



Nutrient resorption of coexistence species in alpine meadow of the Qinghai-Tibetan Plateau explains plant adaptation to nutrient-poor environment

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ABSTRACT

Nitrogen (N) and phosphorus (P) resorption from senescing organs are important plant nutrient conservation mechanisms. However, whether nutrient resorption can indicate plant adaptation to nutrient-poor environment remains a controversy. We quantified nutrient resorption efficiency of major species in an alpine meadow of the Qinghai-Tibetan Plateau. N and P resorption for these species averaged 65.2% and 67.4%, respectively, which was at the high end of the values of global scale. Among three life forms, sedges contained least N and P and had highest resorption efficiency, indicating sedges had a competitive advantage over grasses and forbs in this nutrient-poor environment. This result was consistent with the fact that sedge was the typically dominant plant functional group in Qinghai-Tibetan Plateau. By fitting the allometric equations ($[\text{nutrient}]_{\text{senescent}} = A([\text{nutrient}]_{\text{live}})^B$) separately for N and P, we found much smaller $B(N)$ than $B(P)$, which suggested that relative to the resorption from senescent leaves, the cost of N uptake from soils increased more quickly than that of P as resource availability decreased. This phenomenon was contrary to the corresponding N and P acquisition pattern of the tropical ecosystem, which matched the large geographical gradients of N vs. P limitation (N for alpine ecosystem, while P for tropical ecosystem). This study suggests that surveying leaf nutrient concentration and resorption could provide indicative information about plant adaptation to nutrient-poor soil within and across ecosystems. Our finding offers insights to nutrient management and ecosystem restoration in nutrient-poor environment and delivers information for upcoming meta-studies and model simulation of global leaf nutrient resorption.

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1. Introduction

Nitrogen (N) and phosphorus (P) are important nutrients in plant metabolic processes: N is an important component of protein; P is a key element in cellular energy transfer and a structural element in nucleic acids. N and P are also the primary nutrients that restrict plant growth in many natural environments (Aerts and Chapin, 2000; Chapin, 1980; Koerselman and Meuleman, 1996). In order to reduce dependence on current nutrient uptake, plants can resorb nutrients from senescing leaves prior to abscission and store them into other plant tissues for reuse. Resorption efficiency (RE), defined as percentage of nutrient reduction between live and

senescent leaves, is used to quantify the resorption capacity of plant (Lü et al., 2011). Across a wide range of perennial life forms, plants reutilize an average of 50% of N and P content in live leaves before the leaf falls, although there is much variability (Aerts, 1996; Aerts and Chapin, 2000; Killingbeck, 1996; McGroddy et al., 2004). So far, leaf nutrient resorption has been remarkably well studied. However, the studied species are mostly from temperate regions (Aerts, 1996; Killingbeck, 1996; Kobe et al., 2005; Rejmankova, 2005; Yuan and Chen, 2009). To the best of our knowledge, very little information exists about the nutrient-resorption characteristics of species on the Qinghai-Tibetan Plateau.

The Qinghai-Tibetan Plateau is regarded as the world's "third pole" (Fig. 1), with an average elevation of over 4000 m, and about 35% of its area is alpine meadow (Xu et al., 2011). Herbaceous perennial plants on Qinghai-Tibetan Plateau are in climatically extreme environments and nutrient-poor conditions, in a location which is expected to be susceptible to climate warming and

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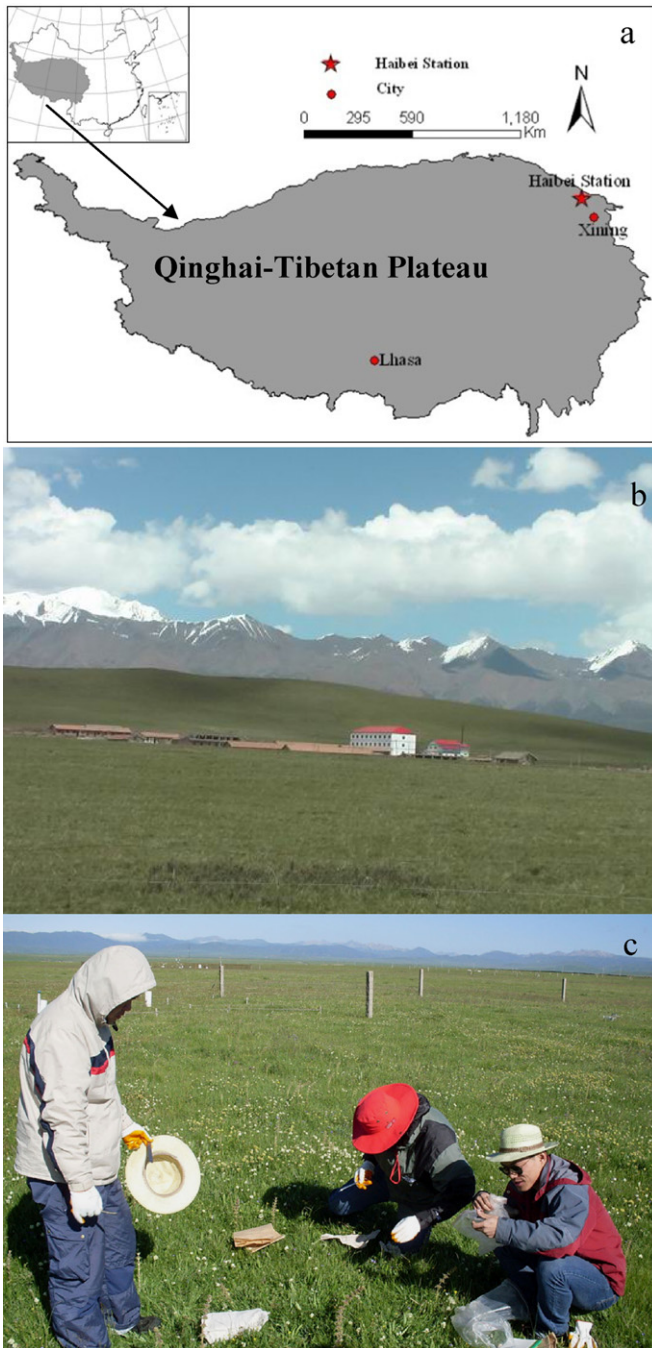


