63	198.62	110.43	14.36	0.87	11.29	27.42	197.43
	CV (%)	2.87	6.45	4.59	7.69	4.89	9.51	6.38	5.42	9.34	4.52	8.35	14.53
16 years	Average	451.97b	40.44c	1.96b	11.18b	20.63b	230.78b	185.47c	17.52b	0.69b	10.59b	25.33b	267.97b
	SE	3.24	0.68	0.43	2.18	3.41	8.39	6.32	3.75	2.13	4.52	3.45	4.39
	Minimum	421.57	32.39	1.34	7.32	16.39	218.36	162.38	11.29	0.38	6.89	20.24	224.87
	Maximum	479.62	47.58	2.38	16.39	23.32	266.38	192.38	21.34	0.97	13.45	29.41	296.31
	CV (%)	5.73	3.41	8.43	4.38	3.97	11.26	5.29	8.99	4.32	7.22	4.82	11.49

SE: standard error CV: coefficient variation, Eh: *Epilobium hirsutum,* Am: *Astragalus mahoschanicus* and Hr: *Hippophae rhamnoides*
Values within a row followed by different letters are significantly different (P < 0.05), S.E. means standard error of mean

Correlation between C P N and its stoichiometry in the senescent leaves

There existed significant positive correlation between organic carbon, total nitrogen and total phosphorus of the senescent leaves of 4 years vegetation succession (*Fig. 2*). The correlation between C:N and N:P ratios did not reach the significant level ($p > 0.05$), while there was a significant positive correlation between C:P ratio and C:N ratio ($p < 0.05$). Meanwhile, the nutrient traits and correlation of senescent leaves of 8 years vegetation succession had similar change trends as the four-year vegetation succession. And all reached the significant level ($p < 0.05$). These results may be closely related to limited P supply. However, negative correlation was observed between organic carbon and total nitrogen, between total nitrogen and total phosphorus, between C:N ratio and N:P ratio, and also between organic carbon and total nitrogen of the senescent leaves of the sixteen-year vegetation succession, but the latter did not reach the obvious significant level. Correlation analysis showed that total nitrogen was closely related to total phosphorus ($p < 0.001$). In addition, the index of organic carbon increased with the index of total phosphorus. Negative correlation was observed

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between C:N ratio and N:P ratio. The index of N:P ratio and C:P ratio showed a positive correlation ($p < 0.05$). The similar change trends were observed as between C:N ratio and C:P ratio.

Comparing the correlation between the organic carbon and total nitrogen of the senescent leaves, the results showed that a positive correlation existed at the 4 years vegetation succession. As the years of vegetation succession increased, the correlation showed decreasing trends. The similar positive correlation trends was showed between total nitrogen and total phosphorus, and also between organic carbon and total phosphorus. Comparing the correlation between the stoichiometry of the senescent leaves of the three different stages of vegetation successions, the results showed an obviously significant exponential positive correlation between C:N ratio and N:P ration of the four-year and the eight-year vegetation succession, while the 16 years vegetation succession showed exponential positive correlation between C:N ratio and N:P ration, but did not reach the obviously significant level. Meanwhile, a positive correlation existed between N:P ratio and C:P ratio and both reached the obviously significant level. As the years of vegetation succession increased, the correlation efficiency showed decreasing trends. Regarding the four-year senescent leaves and the eight-year senescent leaves, the correlation between C:N ratio and C:P ratio changed from the positive correlation to the negative correlation. The sixteen-year senescent leaves showed a positive correlation between the C:N ratio and the C:P ratio.

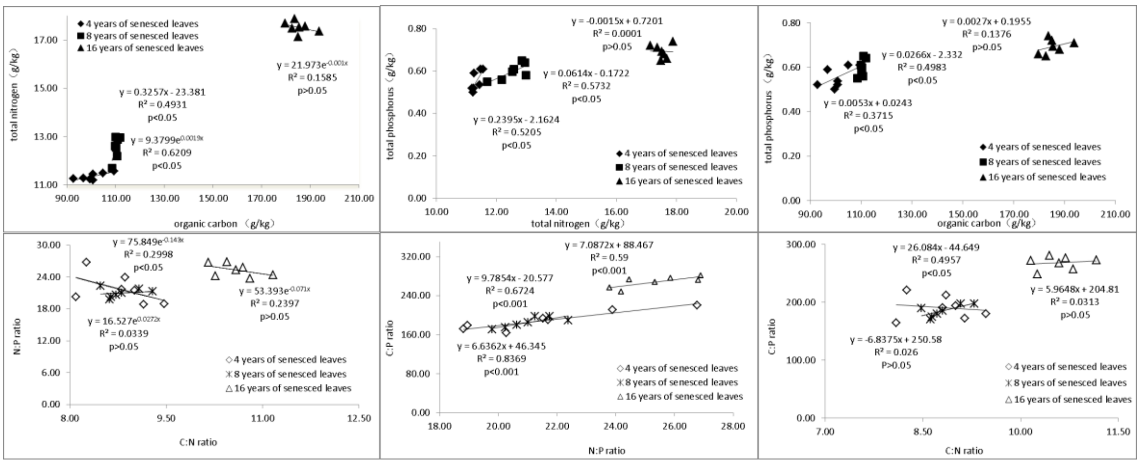

Figure 2. *Correlation between the organic carbon, total nitrogen, total phosphorus and its stoichiometry in senescent leaves of the three different stages of vegetation successions*

