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Patterns of nitrogen resorption in functional groups in a Tibetan alpine meadow

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Abstract Nutrient resorption from senescing leaves is an important plant nutrient conservation mechanism. Effects of functional groups on nitrogen resorption efficiency (NRE) are well known in woody perennials in forest ecosystems, but less is known from other ecosystems. We investigated green and senesced leaf nitrogen (N) concentrations of different functional groups in a Tibetan alpine meadow. We found legumes contained higher N in green leaves, with no significant differences in N between graminoids and forbs. Graminoids contained the lowest amount of N in senesced leaves, followed by forbs and legumes. NRE was higher in graminoids, with no significant difference between legumes and forbs. Our results showed that level of N was related to resorption in this ecosystem, with NRE decreasing as green leaf N concentration increased, regardless of the functional group. Furthermore, we found differences in N concentration in senesced leaves resulted from differences in both green leaf N concentration and NRE across functional groups. Our findings highlight that the ability to minimize N loss by both reducing the N concentration in senescing leaves and increasing NRE could explain the dominance of graminoids in this alpine meadow. Our results indicate that change in the dominance of different functional groups could influence soil N cycling in this ecosystem.

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Introduction

Resource availability is a major driving force in ecosystem structure and function, including species diversity and nutrient cycling (Tilman 1985; Koerselman and Meuleman 1996). Nitrogen is an essential plant nutrient and is also the element that most commonly limits plant growth in terrestrial ecosystems (Chapin 1980). Nutrient resorption from senescing leaves increases the residence time of nutrients within the plant, which is an important nutrient conservation mechanism in plants (Aerts 1996). Nutrient resorption also decreases dependence on the available soil nutrient pool. In addition, the nutrients remaining in senesced leaves directly impact decomposition and nutrient cycling (Hättenschwiler et al. 2005).

Resorption efficiency (RE), the proportion of leaf nutrients withdrawn in green leaves prior to abscission, is usually used to quantify the resorption capacity of plants (Killingbeck 1996). A recent global meta-analysis showed that an average of 62.1 % of foliar N (Vergutz et al. 2012), which is significantly higher than the commonly used value of 50 % (Aerts 1996; Aerts and Chapin 2000), is recycled through resorption in a wide range of functional groups across a variety of climates. Numerous studies on the control of resorption of leaf nutrients (N and phosphorous) reported conflicting results (Aerts 1996; Aerts and Chapin 2000;

Rejmankova 2005). Such inconsistencies may be attributed to data analysis problems, resulting from the non-independence of resorption measures and foliar nutrient contents (Kobe et al. 2005). Based on an allometric scaling relationship, Kobe et al. (2005) and Ratnam et al. (2008) both found that N and P resorption efficiencies decreased with increasing concentrations of leaf P and N across broad environmental gradients. Previous studies reported inverse (Aerts 1996) or no correlation between RE and soil availability (Aerts and Chapin 2000; Lal et al. 2001; Wright and Westoby 2003). Recent global data indicate that plants do not always exhibit higher RE in low-fertility soils (Vergutz et al. 2012). Nitrogen resorption efficiency (NRE) can vary substantially within an ecosystem at small spatial scales (Hättenschwiler et al. 2008). The effect of functional groups on NRE varies (McJannet et al. 1995; Aerts 1996; Ratnam et al. 2008; Jiang et al. 2012; Vergutz et al. 2012), depending on the choice of functional group classification and ecosystem type.

Another index of nutrient resorption in plants is resorption proficiency (RP), the level to which nutrient concentration is reduced in senesced leaves, which is a reflection of biochemical limits to resorption (Killingbeck 1996). RP has been confirmed to be more sensitive to nutrient availability and plant nutritional status than to resorption efficiencies (Killingbeck 1996; Wright and Westoby 2003; Rentería et al. 2005). Potential RP of a species is the lowest nutrient content found in senesced leaves for that species. Concentrations that approach the potential RP, or terminal value, indicate complete resorption. A concentration of approximately 0.3 % N is believed to represent potential RP (Killingbeck 1996). Several studies have reported more proficient resorption in low-nutrient systems along successional or latitudinal gradients (Norris and Reich 2009). Across functional groups there are inconsistent results for nitrogen resorption proficiency (NRP; Killingbeck 1996; Ratnam et al. 2008; Yuan and Chen 2009; Jiang et al. 2012; Vergutz et al. 2012). However, multiple studies have shown lower NRP in N_2-fixers than in non-N_2-fixers (Killingbeck 1996; Yuan et al. 2005; Stewart et al. 2008).