Fig. 1. Location of the sampling site (Haibei station) on the Qinghai-Tibetan Plateau (a); view of the station (b); surveying and sampling in the experiment plot (c).

increasing N deposition. Quantifying plant nutrient resorption on the Qinghai-Tibetan Plateau can not only fill a gap of global nutrient-resorption data sets, but also contribute to understanding of plant adaptation to a severe environment.

Plant traits are considered to be a tool to understand the plant adaptation to a harsh environment (Ma et al., 2010). Plants from low-nutrient habitats are often characterized by low leaf nutrient concentration, slow tissue turnover rates and high nutrient resorption efficiency, which can reduce nutrient losses (Aerts and Chapin, 2000). According to the theory of Aerts (1999), plants adopting these features have successful competitive advantages over others in nutrient-poor environments. This theory, which has been

confirmed by many previous studies, has not yet been adequately tested in Qinghai-Tibetan Plateau. Sedge is the key functional group in the alpine meadow on the Qinghai-Tibetan Plateau (Cao and Zhang, 2001). Therefore, we hypothesize that it should show more adaptive leaf traits compared to other coexistent groups.

Studies on the control of resorption by live leaf nutrient status have yielded conflicting results (Aerts, 1996; Aerts and Chapin, 2000; Kobe et al., 2005; Ratnam et al., 2008; Rejmankova, 2005). Aerts (1996) concluded that there were no nutritional controls on resorption efficiency through comprehensive literature review. Kobe et al. (2005) and Ratnam et al. (2008) both found N resorption efficiency (NRE) and P resorption efficiency (PRE) decreased with increasing concentrations of live leaf N and P. These inconsistent results could be attributed to the data analysis problems in the research of Aerts (1996), arising from the non-independence of resorption measures from leaf nutrient concentrations (Kobe et al., 2005). Kobe et al. (2005) introduced a new analysis technique based on the allometric scaling relationship, which could eliminate the critical statistical problems. In tropical savanna ecosystems of South Africa, Ratnam et al. (2008) analyzed the N and P resorption pattern using Kobe's statistical approach (Kobe et al., 2005) and the energy cost perspective (Wright and Westoby, 2003). In the study of Ratnam et al. (2008), the cost of uptake from soils relative to that of resorption from senescent leaves increases more rapidly for P than for N as resource availability decreases. More recently, Renteria and Jaramillo (2011) also found a similar energy cost pattern in N and P acquisition in a tropical forest in Mexico, which suggested that acquiring P for plants was more difficult than that for N particularly in a dry year. In the alpine meadow ecosystem, the limiting nutrient factor for plant growth is markedly different from that in the tropical ecosystem (N for alpine ecosystem, while P for tropical ecosystem) (Reich and Oleksyn, 2004; Xu et al., 2006). Consequently, we expected that energy cost patterns in N and P acquisition would differ between the two distinctive ecosystems.

Therefore, we surveyed leaf N and P resorption of major species and functional groups in an alpine meadow on the Qinghai-Tibetan Plateau. We hypothesized that: (1) sedge would show lower leaf N and P concentrations and higher nutrient resorption efficiency than grasses and forbs; (2) the N and P acquisition pattern in the alpine meadow was opposite to that of the tropical ecosystem. Additionally, our study can not only report the leaf nutrient resorption on the Qinghai-Tibetan Plateau, but also provide implications for simulating nutrient resorption across large geographical scale. Overall, we intend to elucidate that leaf nitrogen and phosphorus resorption could be an intra- and inter-ecosystems indicator of plant adaptation to nutrient-poor soil.

2. Materials and methods

2.1. Study area and species

The research was conducted in an alpine meadow, located in the Haibei Alpine Meadow Ecosystem Research Station, Northwest Plateau Institute of Biology, Chinese Academy of Sciences (Fig. 1) (37°37'N, 101°20'E and at an altitude of 3250 m above sea level). The local climate is characterized by strong solar radiation with long, cold winters, and short, cool summers. The average annual air temperature was -1.7°C . The mean, maximum and minimum of averaged air temperature were 8.7, 15.6 and 2.5°C , respectively, in summer (from June to August) and -13.2 , -2.2 and -22.1°C , respectively, in winter (from December to February of next year). Annual mean precipitation is 580 mm, about 80% of which is concentrated in the growing season from May to September (Li et al., 2004). The soil is a clay loam with an average thickness of 65 cm.

Table 1
Characteristics of the alpine meadow soil.^a

Depth (cm)	Organic matter (%)	C/N	pH	CaCO ₃ (%)	CEC (cmol kg ⁻¹)	Total N (g kg ⁻¹)	Hydrolyzable N (mg kg ⁻¹)	Total P (g kg ⁻¹)	Available P (mg kg ⁻¹)	Total K (g kg ⁻¹)	Available K (mg kg ⁻¹)
0–10	12.1	10.2	7.3	0	29.9	4.2	103.5	0.9	7.3	21.4	315.0
10–20	8.6	10.6	7.7	0	31.0	3.9	106.8	0.9	3.6	20.8	187.3
20–50	3.1	10.0	8.3	4.3	16.4	1.7	79.0	0.8	0.2	21.8	97.0
50–70	1.3	11.4	8.5	4.8	14.9	0.6	32.9	0.9	7.5	21.4	70.5
70–110	3.5	11.3	8.4	6.4	25.3	1.8	58.7	0.7	1.6	–	116.1

^a Data are cited from Zhang and Cao (1999).