Correlation between C P N and its stoichiometry in the green leaves

The results of correlation analysis of the stoichiometry in the green leaves are showed in *Figure 3*. There was an exponential correlation between the organic carbon and total nitrogen of the green leaves with different vegetation succession years, but correlation co efficiency did not reach the obviously significant difference. While there was a negative correlation between total nitrogen and total phosphorus of the four-year green leaves, the eight-year green leaves and the sixteen-year green leaves showed the opposite trends, there was a positive correlation between total nitrogen and total phosphorus. And the significant difference of these two indices reached the obvious level in the cases of the eight-year green leaves and the sixteen-year green leaves. The

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correlation between organic carbon and total phosphorus showed similar trends as the correlation between total nitrogen and total phosphorus.

There was a significantly negative correlation between C:N ration and N:P ratio of the four-year green leaves, while the correlation between C:N ration and N:P ration of the eight-year and the sixteen-year green leaves showed the opposite correlation trends, there was a positive correlation between C:N ration and N:P ration of the eight-year and the sixteen-year green leaves. As for the correlation between N:P ratio and C:P ratio, there was a positive trend, no matter what the years of vegetation succession was. And all reached the obviously significant difference levels. The correlation between C:N ration and C:P ratio showed similar trends, except for the four-year green leaves that did not reach the obviously significant difference level as the other two vegetation succession stages.

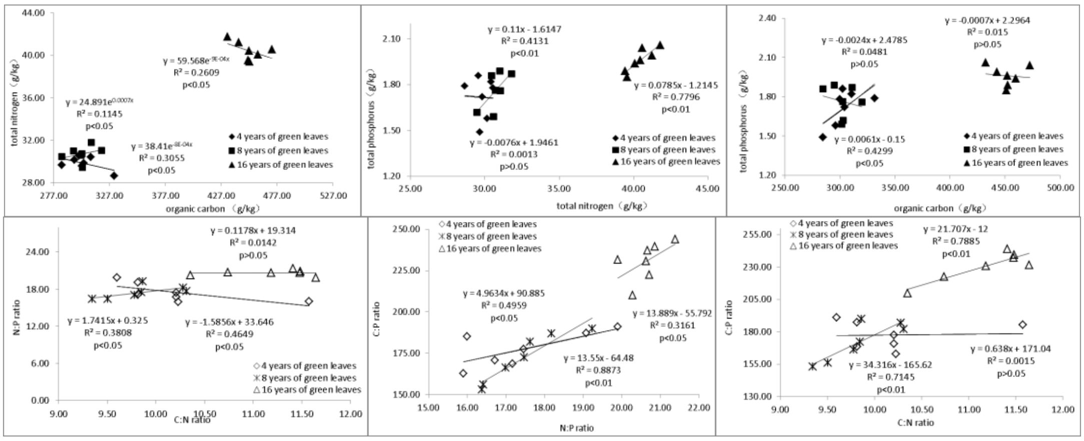

Figure 3. *Correlation between organic carbon, total nitrogen, total phosphorus and its stoichiometry in the green leaves of the three different stages of vegetation successions*

Nutrient resorption efficiencies of the three dominant species and their relationship

It was found that the nutrient resorption efficiencies (CRE, NRE and PRE) were significantly different among different stages of vegetation succession (*Fig. 4*). The four-year of vegetation succession had the high value of nutrient resorption efficiency than those of the eight-year and the sixteen-year of vegetation successions. And the values of nutrient resorption efficiencies decreased in the following order: PRE > NRE > CRE. The value of CRE of the four-year vegetation succession ranged from 0.65-0.69. The value of CRE of the eight-year vegetation succession ranged from 0.61-0.66, The value of CRE of the 16- year vegetation succession ranged from 0.55-0.61. CRE decreased in the following order: the four-year > the eight-year > the sixteen-year. And significant difference existed between the four-year and the eight-year vegetation succession, also between the four-year and the sixteen-year vegetation succession ($p < 0.05$). The value of NRE of the four-year vegetation succession ranged from 0.61-0.63. The value of NRE of the eight-year vegetation succession ranged from 0.57-0.62. The value of NRE of the sixteen-year vegetation succession ranged from 0.55-0.58. The value of PRE of the four-year vegetation succession ranged from 0.66-0.69. In addition, the NRE results of the significant difference tests showed the similar changes as the index of CRE. The value of PRE of the eight-year vegetation succession ranged from 0.65-0.68. The value of PRE of the sixteen-year vegetation succession

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ranged from 0.63-0.66. The value of NRE and PRE all showed the similar trends as that of the four-year vegetation succession, which showed the trend of PRE > NRE > CRE. However, no significance was observed among the stages of vegetation succession with different years as for the index of PRE.