In recent years, numerous studies of nutrient resorption have been conducted mostly in forest ecosystems (Wright and Westoby 2003; Rentería et al. 2005; Ratnam et al. 2008; Rentería and Jaraillo 2011; Wood et al. 2011; Drenovsky et al. 2013; Tang et al. 2013), or on the global scale (Kobe et al. 2005; Vergutz et al. 2012). Much less is known about resorption patterns for different functional groups from other ecosystems, particularly alpine grassland ecosystems. Such information is critical for better understanding the factors regulating nutrient conservation strategies in different ecosystems.

Tibetan alpine meadows have been severely degraded due to overgrazing since the 1970s, resulting in a decrease in grass and sedge cover and an increase in herb cover (Li and Zhou 1998). These functional group shifts may influence nutrient cycling and ecosystem functioning through alteration of nutrient resorption. To our knowledge, few studies have examined whether different functional groups have different N resorption values in this ecosystem (but see Jiang et al. 2012).

In this study, we investigated patterns of nitrogen resorption in three functional groups in a Tibetan alpine meadow. We aimed to determine if there were differences in N concentration in both green and senesced leaves, if there were differences in NRP and NRE, and if nitrogen status influences NRP and NRE.

Material and methods

Study site

The experiment was conducted at the Research Station of Alpine Meadow and Wetland Ecosystems of Lanzhou University, located in Maqu (33°58′ N, 101°53′ E) on the eastern Tibetan Plateau of China (3,500 m a.s.l..). The mean annual temperature (MAT) is 1.2°C, ranging from −10°C in January to 11.7°C in July, with approximately 270 days of frost per year. Mean annual precipitation (MAP), measured over the last 35 years, is 620 mm, occurring mainly during the short cool summer. During 2012, the MAP was 718 mm. The vegetation is characterized as an alpine meadow dominated by graminoids (*Elymus nutans*, *Kobresia capillifolia* and *Scirpus pumilus*), forbs (*Anemone rivularis* var. *floreminore*, *Trollius farreri* and *Ligularia virgaurea*) and legumes (*Thermopsis lanceolata*). In this study area, grazing was limited to the non-productive winter months through the use of fencing. The vegetation was moderately grazed by livestock, including yak and Tibetan sheep. The soil type of the study area was an alpine meadow soil (Chinese soil taxonomy research group 1995).

Data collection

Five 10 × 10 m plots separated by 50 m were established on a large flat area within the study site in May 2012. In one plot, we sampled all but a few infrequent species. Lastly, 42 species were selected for our analysis (Table **1**). Basing on the number and size of leaves, we randomly marked and sampled five to twenty individuals of each species in each plot. If individuals numbered fewer than needed, individuals found in neighboring plot areas were also marked and sampled.

Green and senesced leaves were collected in the field from July to October 2012. In early July, fully expanded green leaves were randomly collected from marked individuals of each species in each plot or in neighboring areas. In early October, similar collections were performed for senesced leaves, which were identified by colours (often red or yellow) different from live leaves. For species with shedding leaves, senesced leaves were collected as dead leaves that were ready to abscise. For species that retained dead leaves on the plants (e.g. all graminoids), leaves that were functionally disconnected from the shoot were cut off and collected. Leaves with obvious evidence of substantial mechanical damage or biotic alteration (e.g. leaves with insects damage or disease) were not sampled.

The samples were air dried in the field before being taken to the laboratory for analysis. In the laboratory, leaf samples were first ground and oven dried at 60°C for 48 h to a constant weight. N concentrations in leaves were analysed using a continuous flow-injection analyser (LACHAT Company). N content and N use efficiency were calculated per unit dry mass of leaf.

Data analysis

We followed the method of Kobe et al. (2005) to evaluate the relationship between N resorption efficiency (NRE) and green leaf N concentrations. N concentration in senesced leaves was related to N concentration in green leaves using a standard allometric equation:

$$[\mathrm{N}]_{\mathrm{senesced}} = \mathrm{A} \times ([\mathrm{N}]\mathrm{green})^{\mathrm{B}} \tag{1}$$

where A is an index of NRE and the scaling exponent B represents how N concentrations in green leaves control resorption efficiency. When B is not different from 1, resorption efficiency is independent of $[\mathrm{N}]_{\mathrm{green}}$ and is equal to (1 – A) × 100 %. A value of B greater than 1 implies a disproportionately greater amount of N in senesced leaves as $[\mathrm{N}]_{\mathrm{green}}$ increases, indicating a decrease in resorption efficiency with increased nutrient status. Conversely, a value of B less than 1 implies that resorption efficiency increases with increasing nutrient status (Kobe et al. 2005). When B is not equal to 1,

$$\mathrm{NRE} = 1 - \frac{\mathrm{A} \times [\mathrm{N}]_{\mathrm{green}}^{\mathrm{B}}}{[\mathrm{N}]_{\mathrm{green}}} \times 100\% \tag{2}$$