The soils, which are classified as Mat Cry-gelic Cambisols according to the Chinese national soil survey classification system (Chinese Soil Taxonomy Research Group, 1995) are wet and high in organic matter. The soils are similar to boreal forests and arctic tundra ecosystems, with a large stock of N in the soils, 95% of which is organic N (Cao and Zhang, 2001). Characteristics of the soils in the experimental alpine meadow are listed in Table 1.

The plant community in this alpine meadow is dominated mainly by *Kobresia humulis*, *Stipa aliena*, *Elymus nutans*, *Saussurea superba*, *Gentiana straminea* and *Potentilla nivea* (Wang et al., 1998). In total, 18 plant species belonging to three life-form groups (sedges, grasses and forbs) were selected in the study (Table 2). The selected species accounted for more than 70% of total aboveground biomass in this alpine meadow (Wang et al., 1998).

In the study of Ratnam et al. (2008), the vegetation is a typical well-wooded savanna, and the dominant tree species are fine-leaved *Acacia nigrescens*, broad-leaved *Combretum imberbe*, *Sclerocarya birrea*, and *Colospermum mopane* with an understory dominated by perennial grasses. The dominant vegetation type in the study of Renteria and Jaramillo (2011) is a highly diverse tropical dry forest with a well developed shrub understory and a strongly seasonal phenology.

2.2. Sampling and chemical analysis

Three plots were randomly selected (5 m × 5 m), and located more than 50 m distant from each other, within the alpine meadow. In one plot, we sampled the plant species as much as we could. Lastly, the 18 species, which were all found in the three plots, were selected in our analysis. In middle of July in 2008, the time of peak biomass, about 10 g mature and fully expanded live leaves of the species were randomly collected from each of three tagged plots. In late September of 2008, recently senesced, brown, but still attached leaves were collected in the same plots, and the sampling standard of senescent leaf was according to the method of Yuan et al. (2005). Leaves are considered to be ready to abscise if they are completely dry yellow without signs of deterioration, which can be removed by a gentle flicking of the branch or leaf, because leaves without an abscission layer are not removed by this method. In order to avoid sampling other tissue, we gently removed the intact senescent leaf from stem.

The samples were immediately taken to the laboratory, oven dried at 60 °C for at least 48 h to a constant weight, and then each species sampled from one of the three plots was bulked and finely ground in a Wiley mill to pass a 60-mesh screen for later analysis. The three plant samples were separately analyzed and the values were averaged for one species. N concentration in leaves was analyzed colorimetrically by the Kjeldahl acid-digestion method. Leaf P concentration was determined after digesting ground leaf material in 37% HCl:65% HNO₃ (1:4, v/v). P was measured colorimetrically at 880 nm after reaction with molybdenum blue (van Heerwaarden et al., 2003). The nutrient concentration and resorption efficiency for a functional group was an arithmetical mean of the species in this group.

3. Calculations and analysis

3.1. N and P resorption efficiencies calculations

The method of Kobe et al. (2005) was used to quantify nutrient resorption efficiency and to detect how N and P resorption efficiencies changed with live leaf N and P concentrations. Across the 18 species (Table 2), a standard allometric equation was employed to relate live and senescent nutrient concentrations (mean value of the three plots):

$$[\text{nutrient}]_{\text{senescent}} = A([\text{nutrient}]_{\text{live}})^B \quad (1)$$

The parameter A is an index of nutrient-resorption efficiency, while the scaling exponent B determines how nutrient concentrations in live leaves control resorption efficiency. $B > 1$ indicates decreasing resorption efficiency with increased nutrient status because $[\text{nutrient}]_{\text{senescent}}$ increases more than proportionately with $[\text{nutrient}]_{\text{live}}$, while $B < 1$ implies increasing resorption efficiency with increased nutrient status. $B = 1$ indicates that $[\text{nutrient}]_{\text{live}}$ has no effect on resorption efficiency (Kobe et al., 2005).

If B is not equal to 1,

$$\text{Resorption efficiency} = 1 - \frac{A[\text{nutrient}]_{\text{live}}^B}{[\text{nutrient}]_{\text{live}}} \times 100\% \quad (2)$$

Log₁₀ transformation of Eq. (1):

$$\text{Log}_{10}([\text{nutrient}]_{\text{senescent}}) = A' + B \times \text{log}([\text{nutrient}]_{\text{live}}) \quad (3)$$

where A' is $\text{log}_{10}(A)$.

For both N and P, log₁₀ transformed values of $[\text{nutrient}]_{\text{senescent}}$ were regressed against log₁₀ transformed $[\text{nutrient}]_{\text{live}}$ and the slope (B) and intercept (A') were estimated. Standardized major axis regression was used for this estimation, which was appropriate because our primary aim was to summarize relationships between the two leaf traits rather than calculating predictive regression equations (Wright et al., 2005). Regression parameters and confidence intervals were computed using the SMATR (Standardized Major Axis Tests & Routines) library (version 1) (Falster et al., 2006; Warton et al., 2006) in Matlab (Matrix Laboratory) (MathWorks, Inc.).