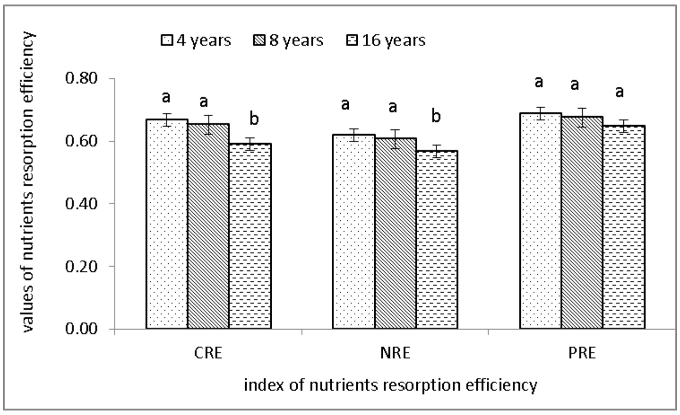

Figure 4. *the values of nutrient (C N P) resorption efficiencies of different vegetation succession years. Error bars represent the standard deviation (SD). Different lowercase letters (a, b) indicate significant differences ($p < 0.05$) among different vegetation succession years*

The three different vegetation succession years showed similar correlation between CRE and NRE as well as PRE (*Fig. 5*). A negative correlation existed between CRE and NRE, also between NRE and PRE. The correlation between CRE and NRE of the four-year vegetation succession reached the obvious significant difference ($p < 0.001$). The correlation between NRE and PRE of the eight-year vegetation succession reached the significant difference ($p < 0.05$). Oppositely, a positive correlation existed between CRE and PRE of the three different vegetation succession years. Meanwhile, the correlation between CRE and PRE of the four-year vegetation succession showed an obvious significant difference ($p < 0.001$).

Nutrient concentration of the rhizosphere soils

The soil organic carbon concentration of the rhizosphere soils increased as the vegetation succession proceeded from the four-year to the sixteen-year (*Fig. 6*). The concentration of soil total nitrogen had similar trends. While, the soil total phosphorus of the rhizosphere soils of the four-year vegetation succession showed the highest value, ranging from 1.49 to 1.63. The value of the rhizosphere soils of the eight-year vegetation succession was the lowest of the early stage of vegetation succession, ranging from 1.08 to 1.13. Soil total phosphorus concentration of the rhizosphere soils of the four-year vegetation succession ranged from 1.35 to 1.56. As the vegetation succession proceeded, the N:P ratio increased in the following order: the four-year < the eight-year < the sixteen-year. While the C:N ratio and C:P ratio had the different change trends as the vegetation succession years increased.

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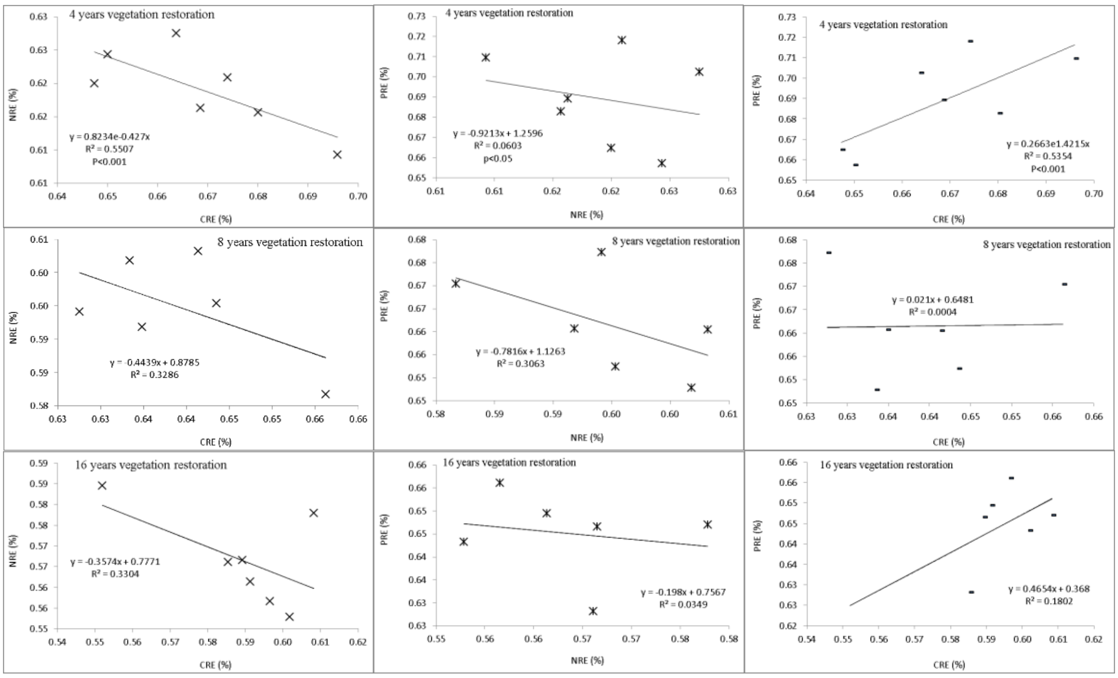