Log_{10} transformation of equation (1):

$$\mathrm{Log}_{10}\left([\mathrm{N}]_{\mathrm{senesced}}\right) = \mathrm{A}' + \mathrm{B} \times \log_{10}\left([\mathrm{N}]_{\mathrm{green}}\right) \tag{3}$$

where A′ is $\log_{10}$ (A).

Log_{10} transformed values of $[\mathrm{N}]_{\mathrm{senesced}}$ were regressed against $\log_{10}$ transformed $[\mathrm{N}]_{\mathrm{green}}$, and the slope (B) and intercept (A′) were estimated. Standardized major axis regression was used for this estimation, which was appropriate when both variables were measured in the same units and was subject to measurement error (Sokal and Rohlf 1995).

Regression parameters and confidence intervals were computed using the SMATR (Standardized Major Axis Tests & Routines) library (version 2.1; Warton et al. 2006) in R. To evaluate if different functional groups displayed similar or contrasting patterns, we tested for homogeneity of slopes to determine if a common slope fit the data for all functional groups (Warton et al. 2006). When slope homogeneity was observed, we additionally tested for differences in Y intercepts and for shifts along the major axis between functional groups (Warton et al. 2006). Multiple comparisons for mean value of N concentration in green and senesced leaves and NRE among functional groups were carried out using Tukey's unequal n HSD test.

Results

N concentrations in green and senesced leaves

N concentration was significantly different in both green and senesced leaves among species ($F = 256.1$, $P < 0.0001$; $F = 346.4$, $P < 0.0001$). Mean values of N concentrations were 22.1 $\mathrm{mg{\cdot}g^{-1}}$ and 11.6 $\mathrm{mg{\cdot}g^{-1}}$ in green and senesced leaves, respectively (Table **1**). The highest N concentration in green leaves (35.2 $\mathrm{mg{\cdot}g^{-1}}$) and senesced leaves (26.3 $\mathrm{mg{\cdot}g^{-1}}$) were both found in

Table 1 Nitrogen concentration in green leaves (N_g) and senesced leaves (N_s), and nitrogen resorption efficiency (NRE) of 42 species in a Tibetan alpine meadow. Values are means of five replicates, and standard deviations are in parentheses.