3.2. Statistical analysis

Pearson correlation was used for quantifying relationships between two nutrient concentrations ($[\text{N}]_{\text{live}}$ vs. $[\text{P}]_{\text{live}}$; $[\text{N}]_{\text{senescent}}$ vs. $[\text{P}]_{\text{senescent}}$; $[\text{N}]_{\text{live}}$ vs. $[\text{N}]_{\text{senescent}}$; $[\text{P}]_{\text{live}}$ vs. $[\text{P}]_{\text{senescent}}$) across the 18 species. We used the Tukey HSD for unequal n test to detect the difference of the three life forms in nutrient concentrations, resorption efficiencies and N:P ratios. These analyses were conducted using the statistical program Statistica 6.0 (StatSoft Inc.).

Table 2
N and P concentrations and N:P ratios of live and senescent leaves; and nutrient resorption efficiencies of 18 species in an alpine meadow on the Qinghai-Tibetan Plateau, China.

Life form	Species	Live			Senescent			Resorption	
		N (mg g ⁻¹)	P (mg g ⁻¹)	N:P	N (mg g ⁻¹)	P (mg g ⁻¹)	N:P	N (%)	P (%)
Sedges	<i>Kobresia humulis</i>	18.5 (0.2)	1.1 (0.13)	17.3	5.5 (0.0)	0.2 (0.01)	30.3	67.4	78.9
	<i>Scirpus distigmaticus</i>	13.5 (0.4)	0.8 (0.01)	16.7	2.9 (0.1)	0.1 (0.00)	36.5	72.0	85.0
	<i>Carex alrofusca</i>	18.0 (0.2)	1.3 (0.02)	13.4	5.3 (0.2)	0.2 (0.00)	23.0	67.9	72.2
Grasses	<i>Elymus nutans</i>	24.8 (0.5)	1.6 (0.08)	15.1	7.5 (0.3)	0.5 (0.01)	15.3	62.5	64.5
	<i>Festuca ovina</i>	13.0 (0.1)	0.9 (0.08)	15.3	6.3 (0.4)	0.3 (0.01)	20.8	72.6	84.1
	<i>Stipa aliena</i>	19.7 (0.3)	1.2 (0.03)	16.4	5.2 (0.1)	0.2 (0.01)	23.6	66.5	75.7
	<i>Koeleria cristata</i>	24.0 (1.0)	1.7 (0.01)	13.9	6.5 (0.5)	0.6 (0.03)	11.8	63.1	62.1
	<i>Poa orinosa</i>	18.1 (0.3)	1.0 (0.02)	17.6	7.2 (0.5)	0.5 (0.01)	15.3	67.8	79.9
Forbs	<i>Saussurea superba</i>	21.3 (0.5)	1.6 (0.02)	13.4	9.4 (0.4)	0.6 (0.00)	14.8	65.2	65.8
	<i>Taraxacum monogolicum</i>	30.7 (0.6)	1.9 (0.12)	15.8	11.6 (0.5)	0.8 (0.01)	13.9	58.4	56.4
	<i>Gentiana straminea</i>	24.5 (0.5)	1.9 (0.04)	12.8	10.4 (0.1)	0.9 (0.02)	12.1	62.7	57.2
	<i>Potentilla anserina</i>	20.9 (0.3)	2.0 (0.04)	10.7	8.5 (0.2)	0.9 (0.03)	9.9	65.5	56.1
	<i>Potentilla nivea</i>	23.1 (1.0)	1.8 (0.02)	13.1	9.0 (0.2)	0.7 (0.02)	13.0	63.7	61.3
	<i>Lancea tibetica</i>	18.6 (0.4)	1.4 (0.02)	13.7	10.2 (0.6)	0.7 (0.02)	13.7	67.4	71.7
	<i>Ligularia virgaurea</i>	24.0 (0.8)	1.7 (0.05)	14.0	6.4 (0.1)	0.4 (0.00)	15.3	63.1	62.3
	<i>Aster flaccidus</i>	23.5 (1.0)	1.7 (0.02)	13.6	7.5 (0.1)	0.6 (0.00)	12.6	63.5	62.3
	<i>Saussurea nigrescens</i>	23.0 (0.3)	1.5 (0.00)	15.1	9.1 (0.4)	0.7 (0.01)	13.4	63.8	67.6
	<i>Morina chinensis</i>	27.9 (1.1)	2.2 (0.05)	12.8	9.0 (0.3)	0.7 (0.01)	13.7	60.2	49.4

Values between brackets are the standard error of the mean ($n=3$), and the mean is an average of three samples from separated plots.

4. Results

4.1. Nutrient concentration in leaves

Considerable differences of nutrient concentration in live and senescent leaves were observed (Table 2). The average nutrient concentration in the 18 species were 21.5 mg g⁻¹ for N and 1.5 mg g⁻¹ for P in live leaves, and 7.6 mg g⁻¹ for N and 0.5 mg g⁻¹ for P in senescent leaves (Table 3). Among the three life forms, mean values of N and P concentrations in live and senescent leaves were in the same order of sedges < grasses < forbs. Mean N and P in senescent leaves of forbs were significantly higher than that of the other two groups ($P < 0.05$) (Table 4). N and P in senescent leaves were positively correlated ($r = 0.95$, $P < 0.0001$), and more strongly than that in green leaves ($r = 0.87$, $P < 0.0001$) (Table 5). Both in live leaves and senescent leaves, sedges had a higher N:P ratio than the other two groups, and this difference was significant in senescent leaves ($P < 0.05$) (Table 4). With senescent leaves, N:P ratios increased in most of the species, especially in sedges (Table 2).

4.2. Nutrient-resorption efficiency

The average of NRE and PRE of the 18 species was 65.2% and 67.4%, respectively (Table 3). There was also large variation of NRE and PRE in these species. NRE ranged from 72.6% in *Festuca ovina* to 58.4% in *Taraxacum monogolicum*, and PRE ranged from 85% in *F. ovina* to 49.4% in *Morina chinensis* (Table 2). The values of NRE and PRE followed the same order of sedges > grasses > forbs (Table 4). Among the three life forms, PRE of forbs was significantly lower than that of sedges ($P < 0.05$) (Table 4).