Figure 5. *The correlation between CRE, NRE and PRE*

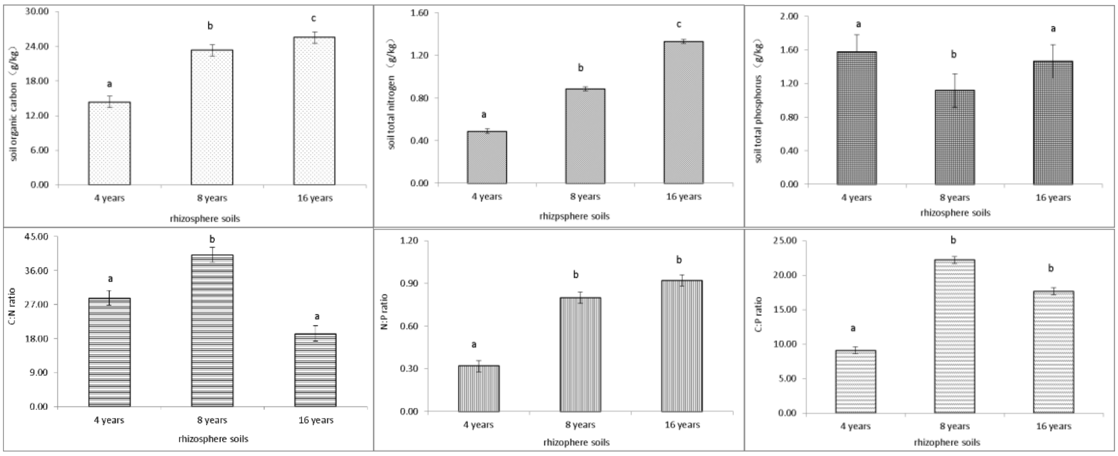

Figure 6. *The characteristics of carbon, nitrogen, phosphorus concentrations and its stoichiometry of the rhizosphere soils. Error bars represent the standard deviation (SD). Different lowercase letters (a–c) indicate significant differences (p < 0.05) among different rhizosphere soils*

Correlation between the stoichiometry and CRE, NRE and PRE of the rhizosphere soils

A negative correlation was found between C:N ratio and N:P ratio, and those of the rhizosphere soils of the eight-year and the sixteen-year vegetation succession reached the obvious significant negative correlation level ($p < 0.001$). Positive correlation between N:P ratio and C:P ratio, and positive correlation between C:N ratio and C:P ratio were observed. However, the correlation between C:N ratio and C:P ratio did not reach a significant level ($p > 0.05$).

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As for the correlation between CRE and NRE of the rhizosphere soils of the four-year and the 16- year vegetation succession, there existed a significant negative correlation (*Fig. 7*). The CRE and NRE of the rhizosphere soils of the eight-year vegetation succession showed a positive correlation. The correlation between NRE and PRE of the rhizosphere soils of three different years of vegetation succession had the similar change trends as the correlation between CRE and NRE of the rhizosphere soils. While, there was a positive correlation between CRE and PRE of the four-year and the eight-year vegetation succession. The correlation between CRE and PRE of the rhizosphere soils of the sixteen-year vegetation succession showed a negative correlation.

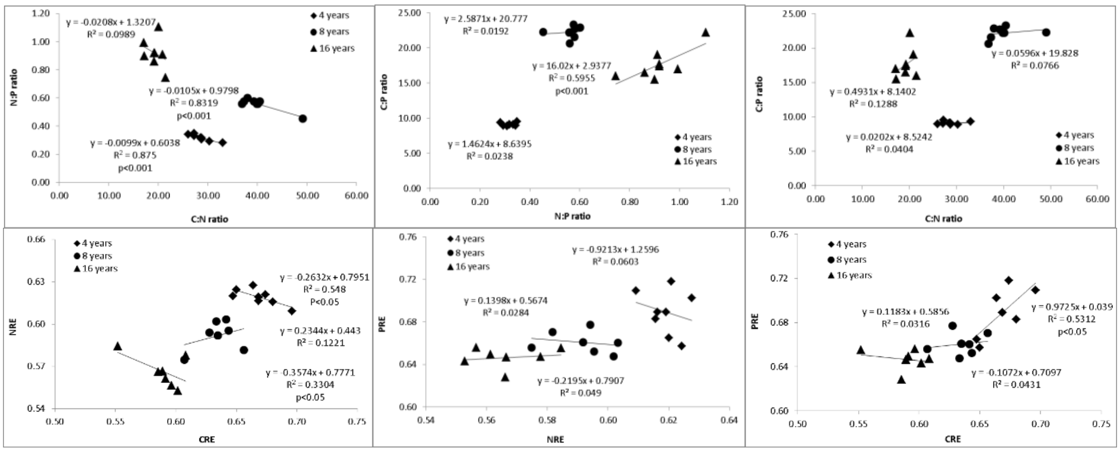

Figure 7. *Relationship between the stoichiometry and CRE, NRE and PRE of the rhizosphere soils*