Functional group	Species	N_g [mg·g^{-1}]	N_s [mg·g^{-1}]	NRE [%]
Legumes	*Astragalus polycladus*	34.4 (0.2)	24.8 (0.1)	28.0 (7.6)
	Gueldenstaedtia diversifolia	26.9 (1.3)	13.8 (0.6)	48.5 (4.4)
	Melissilus ruthenicus	34.8 (1.8)	20.9 (0.8)	40.0 (2.2)
	Oxytropis kansuensis	28.3 (3.0)	14.9 (1.5)	47.4 (6.9)
	Thermopsis lanceolata	35.2 (1.7)	26.3 (1.8)	25.4 (1.4)
Graminoids	*Carex enervis*	22.8 (0.6)	11.1 (0.4)	51.5 (1.6)
	Deschampsia caespitosa	21.6 (0.5)	6.1 (0.6)	71.7 (2.4)
	Elymus nutans	20.5 (0.4)	9.3 (0.3)	54.7 (5.9)
	Kobresia capillifolia	22.3 (0.8)	9.5 (0.4)	57.7 (0.5)
	Kobresia setchwanensis	19.0 (0.6)	6.8 (0.5)	64.4 (2.8)
	Koeleria glauca	23.1 (0.6)	8.0 (0.2)	65.5 (0.4)
	Poa pachyantha	16.0 (0.6)	5.4 (0.2)	66.4 (0.7)
	Scirpus pumilus	14.3 (0.4)	4.0 (0.3)	72.3 (16.7)
Forbs	*Allium beesianum*	18.2 (0.5)	5.8 (0.4)	68.5 (2.7)
	Anaphalis lactea	13.0 (0.5)	8.1 (0.4)	37.5 (1.4)
	Anemone rivularis	25.8 (0.3)	14.8 (1.0)	42.6 (3.4)
	Anemone trullifolia	22.0 (0.9)	10.9 (0.5)	33.1 (3.3)
	Artemisia mongolica	32.1 (0.5)	12.1 (0.3)	62.4 (0.9)
	Aster diplostephioides	15.0 (0.3)	8.1 (0.3)	46.1 (0.9)
	Chamaesium spatuliferum	25.3 (0.7)	10.3 (0.1)	59.2 (1.0)
	Delphinium kamaonense	21.0 (0.5)	9.2 (0.3)	56.1 (1.8)
	Euphorbia esula	20.1 (0.4)	17.5 (0.3)	12.6 (1.1)
	Gentiana macrophylla	21.6 (0.4)	12.1 (0.3)	44.1 (1.1)
	Gentianopsis barbata	23.0 (0.7)	11.9 (0.8)	48.5 (3.2)
	Geranium wilfordii	27.9 (1.0)	12.5 (0.8)	55.0 (1.7)
	Lamiophlomis rotata	17.3 (0.9)	11.0 (0.2)	36.7 (3.1)
	Ligularia virgaurea	19.6 (0.4)	7.4 (0.7)	62.5 (2.9)
	Pedicularis kansuensis	22.9 (0.6)	17.4 (0.4)	23.8 (2.9)
	Pedicularis semitorta	21.4 (0.9)	16.4 (0.7)	23.1 (2.6)
	Pedicularis szetschuanica	27.3 (0.9)	22.7 (0.6)	16.8 (2.0)
	Polygonum viviparum	23.9 (0.2)	10.1 (0.1)	57.5 (0.3)
	Potentilla anserina	21.7 (0.2)	7.3 (0.2)	66.5 (9.3)
	Potentilla fragarioides	22.2 (0.4)	15.6 (0.5)	29.7 (2.1)
	Saussurea lanuginosa	15.9 (0.5)	7.6 (0.4)	52.6 (1.6)
	Saussurea nigrescens	17.9 (0.2)	9.3 (0.3)	48.2 (1.6)
	Saussurea pachyneura	14.5 (0.4)	8.1 (0.3)	43.8 (3.0)
	Saussurea stella	14.4 (0.4)	7.3 (0.1)	49.5 (1.3)
	Scutellaria baicalensis	25.5 (0.8)	10.5 (0.5)	58.9 (0.7)
	Taraxacum mongolicum	23.0 (0.3)	11.6 (0.8)	49.6 (4.1)
	Thalictrum alpinum	18.0 (1.0)	10.3 (0.5)	42.7 (1.7)
	Trollius farreri	20.2 (0.4)	11.6 (0.2)	42.4 (0.9)
	Veronica eriogyne	18.7 (0.4)	9.0 (0.3)	51.7 (0.9)
Across all functional groups		22.1 (5.5)	11.6 (5.1)	48.4 (14.8)

Table 2 Means of N concentration in green leaves (N_g) and senesced leaves (N_s), and N resorption efficiency (NRE) for different plant functional groups in a Tibetan alpine meadow. Values are presented as means of five replicates and standard error are in parentheses; *n* – number of species. Within any column, different letters indicate significant differences ($P < 0.05$) between functional groups based on post hoc comparisons (Tukey HSD unequal *n* tests).

Functional group	*n*	N_g [$mg \cdot g^{-1}$]	N_s [$mg \cdot g^{-1}$]	NRE [%]
Legumes	5	31.9 (1.8)^a	20.1 (2.5)^a	37.9 (4.8)^b
Graminoids	8	19.9 (1.2)^b	7.5 (0.8)^c	63.0 (2.7)^a
Forbs	29	21.0 (1.0)^b	11.3 (0.7)^b	46.2 (2.6)^b

Thermopsis lanceolata, and the lowest N concentration of green and senesced leaves were found in *Anaphalis lactea* (13.0 $mg \cdot g^{-1}$) and in *Scirpus pumilus* (4.0 $mg \cdot g^{-1}$), respectively (Table 1).

Mean N concentration differed significantly among functional groups in both green and senesced leaves. N concentration of green leaves was highest for legumes. However, no differences were detected between graminoids and forbs for green leaf N concentration (Table 2). Mean senesced leaf N concentration (NRP) was lowest for graminoids (7.5 $mg \cdot g^{-1}$), intermediate for forbs (11.3 $mg \cdot g^{-1}$) and highest for legumes (20.1 $mg \cdot g^{-1}$; Table 2).