4.3. Allometries between leaf traits

Across 18 species, N concentrations increased more slowly than P concentrations in both live and senescent leaves ($B < 1$) (Fig. 2a and b, and Table 5). The values of B estimated from the allometric relationships between nutrient concentration in live and senescent leaves were both significantly greater than 1 ($B = 1.48$ for N; $B = 2.22$ for P) (Fig. 2c and d, and Table 5), suggesting that disproportionately more nutrient remained in senescent leaf as live leaf nutrient concentrations increased, that is to say,

nutrient-resorption efficiencies decreased with an increase of live leaf nutrient concentrations.

The B (N) was much lower than B (P) in the alpine meadow we surveyed. In contrast, the B value of N and P in the tropical savanna ecosystem showed opposite characters ($B = 2.03$ for N; $B = 1.19$ for P) (Fig. 3) (Ratnam et al., 2008). Interestingly, the magnitude of difference between the two exponents was relatively smaller ($B = 1.3$ for N; $B = 1.51$ for P) from analyzing the compiled global database of previous publications by Kobe et al. (2005). Overall, the ratio of B (P) to B (N) followed the order of alpine meadow > global data set > tropical savanna (Fig. 3).

5. Discussion

5.1. Nutrient concentration in leaves

The average of N and P concentrations in live leaves for the 18 plant species was 21.5 mg g⁻¹ (ranged from 13 mg g⁻¹ to 30.7 mg g⁻¹) and 1.5 mg g⁻¹ (ranged from 0.8 mg g⁻¹ to 2.2 mg g⁻¹), respectively (Table 3). Our mean N and P concentrations were lower than results of a large scale survey of leaf N and P concentrations across Qinghai-Tibetan Plateau grassland (with an average of 28.6 mg g⁻¹ for N and 1.9 mg g⁻¹ for P) (He et al., 2006, 2008). Compared with an average of the global data set (20.1 mg g⁻¹ for N, 1.8 mg g⁻¹ for P) (Reich and Oleksyn, 2004), live leaf N concentration in the alpine meadow was still slightly larger. Higher live leaf N concentration in this study from a cold ecosystem in Tibet with low mean annual temperature is consistent with the temperature-plant physiological hypothesis (Reich and Oleksyn, 2004), which states that leaf N should decline with increasing temperature because cold climates may favor high leaf N to compensate for the low efficiency of physiological processes at low temperature. An additional explanation is that increasing MAT (Mean Annual Temperature) has stronger effects on plant growth than on soil N mineralization, thus leading to N dilution in mature green leaves (Aerts et al., 2007). Koerselman and Meuleman (1996) argued that critical values of N:P ratio could be used to indicate community-level N or P limitations: N:P < 14 is generally a sign of N-limitation, while N:P ratio > 16 is indicative of P-limitation. The N:P ratios of mean live leaves of the major plant in the alpine was relatively low (14.5) (Table 3), which was near the low threshold for N limitation.

Table 3

Mean value, SD and coefficient of variation (CV; defined as $SD/mean \times 100$) of N and P concentrations and N:P ratios of live and senescent leaves; and nutrient resorption efficiencies of 18 species.

	Live			Senescent			Resorption	
	N ($mg\ g^{-1}$)	P ($mg\ g^{-1}$)	N:P	N ($mg\ g^{-1}$)	P ($mg\ g^{-1}$)	N:P	N (%)	P (%)
Mean	21.5	1.5	14.5	7.6	0.5	17.2	65.2	67.4
SD	4.5	0.4	1.8	2.2	0.3	7.0	3.7	10.3
CV	21.1	26.2	12.6	29.0	46.4	41.0	5.6	15.2

Table 4

Mean value of N and P concentrations, N:P ratios of live and senescent leaves and nutrient resorption efficiencies for different plant life forms.

Life form	n	Live			Senescent			Resorption	
		N ($mg\ g^{-1}$)	P ($mg\ g^{-1}$)	N:P	N ($mg\ g^{-1}$)	P ($mg\ g^{-1}$)	N:P	N (%)	P (%)
Sedges	3	16.7 (1.6)a	1.1 (0.15)a	15.8 (1.2)a	4.6 (0.8)a	0.2 (0.04)a	30.0 (3.9)a	69.1 (1.5)a	78.7 (3.7)a
Grasses	5	20.0 (2.1)a	1.3 (0.17)a	15.6 (0.6)a	6.5 (0.4)a	0.4 (0.06)a	17.4 (2.1)b	66.5 (1.8)a	73.2 (4.3)ab
Forbs	10	23.7 (1.1)a	1.8 (0.08)b	13.5 (0.4)a	9.1 (0.5)b	0.7 (0.04)b	13.2 (0.5)b	63.4 (0.8)a	61.0 (2.1)b

Values between brackets are the standard error of the mean; n, number of species.

Within any column, different letters indicate significant differences ($P < 0.05$) between life forms based on post hoc comparisons (Tukey HSD for unequal n tests).

Consequently, the soil of the alpine meadow was mostly limited in N rather than P. Admittedly, this inference may face uncertainty because the mean N:P ratio is an arithmetical mean rather than a weighted value. A more reasonable calculation of community-level N or P limitations should be based on a biomass-weighted N:P ratio.