Discussions

Characteristics of nutrient resorption efficiencies

Plant nutrient resorption, a process by which plant withdraws nutrients from senescent structures to developing tissues, can significantly affect plant growth, litter decomposition and nutrient cycling. Leaf nutrient resorption is a key component of nutrient conservation strategies to increase plant fitness and improve nutrient cycling especially in nutrient-poor environment (Vergutz et al., 2012). Also nutrient resorption is a nutritional trade-off mechanism in plant, contributing to meet the demand of tissue regrowth, chemical composition balance and biomass production (Du et al., 2017; Jiang et al., 2019). In general, nutrient resorption varied greatly among different plant functional types, mainly related to the plant inherent characteristics and surrounding environment conditions. We hypothesized that the nutrient resorption patterns of leaves were different among different stages of primary vegetation succession process. We found that the nutrient resorption efficiency was higher in the case of the four-year vegetation succession than that of the eight-year and the sixteen-year vegetation succession. Also the low value of CRE of the eight-year and the sixteen-year vegetation succession could probably be attributed to the non-structural carbohydrate contents in plants body for nutrient reflow was low during senescence. Meanwhile, many previous studies demonstrated that NRE was lower than PRE. This could be attributed to the fact that plant might either expend less energy to obtain N than P from the soil or y resorption of P is easier from aging leaves than absorption of P from the soil (Chen et al., 2015). Kimmins (1976) reported that the prolongation of plant

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leaf lifespan promoted the transfer of nutrients from green leaves to senescent leaves, which enhanced their viability in low temperature environments. Moreover, if the time that leaves remain on the plant body increases, forcing the cost of maintaining plant growth and photosynthesis to increase, then it will result in increased nutrient use efficiencies (Aerts and Chapin, 2000). Meanwhile, Aerts (1999) suggested that low tissue concentration and high nutrient-resorption efficiency were the successfully competitive strategies for species living in nutrient-poor environment. In Tilman's competition theory, plant species are more competitive if they can reduce the limiting resources to a lower level than their competitors (Tilman, 1982). Thus, our stoichiometric results provide additional evidence verifying the theory of Aerts (Aerts et al., 1999) and Tilman on the Hailuogou glacier forehead at the southeast edge of the Qinghai-Tibetan Plateau and help to explain why Epilobium hirsutum, which was the dominant species in the four-year vegetation succession sites was first appeared and became the typically dominant plant functional group, then replaced by Astragalus mahoschanicus and Hippophae rhamnoides, which were the dominant species of the eight-year and the sixteen-year vegetation succession, respectively, after several years in this cold alpine region.

Relationships among nutrient contents, stoichiometry ratios and NuRE

Different nutrient elements, such as C, N and P, often display different variations along the primary vegetation succession chronosequence (Liang et al., 2018). Similarly, the restriction of soil P regulates the absorption of N by plant roots (Schreeg et al., 2014). These results indicate that there were mutual driving effects between N and P content of plants and soil. Therefore, the leaf PRE and NRE were driven synchronously by N and P content of plants and soils among three different years of vegetation succession. Significant positive correlations between senescent leaves and green leaves and senescent leaves and soil in C, N, and P contents were observed in our study, which essentially agreed with previous studies (Drenovsky et al., 2019). These findings may be due to the positive plant-soil feedback through litter decomposition, manifesting the important role of leaf litter in the nutrient cycling between plants and soil (Yang et al., 2018).

Our research suggests that the three different years of vegetation succession in Hailuogou glacier forehead showed different relationship between the nutrient characteristics, their stoichiometries and nutrient resorption efficiencies. Both nutrients of rhizosphere soils and green leaves obviously influenced nutrient resorption efficiencies of the three different years of vegetation succession in the glacier forehead along a glacial chronosequence. The data suggest that at the beginning 3-4 years along a glacial chronosequence, *Epilobium hirsutum* was the dominant species and the soil nutrients were all at a low level. Regression relationship was used to study the correlations among the C, N, and P contents in green leaves, senescent leaves, and rhizosphere soils of the three different years vegetation succession (*Fig. 8*). As for the dominant species of *Epilobium hirsutum*, which was the key species of the four-year vegetation succession in the Hailuogou glacier forehead, concerning the relationships between soil and green leaves, between soil and senescent leaves, and between green and senescent leaves, there were significant positive correlations in C, N, and P contents ($p < 0.05$), and correlations for P always ranked the highest. As for the stoichiometry ratio, only the C:N ratio of the senescent leaves, N:P ratio of the soil and C:P of the soils had positive correlation with other stoichiometry ratios. Meanwhile, considering the nutrient resorption efficiencies, the CRE was significantly positively correlated with the C contents in green leaves of the C N P contents, and the NRE was significantly

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positively correlated with the N contents in green leaves of the C N P contents, other indices of C N P contents had a negative correlation with nutrient resorption efficiencies. The results also showed that the C:P ratio of the senescent leaves had less relationship with other indices, also the nutrient resorption efficiencies had less relationship with its stoichiometry. The C N P of the soils had positive correlation with the C contents of the green leaves, with C:P ration, and CRE. The NRE had nearly no correlation with the C N P of the senescent leaves. The PRE was significantly negatively correlated with the N, and P contents in green leaves, senescent leaves. But there was less correlation between PRE and the C N P of the soils.