N resorption efficiency

Both species and functional groups significantly affected NRE ($F = 243.2$, $P < 0.0001$; Table 2). The average of NRE was 48.4 %, ranging from 12.6 % in *Euphorbia esula* to 72.3 % in *Scirpus pumilus* (Table 1). NRE was highest in graminoids, while no significant difference was found between legumes and forbs (Table 2).

Allometric relationships between N concentrations in green and senesced leaves

N concentration in senesced leaves was positively correlated with N concentration in green leaves across functional groups (Table 3; Fig. 1). The value of B estimated from allometric relationships between senesced and green leaves was greater than 1 across functional groups (Table 3), suggesting disproportionally more N remained in senesced leaves, as green leaf N concentration increased and NRE decreased with increasing N concentration in green leaves. Major axis regressions used for different functional groups indicated no difference in slopes (test for slope heterogeneity, $P = 0.20$), but there were significant differences in intercepts and shifts in elevation along the common slope (Wald Statistic = 12.82, $P = 0.002$). Additionally, functional groups were shifted significantly in their position along the common slope (Wald Statistic = 27.37, $P = 0.00$), as evidenced by N concentrations in both senesced and green leaves being highest in legumes (Table 2).

Discussion

Nitrogen concentration in green and senesced leaves

The average N concentration in green leaves of 42 species was 22.1 $mg \cdot g^{-1}$, similar to that reported in the Tibetan alpine meadow (21.5 $mg \cdot g^{-1}$; Jiang et al. 2012) and larger than the average from a global data set (20.1 $mg \cdot g^{-1}$ and 18.4 $mg \cdot g^{-1}$; Reich and Oleksyn 2004; Vergutz et al. 2012). We found that the N concentration in green leaves differed significantly among plant functional groups, with a higher level for legumes and

Table 3 Summary of Pearson's correlation coefficients (R^2) and standardized major axis regression parameters relating N_g to N_s. The descriptions of N_g, N_s and NRE were referred to Table 2. * < 0.05, ** < 0.01, *** < 0.01. 95 % *CI*, 95 % confidence interval.

Functional group	*n*	R^2	Intercept [mean and 95 % *CI*]	Slope [mean and 95 % *CI*]
Log N_s vs log N_g				
Legumes	5	0.91*	−2.12 (−3.97, −0.27)	2.27 (1.35, 3.82)
Graminoids	8	0.74**	−1.62 (−2.87, −0.37)	1.91 (1.12, 3.11)
Forbs	29	0.35***	−0.89 (−1.50, −0.28)	1.46 (1.06, 2.00)
Across all functional groups	42	0.54***	−1.21 (−1.69, −0.73)	1.68 (1.36, 2.08)

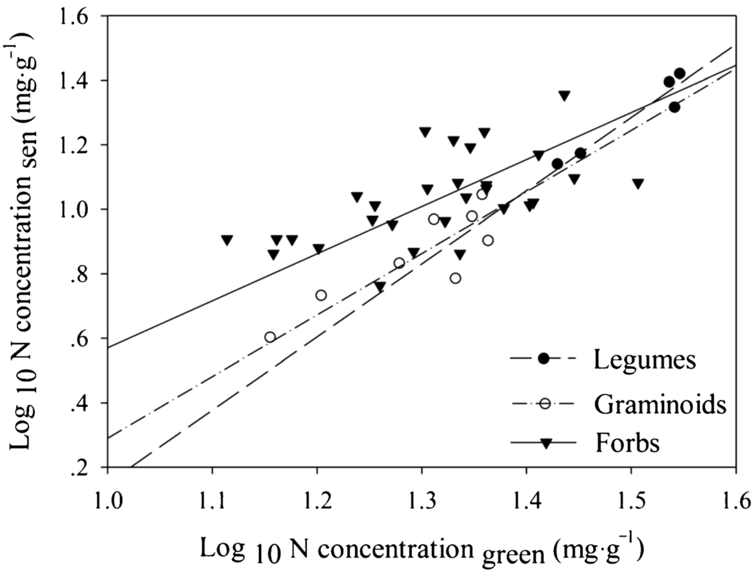

Fig. 1 Allometric relationships between N concentration in green and senesced leaves among different functional groups. Lines refer to standardized major axis (SMA) line-fitting.

with no difference between graminoids and forbs, which is consistent with previous studies (Killingbeck 1996; Killingbeck and Whitford 2001; Wright and Westoby 2003) and the results reviewed recently by Vergutz et al. (2012). Numerous studies have demonstrated that N concentration differed between deciduous, evergreen and coniferous functional groups in mature leaves in forests (Aerts 1996; Diehl et al. 2003; Kobe et al. 2005; Vergutz et al. 2012; Chen et al. 2013). We also demonstrated differences between the functional groups of legumes, forbs and graminoids in alpine grasslands.