Across the 18 species, live leaf N and P were highly positively correlated (Table 4). This result was consistent with previous studies (Güsewell, 2004; Garten, 1976; Han et al., 2005; Thompson et al., 1997). The strong correlation between concentrations of N and P may result from the most basic biochemical processes and metabolic activities shared among terrestrial plants (Duarte, 1992). The scaling exponent B estimated from the allometric relationship between N and P concentration in live leaves was 0.76 (Table 5), which agreed very well with the result of Reich and Oleksyn (2004), Niklas (2006), and Niklas et al. (2005), and followed the famous quarter-power scaling rules (West et al., 1997). This indicates that quick returns on investments of carbon and nutrients for plant growth (Wright et al., 2004), because rRNA (P) represents the protein-output 'machinery' for plant growth, while protein (N) represents 'overhead' in the growing process (Niklas et al., 2005). Moreover, the fact that the N:P ratio increased during senescence especially at the low nutrient concentration level, pointed out that P was preferentially reabsorbed over N and resulted in smaller log-log slope of the standardized major axis for senescent leaves than that of live leaves (Fig. 2a and b, and Table 5). This disproportionately greater resorption of P relative to N in the alpine meadow could be an important strategy for nutrient conservation on the nutrient poor soil (Richardson et al., 2008). The higher leaf N:P ratio for sedges than the other functional groups might be explain by several hypotheses, including plant growth hypothesis (Elser et al., 2000; Güsewell, 2004), and resource allocation to plant organs (Kerkhoff et al., 2006) and nutrient niche partitioning (McKane et al., 2002; Xu et al., 2011).

Killingbeck (1996) suggested that in senescent leaves, nutrient concentration values less than $7\ mg\ g^{-1}$ for N and $0.5\ mg\ g^{-1}$ for P could be considered as 'complete resorption', and values greater than $10\ mg\ g^{-1}$ for N and $0.8\ mg\ g^{-1}$ for P could be regard as 'incomplete resorption'. According to this criterion, sedges and grasses could resorb nutrient completely, while forbs fell in intermediate between complete and incomplete resorption (Table 4). This difference may be attributed to the longer growth stage of forbs than that of sedges and grasses (Wang and Shi, 2001). To confirm the speculation, the elaborate nutrient-resorption process of the three functional groups, especially in the shedding period under cold climate condition, needs further comparison.

5.2. Nutrient-resorption efficiency

The plant species in our study site showed relatively high NRE and PRE. The average of the 18 species NRE and PRE was 65.2% and 67.4%, respectively, comparable to the values of other sub-arctic plant species (Freschet et al., 2010; Quested et al., 2003; van Heerwaarden et al., 2003). Nutrient-resorption efficiency of most alpine-cold species showed obviously higher values than the average values of global scale compiled by Aerts (1996) and more recently by Yuan and Chen (2009). The relatively higher nutrient-resorption efficiency implied species seemed well adapted to nutrient stress by high internal N and P recycling (Norris and Reich, 2009; Freschet et al., 2010), although this inference remained a controversy because it was just based on the comparison of species originally growing in low-fertility habitats with that growing in high-fertility habitats, which could not distinguish the confounding effects of species and environments on nutrient-resorption efficiency (Kobe et al., 2005).

There was a strong positive correlation between NRE and PRE (data not shown) and between N and P concentration in senescent

Table 5

Summary of Pearson's correlation coefficients (r) and standardized major axis regression parameters relating N and P concentrations in live and senescent leaves, respectively; and relating nutrient concentrations in live and senescent leaves ($n = 18$).

Nutrient	r	Intercept	Slope (mean and 95% CI)
$\log_{10}P_{live}$ vs. $\log_{10}N_{live}$	0.87****	1.20	0.76 (0.62, 0.95)
$\log_{10}P_{sen}$ vs. $\log_{10}N_{sen}$	0.95****	1.04	0.51 (0.43, 0.60)
$\log_{10}N_{live}$ vs. $\log_{10}N_{sen}$	0.68**	-1.10	1.48 (1.02, 2.17)
$\log_{10}P_{live}$ vs. $\log_{10}P_{sen}$	0.80****	-0.71	2.22 (1.62, 3.05)

95% CI, 95% confidence interval.