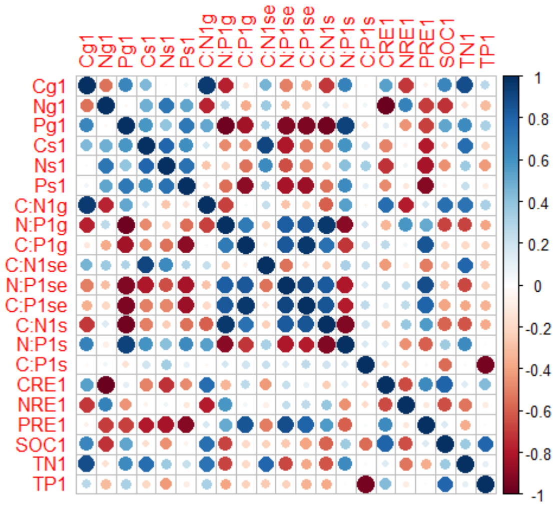

Figure 8. *Correlation among C N P and its stoichiometry ratios and NuRE of dominant species. 1: the four-year vegetation restoration, Cg: organic carbon concentration of the green leaf, Ng: total nitrogen concentration of the green leaf, Pg: total phosphorus concentration of the green leaf, Cs: organic carbon concentration of the senescence leaf, Ns: total nitrogen concentration of the senescence leaf, Ps: total phosphorus concentration of the senescence leaf. The same below. Pearson's correlation coefficients between nutrient resorption efficiency and nutrient contents, stoichiometry ratios in leaves and soil. NRE, N resorption efficiency, PRE, P resorption efficiency. Blue indicates a positive correlation between the two variables, and red indicates a negative correlation. The darker the color of the circle is, the greater the absolute value of the correlation coefficient. The larger the size of the circle is, the greater the absolute value of the correlation coefficient. The notes in figure 9 and 10 were the same.*

A positive correlation was observed between the C N P contents of the green leaves and senescent leaves of the eight-year vegetation succession in the Hailuogou glacier forehead. But the indices did not reach the obviously significant difference (*Fig. 9*). Meanwhile, a negative correlation was observed between C N P contents and its stoichiometry. The correlation between the stoichiometries of the green leaves and senescence leaves showed the positive correlation. Also the nutrients resorption efficiency (CRE and NRE) and the C N P contents of the green leaves and senescent leaves showed negative correlation. The PRE showed the opposite correlation. The SOC of the soils were positively associated with C N P contents of the green leaves and senescent leaves and with nutrients resorption efficiency of carbon and nitrogen, but negatively associated with its stoichiometries of the green leaves and senescent leaves and with PRE. Negative correlation was observed between TN, TP and CNP contents of the green leaves.

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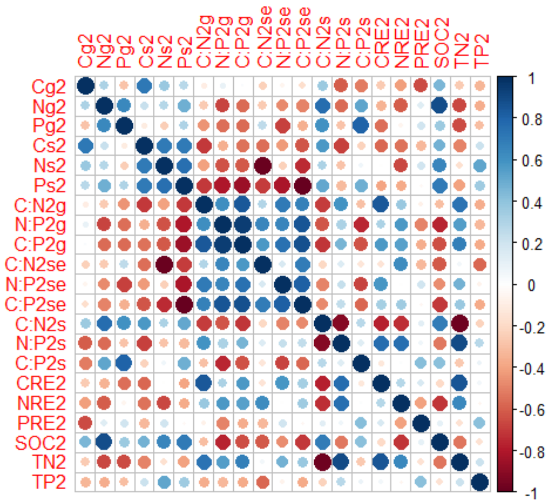

Figure 9. *Correlation among C N P and its stoichiometry ratios and NuRE of dominant species. 2: the eight-year vegetation restoration*

A negative correlation was observed between C, N and P contents of the green leaves and senescent leaves of the sixteen-year vegetation succession in the Hailuogou glacier forehead (*Fig. 10*). While there was a positive correlation between N and P contents of the green leaves, and N contents of the senescent leaves negatively associated with C and P contents. There was no significant correlation between the stoichiometries of the rhizosphere soils. Also there was no significant correlation among the C N P contents of the rhizosphere soils. CRE was negatively associated with N P contents of the green leaves, while positively associated with C content of the green leaves. NRE was positively associated with N P contents of the green leaves, but negatively associated with its stoichiometries, except the index of C P ratio of the senescent leaves. C N P contents positively associated with SOC and TN of the rhizosphere soils.

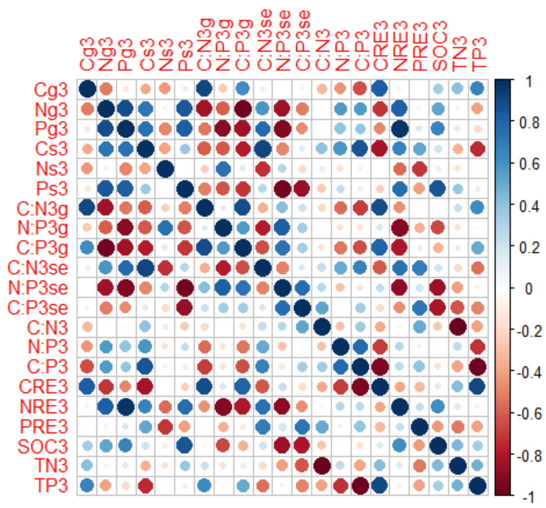

Figure 10. *Correlation among C N P and its stoichiometry ratios and NuRE of dominant species. 3: the sixteen-year vegetation restoration*