Our results confirmed that N concentration in senesced leaves (N resorption proficiency, NRP) differed across plant functional groups. Legumes, as expected, were the least proficient at resorbing N, while forbs were intermediately proficient, and graminoids were the most proficient. Lower NRP in legumes, as many studies have indicated (Yuan et al. 2005; Stewart et al. 2008), is likely due to the fact that N-fixers have little need for tight internal N recycling. In contrast to legumes, graminoids, the dominant functional group in this ecosystem, had a strong ability to minimize N loss by reducing N concentration in senesced leaves, and thus had a competitive advantage over other functional groups. Compared to values reported by Killingbeck (1996), graminoids could resorb N completely, while senesced leaf N in legumes and forbs were both indicative of incomplete resorption. NRP is directly related to decomposition (Moretto and Distel 2003; Cornwell et al. 2008). Therefore, change in the dominance of different functional groups could influence soil N cycling in this ecosystem.

Nitrogen resorption

N concentration in senesced leaves was considerably lower than in green leaves for all species (Table 1), indicating the widespread existence of N resorption as an N-conserving mechanism in the alpine meadow ecosystem. The average of the 42 species NRE was 48 %, which was comparable to the average global value of 50 % determined by Aerts (1996), but lower than recent value of 62.1 % estimated by Vergutz et al. (2012). Across functional groups, N resorption efficiency (NRE) decreased with increasing green leaf N concentration (Fig. 1), which is consistent with three reviews (Aerts 1996; Kobe et al. 2005; Vergutz et al. 2012). Our results provided evidence that N resorption patterns in this ecosystem were influenced by plant nutritional status. A decrease in resorption efficiency with increasing foliar N concentration might be explained by the possibility that uptake from the soil is less costly than resorption (Franklin and Ågren 2002; Wright and Westoby 2003) and that the ratio of soluble to insoluble forms of N in leaves decreases with increasing foliar N concentration (Pugnaire and Chapin 1993). However, the relative costs of N resorption versus uptake from soil and the proportion of N in different forms are both not known.

Furthermore, we found that functional groups differed in NRE, with levels higher in graminoids than in forbs and legumes (Table 2), which was also indicated by significant differences in the regression intercepts among functional groups (Fig. 1). Vergutz et al. (2012) reported that graminoids had the highest NRE globally across functional groups at 74.6 %, which was higher than the result (63 %) from our study. Our results, consistent with a recent study reported by Vergutz et al. (2012), showed that differences among functional groups could be large within alpine grasslands. The variation in NRE among functional groups can result from differences in the size of the non-leaf nutrient pool (Kull and Kruijt 1999) because NRE depends on the transfer of N between leaf and other plant pools. The smaller non-leaf pools in graminoids could lead to a greater need for nutrient resorption compared to other functional groups (Table 2). We found legumes resorbed less N than other functional groups, which may be due to their N_2-fixing ability. Plants with N_2-fixing symbionts have low NRE (Killingbeck 1993; Singh 2004; Stewart et al. 2008; Vergutz et al. 2012). Finding no difference in NRE for N_2-fixers and forbs was consistent with results of another study (Vergutz et al. 2012). Within forbs, hemiparasitic species such as Pedicularis sp. had lower NRE than many other forbs in this study (Table 1), similarly indicated by another study (Quested et al. 2003). In general, our results suggested that functional relationships between N concentration in green and senesced leaves and specific patterns of resorption varied depending on plant functional group.

Conclusion

In the Tibetan alpine meadow, our results suggested variability in N conservation strategy among functional groups. Graminoids tended to minimize N loss by both reducing N concentration in senesced leaves and increasing N resorption efficiency, which could contribute to the competitive advantage of graminoids over forbs, which makes gaminoids the typically dominant plant functional group in this ecosystem. Furthermore, resorption proficiency differences among functional groups indicated that any change in the dominance of different functional groups could influence soil N cycling. Therefore, future work is needed to evaluate how grazing-inducing shifts in species and functional groups affect litter decomposition and soil nutrient dynamics in Tibetan alpine meadows.

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