** $P < 0.01$.

**** $P < 0.0001$.

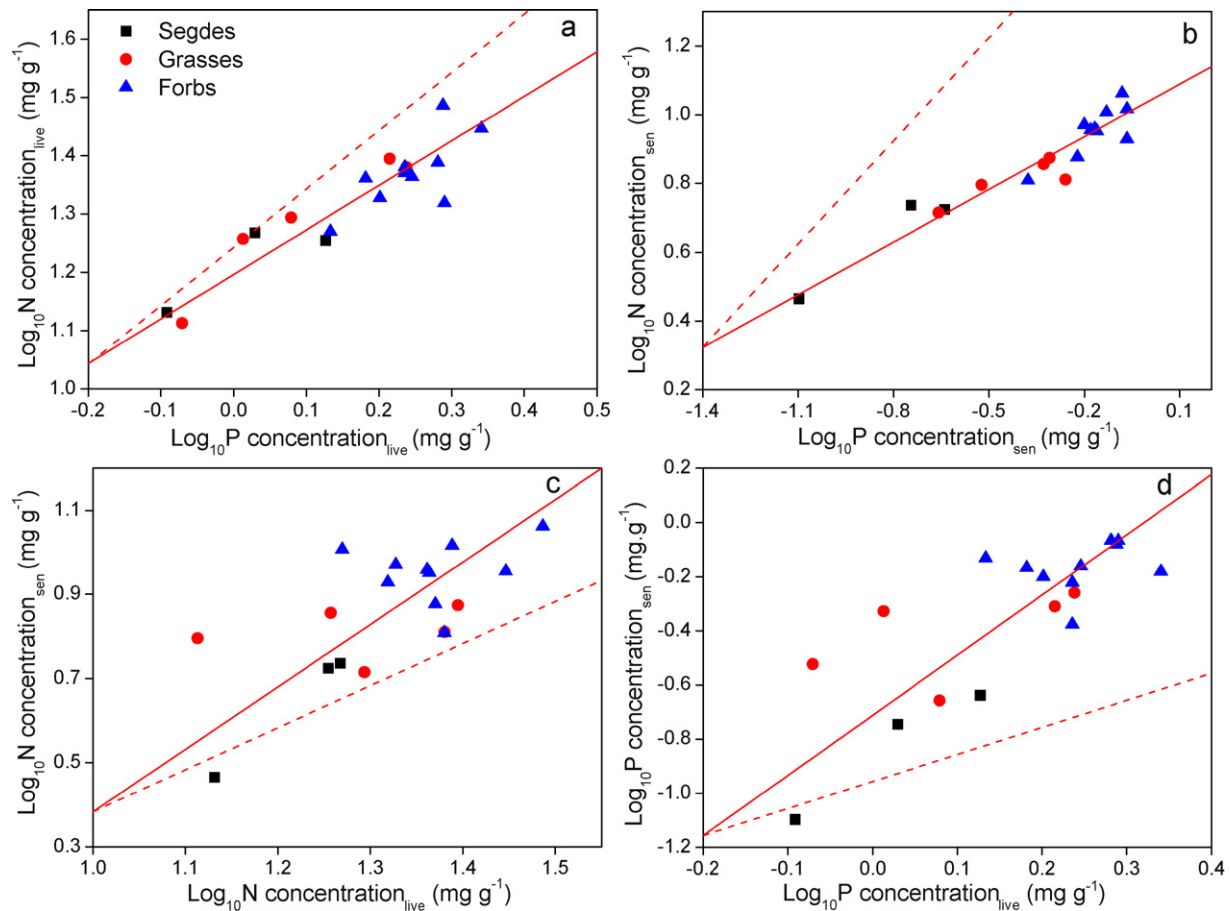


Fig. 2. Allometric relationship between P concentrations and N concentrations in live leaves (a) or in senescent leaves (b); allometric relationship of N (c) or P (d) concentrations in live and senescent leaves. Solid lines were standardized major axis regression curves (for a summary of regression statistics, see Table 5). Dash line passed through the same y-axis intercept as the corresponding solid line, and the slope of the dash lines equaled 1.

leaves (Table 5). These results suggest that N and P resorption may be controlled by correlating mechanisms, which are supported by the statements of Hawkins and Polglase (2000) that strong correlations between N and P resorption are more likely to be found in nutrient-limited sites where resorption is dependent on hydrolysis of organic substrates in live leaves. The CV (CV, coefficient of variation: defined as standard deviation/mean \times 100%) of NRE was smaller than that of PRE (Table 3), which was consistent with previous studies (Aerts and Chapin, 2000; McGroddy et al., 2004). This phenomenon can be explained by two-pool model for N and P mobility in leaf tissue (Lajtha, 1987; Pugnaire and Chapin, 1993). In this model, both foliar N and P occur in two pools: a metabolically active mobile pool, and an immobile pool of structurally bound compounds. Compared with P, the ratio of the active pool to immobile pool for N was much smaller so that N is more difficult for plant to resorb, which resulted in the smaller CV of NRE (McGroddy et al., 2004). Additionally, PRE was higher than NRE for sedges and most grasses, while NRE was higher than PRE for most forbs (Table 2). The phenomena may result from a differentiation between active pool and immobile pool in leaf N and P of the three groups.

5.3. Plant traits comparison of three functional groups

Plant traits are the results of long-term interactions between plants and the environment, reflecting the adaptation of plants to minimize the negative influence of harsh environments. Sedges, which are the key plant functional group in alpine meadow on

the Qinghai-Tibetan Plateau (Wang and Shi, 2001), show different plant traits with others (Table 4). In a previous survey on the Qinghai-Tibetan Plateau (Nyainqentanglha Mountain, about 300 km north-west of Lhasa), Ma et al. (2010) found sedges had higher single leaf area and more fine roots than forbs and grasses. Meanwhile, specific leaf areas and leaf areas of sedges increased with the increase of elevation, while forbs and grasses showed opposite trends. Thus, Ma et al. (2010) argued sedges had a competitive advantage over other functional groups in this harsh environment. In our research, we found sedges contained less N and P in leaves and had higher resorption efficiency than grasses and forbs (Table 4). 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 (Tilman, 1982), plant species are more competitive if they can reduce the limiting resources to a lower level than their competitors. Thus, our stoichiometric results provide additional evidence verifying the theory of Aerts (1999) and Tilman (1982) on the Qinghai-Tibetan Plateau and help to explain why sedges are the typically dominant plant functional group in this alpine-cold region (Sasakia et al., 2010).

5.4. Interpreting energy cost difference of N and P acquisition in contrast biome

Nutrients in new leaves come from two sources: from the soil, and from senescent leaves through resorption (Wright and

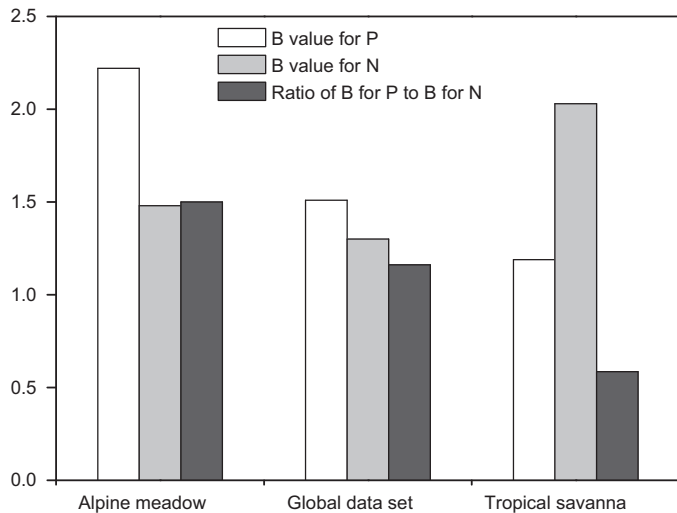


Fig. 3. Comparison of B values (the scaling exponent derived from the allometric equation) in the alpine meadow ecosystem (our study) with those of the global data set (Kobe et al., 2005) and the tropical savanna ecosystem (Ratnam et al., 2008).