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Variations in C, N, P stoichiometry along the chronosequence of Hailuogou glacier forehead

The climate of Hailuogou gully glacier belongs to the monsoon temperate glacier, with high temperature, heavy precipitation, with better water and heat resources when compared to the glaciers of high altitudes in Europe and northern America. It supplied a better environment to the early pioneer species to grow there. The study of primary vegetation succession on glacier foreland in Alaska indicated that the early pioneer species appeared after more than ten years of glacial deglaciation, only the shrubs and herbs, after fifteen to twenty years the arbors appeared in the community (Chapin et al., 1994). First, Epilobium hirsutum, which belonged to the dominant species in the four-year vegetation succession, appeared. Later in the six to eight years period, *Astragalus mahoschanicus,* which belonged to the dominant species in the eight-year vegetation succession became the key species and the shrubs appeared. *Hippophae rhamnoides*, which belonged to the dominant species in the sixteen-year vegetation succession, became the dominant species in the eight to sixteen years period and the rate of primary vegetation succession has become quicker.

Relative nutrient allocation among organs and their responses to environmental factors could vary among species (Poorter et al., 2012). Species with extensive root systems can achieve maximum nutrient uptake and greater spatial occupation, and may not need to evolve efficient nutrient conservation patterns (Miao, 2004). Some studies showed that species with relatively lower foliar resorption had higher underground biomass, spatial expansion and root nutrient capture than species with higher resorption efficiency (Kou et al., 2017; Peng et al., 2019). Whether there is a trade-off between leaf nutrient resorption and nutrient allocation to roots remains unexplored. At the early stage of the primary vegetation succession in Hailuogou glacier forehead, the soil nutrients were very poor. As the process of primary vegetation succession advanced, the *Astragalus mahoschanicus* became the dominant species in the eight-year vegetation succession, because its biological nitrogen fixation. The nutrient contents of different organs reflected the absorption, transportation and usage of the elements. The nitrogen and phosphorus were two restricting factors to the rate of primary vegetation succession (Zhou et al., 2020). Leaf is an important vegetative organ as it produces organic matter with photosynthesis (Wang et al., 2017). Comparing the nutrient contents of leaves and its relation to the stoichiometrics could better understand the usage and location regulation of the plants. Meanwhile, taking the two species (*Epilobium hirsutum* and *Astragalus mahoschanicus)* as the examples, which were considered as the dominant species in the four-year and the eight-year vegetation succession, respectively. They were perennial herbs, when compared to the annual herbs, which had longer leaf lifespan and higher nutrient contents. Our research showed that the mean values of organic carbon contents of the three species were all lower than that of the global mean value (409.63 g/kg). Nitrogen and P are tightly coupled and interact from cell to ecosystem level (Elser et al., 2000) to maintain stoichiometric homeostasis (Yu et al., 2010). While the TN contents of *Epilobium hirsute* was lower than those indices of China and global scales, the TN contents of Astragalus mahoschanicus and *Hippophae rhamnoides* were all higher than those indices of China and global scales. On reason for this is that *Astragalus mahoschanicus* and *Hippophae rhamnoides* are two plants that are able to fix nitrogen biologically. As for Astragalus mahoschanicus, the biological nitrogen fixation mechanism is based on the nodule bacteria Rhizobium. While the biological nitrogen fixation mechanism of *Epilobium hirsutum* is due to the Frankia.

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Although they have two different biological nitrogen fixation processes, they showed similar higher efficiency of biological nitrogen fixation. So the soil nutrient content improved with the appearance of Astragalus mahoschanicus and *Epilobium hirsutum* in the community. On the other hand, as the primary vegetation succession on glacier foreland proceeded, the species of *Epilobium hirsutum* was replace by *Astragalus mahoschanicus* and *Hippophae rhamnoides*, the soil structure and nutrient content improved. In conclusion, this study showed that as the years of primary vegetation succession proceeded, the nutrient concentrations in both green and senescent leaves was enhanced, thus litter quality increased that had positive effects on litter decomposition, producing a positive vegetation soil feedback, and accelerating global nutrient cycle. When compared the phosphorus contents of the three dominant species during the early vegetation succession, the mean value of total phosphorus of *Epilobium hirsutum* was lower than the indices of China and the global scales (*Table 2*). N:P resorption stoichiometry in plants is important in exploring nutrient cycling at various spatial scales (Reed et al., 2012). Our results showed that the trends of N:P ratios were the followings: *Epilobium hirsutum* (the four-year vegetation succession) < *Astragalus mahoschanicus* (the eight-year vegetation succession) < *Hippophae rhamnoides* (the sixteen-year vegetation succession). When the N:P ratio was less than 14, which indicated that this growth of species was restricted by the element of nitrogen. The mean value of total phosphorus of *Astragalus mahoschanicus* was higher than the indices of China and the global scales. However, the N:P ratio changed between 14 and 16, which indicated that the growth of species was restricted by the element of nitrogen and phosphorus. Meanwhile, although the mean values of total phosphorus of *Hippophae rhamnoides* was higher than the indices of China and the global scales, the N:P ratios were more than 16, which indicated that the growth of *Hippophae rhamnoides* was restricted by the element of phosphorus. Phosphorus limitation may be a long-term nutrient balance constraint in this region. As the vegetation primary succession on glacier forehead in Hailuogou proceeded, the restricted element changed from nitrogen to phosphorus. Several studies have shown that N fixing species promote N mineralization and absorption, which in turn increase N efficiency (Chavez-Vergara et al., 2015; Ren et al., 2017). The species of biological nitrogen fixation played an important part in the primary vegetation succession process. Simultaneously, we found that the N:P ratio of plants was significantly higher than that of non-N-fixing plants. As perennial plants grow, a series of processes affect the allocation and utilization of resources (Vergutz et al., 2012). A correlation was observed between growth rate and nutrients location. rRNA is needed to compose protein for fast growth rate and phosphorus is a main component of the rRNA. In addition, the plant's own efficiency in synthesizing proteins and nucleic acids is reduced as the plant ages, reducing the plant growth rate, and thereby stimulating the resorption strategies of senescent leaves for plant growth. The growth rate of *Epilobium hirsutum* was faster than that of other two species, thus it became the first pioneer species of the glacier foreland. Therefore, the phosphorus contents of the dominant species decreased as the primary vegetation succession on glacier foreland proceeded, which showed the ranks of *Epilobium hirsutum* > *Astragalus mahoschanicus* > *Hippophae rhamnoides*. Meanwhile, the trends of C:N ratios were the followings: *Epilobium hirsutum* (the four-year vegetation succession) > *Hippophae rhamnoides* (the sixteen-year vegetation succession) > *Astragalus mahoschanicus* (the eight-year vegetation succession). The low value of N:P ratio and high value of C:N ratio in the organs of the plants body

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showed the higher growth rate and propagation rates, which is a growth competition strategy. Epilobium hirsutum showed this strategy and become the dominant species on the glacier foreland first. While the high value of N:P ratio and low value of C:N ratio in the organs of the plants body showed the slower growth rate and high carbon assimilation efficiency, which is a resource protective strategy (Elser et al., 2000). Therefore, when the vegetation succession proceeded, the other two species *Hippophae rhamnoides* and *Astragalus mahoschanicus* replaced *Epilobium hirsutum*, which could compel the vegetation succession process better.

Consequently, further explorations were still needed on the limitation of elements to compel the velocity of the primary vegetation succession process on the Hailuogou glacier forehead. Yet, how global change will alter nutrient resorption of plants in alpine ecosystems remains unclear (Brant and Chen, 2015).

Table 2. *Mean values of OC, TN and TP and nutrients ratios of different organs of the three dominant species in the Hailuogou glacier forehead and other study regions*

Study areas	OC (g/kg)	Samples quantity	TN (g/kg)	Samples quantity	TP (g/kg)	Samples quantity	C:N ratio	N:P ratio	Samples quantity	References resource
The four-year	202.45	25	13.18	25	1.28	25	15.36	10.29	25	This study
The eight-year	266.37	25	18.78	25	1.22	25	14.18	15.41	25	This study
The sixteen-year	301.72	25	19.96	25	1.19	25	15.12	16.74	25	This study
China			18.63	554	1.21	745	0	14.4	894	Han et al., 2005
Global scale			18.34	1251	1.42	923	0	11.8	894	Reich et al, 2004
Global scale			17.66	398	1.58	406		11	325	Elser et al., 2000

Conclusions

In summary, we quantified C, N and P and its stoichiometrics of the leaves and rhizosphere soils and the nutrient resorption efficiencies of three dominant species along a chronosequence of primary vegetation succession on the Hailuogou glacier forehand. From the comparison of three different years of vegetation succession during the early succession stages, we found *Epilobium hirsutum* as the dominant species in the four-year vegetation succession, showing growth competition strategy and firstly become the dominant species in the early vegetation succession stage on the glacier foreland. With low value of N:P ratio and high value of C:N ratio in the organs of the plants body. Consequently, as the primary vegetation succession compelled, the eight-year and the sixteen-year vegetation successions, which had high value of N:P ratio and low value of C:N ratio in the organs of the plants body, replaced the four-year vegetation succession. The eight-year and the sixteen-year vegetation successions had competitive advantages over 4 years vegetation succession and better compel the succession process in this glacier forehead alpine region with high altitude and cold temperature.

Our research also suggested that both species and level of nutrients insufficiency influenced nutrient resorption in the glacier forehead region. These data suggest that it may be difficult to predict, at the family-level, species responses to environmental perturbations and stressors. The soil available phosphorus and moisture may be the main drivers for nutrient resorption efficiencies. Future work should focus on the role of nutrient resorption in whole-plant nutrient budgets, as well as controlled field studies. Understanding links between plant nutrient budgets and mechanism of species competition may help us better predict species responses to the speed of primary vegetation succession process in glacier forehead region and similar regions in the world.

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Additionally, our study can not only report the characteristics of leaves nutrient resorption on the glacier forehead in the southeast of the Qinghai-Tibetan Plateau, but also provide implications for simulating nutrient resorption across large geographical scale.

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