Westoby, 2003; Rejmankova, 2005). Nutrient acquisition by plant from the two sources both needs to invest energy. Nutrient resorption can reflect the trade-offs of energy cost for plant to invest in acquiring nutrient either from soil or from senescent leaves. Thus, our result that nutrient-resorption efficiency decreases with increase of nutrient concentration ($B > 1$) (Fig. 2c and d, and Table 5) suggests with increasing nutrient availability, resorbing nutrients from senescent leaves is more expensive for plants than acquiring them from soil (Kobe et al., 2005).

Generally, the soil of tropical ecosystem is limited by P because the soil becomes depleted in P caused by its greater soil age; conversely, higher latitudes soil (such as in alpine and boreal ecosystems) is typically younger and low in N (Walker and Syers, 1976; Vitousek and Sanford, 1986; Courtney and Harrington, 2010). The much smaller value of B (N) than B (P) (1.48 for N; 2.22 for P) (Table 5) implies that relative to the resorption from senescent leaves, the cost of uptake of N from soils increases much more quickly than that of P as resource availability decreases (Ratnam et al., 2008). The energetic cost of N and P acquisition in tropical ecosystem showed an opposite pattern (Fig. 3). Such evidence of the two ecosystems appeared to be very reasonable because it matched the latitudinal gradients in N vs. P limitation (Reich and Oleksyn, 2004; Vitousek et al., 2010). Interestingly, in the similar analysis of a global data set (Kobe et al., 2005), the magnitude of the difference between the two exponents was much smaller, presumably because it split the geographical difference. However, the B (N) was still slightly lower than B (P) (Fig. 3), implying N limitation might exist globally. This inference was corresponded to the conclusion of a comprehensive meta-analysis of global nitrogen addition experiments that N limitation of net primary production in terrestrial ecosystems was globally widespread (LeBauer and Treseder, 2008). Consequently, adopting the ratio of B (P) to B (N) to assess the poleward trend of N vs. P limitation seems to make sense logically.

Soil organic N serves both as an important mineralization substrate and as a direct source of N for a variety of plant in arctic and alpine areas (Kielland, 1994; Lipson and Näsholm, 2001; Näsholm et al., 2009; Schimel and Chapin, 1996; Schimel and Bennett, 2004). We speculate that the cost of organic N uptake is much greater than that of inorganic N, which might be an additional reason for the pattern of energetic cost in N and P acquisition in our research. There are two lines of evidence to support our speculation. First,

organic N in soils is much less mobile than inorganic N (Owen and Jones, 2001), due to organic N being sorbed to the soil particles, greatly reducing its rate of diffusion (Jones and Hodge, 1999). Second, sedges, which all lay at the left end of the equation curve estimated by the standardized major axis regression (Fig. 2c), indicated that, relative to the resorption from senescent leaves, the cost of N uptake was higher for sedges than forbs or grasses. This inference corresponded with the results of a ^{15}N -labeled organic N addition experiment in the same alpine meadow that sedges showed a greater capacity to take up organic N than forbs or grasses (Xu et al., 2004, 2006). We inferred that the relatively higher organic N uptake resulted in more expensive energy cost in N acquisitions for sedges.

Limitations of this study include: (1) We estimated the energetic cost pattern of N and P acquisition in one site on the Qinghai-Tibetan Plateau, and compared this pattern to two corresponding studies (Kobe et al., 2005; Ratnam et al., 2008). (2) The N and P resorption was measured over one growing season, and the energy cost pattern might be affected by yearly variation of meteorology factors (Renteria and Jaramillo, 2011). Therefore, further surveys about the energetic cost pattern of N and P acquisition are warranted across a range of soils and plant communities (especially in high-priority ecosystems such as tropical and high-latitude regions) for longer time periods. However, our results suggested that plants across large geographical regions would employ different resorption strategies to adapt to the local soil nutrient status, and the two exponents for N and P in Eq. (1) is a promising new candidate for indicating latitudinal gradients in N vs. P limitation.

6. Conclusion

In summary, we quantified the leaf N and P resorption efficiency in the alpine meadow on the Qinghai-Tibetan Plateau (average 65.2% for N and 67.4% for P), which were at the high end value of the global range. From the comparison within the target ecosystem, we found sedges contained less N and P and had higher resorption efficiency than the grasses and forbs, which should contribute to the fact that sedges had a competitive advantage over grasses and forbs in the alpine meadow. As expected, we found the contrasting energetic cost patterns in N and P acquisition between the alpine meadow and the tropical ecosystem, which might cast new light on the different nutrient resorption strategies across large geographical gradients of N vs. P limitation. Overall, linking our data set with previous researches, we suggest that leaf N and P resorption appear to explain plant adaptation to nutrient-poor soil, within and between ecosystems. However, there remains a need to better understand plant nutrient resorption particularly in tropical and high-latitude regions using the energy cost perspective. Overall, our findings provide implications for nutrient management in nutrient-poor habitats and information for upcoming meta-studies and model simulations of global leaf nutrient resorption.

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