Nitrogen (N) and phosphorus (P) resorption of two dominant alpine perennial grass species in response to contrasting N and P availability

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ABSTRACT

Nutrient additions may affect plant nutrient resorption and hence alter plant community composition and nutrient cycling in ecosystems. However, there is still much debate about how changes in nutrient availability affects nutrient resorption. Field experiments were conducted in 2013 on the Kunlun Mountain alpine grassland in northwestern China to investigate the variation between two dominant grasses *Stipa capillata* and *Seriphidium rhodanthum* in term of their nutrient resorption response to contrasting N and P addition levels. Results showed increasing N addition reduced N resorption efficiency and proficiency, and the N:P resorption ratio for both grass species, but increased P resorption efficiency and proficiency for only *S. rhodanthum*. Phosphorus addition increased P and N resorption efficiency of *S. rhodanthum*. In contrast, P addition decreased P resorption efficiency but had no impact on N resorption efficiency of *S. capillata*. Our results suggest that nutrient resorption responses to nutrient availability differed between perennial grass species. For both species, P additions reduced P resorption proficiency but increased N resorption proficiency. Thus, nutrient resorption is sensitive to soil nutrient availability and is an important strategy for nutrient conservation strategy for alpine grasses.

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1. Introduction

Nitrogen (N) and phosphorus (P) are important nutrients in terrestrial ecosystems and they control many biogeochemical processes. Atmospheric N deposition is rapidly increasing due to increased human activities (i.e. fossil fuel combustion and fertilizer application), leading to an increased availability of N in many environments (Galloway et al., 2004). Therefore, previously N-limited vegetation has become enriched with N and limited by other mineral elements (Falkengren-Grerup and Diekmann, 2003). Similarly, human activities have increased P inputs and influenced P-limitations of plants (DeLONGE et al., 2008). Hence, anthropogenic activities can alter the status of plant nutrient limitation and both N and P cycles in an ecosystem, such as grasslands (Lü and Han, 2010; Lü et al., 2011).

Nutrient resorption from senescing plant tissues is a process that enables a plant to re-use nutrients directly and be less dependent on external nutrient supply, and is one of the most important mechanisms of nutrient conservation. It can be quantified by nutrient resorption efficiency and nutrient resorption proficiency (Killingbeck, 1996; Lü et al., 2012). Nutrient resorption efficiency is the percentage of the amount resorbed during leaf senescence from green leaves (Wang et al., 2014). Nutrient resorption proficiency is defined as the nutrient concentrations of senesced tissue (Killingbeck, 1996), and generally decreases with increased soil resource availability (Lü et al., 2012, 2013). Global climate change and human activities can have significant impacts on the nutrient resorption process. For example, N and water additions generally decreased N resorption efficiency but increased P resorption efficiency of grass species in a semi-arid grassland in China (Lü and Han, 2010). Furthermore, the nutrient resorption patterns can influence nutrient concentration in litter and thus have an impact on nutrient cycling dynamics in an ecosystem, as shown in a grassland ecosystem in China (Lü et al., 2011).

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Nutrient resorption responses to varying nutrient availability, especially for N and P, have been extensively studied. By combining all available data from publications, Aerts (1996) reported the nutrient resorption efficiency of 50.3% for N ($n = 287$) and 52.2% for P ($n = 226$). Moreover, 63% cases of N resorption efficiency ($n = 60$) and 57% cases of P resorption efficiency ($n = 37$) showed no response to increased nutrient supply, suggesting that nutrient resorption efficiency is weakly controlled by nutrient availability. However, recent studies indicate that the N and P resorption efficiencies exhibited various trends depending on plant growth-forms, species and ages (Lü et al., 2013; Wang et al., 2014), and can be altered by nutrient or water supply (Lü and Han, 2010; Van Heerwaarden et al., 2003). For example, N fertilizer addition increased internal N use efficiency of both fast-growing and slow-growing poplar species, with the former being more sensitive (Li et al., 2012). The internal N and P use of poplar genotypes also showed different response to P and/or N deficiency, suggesting different genotype may employ different strategies to cope with N and P starvation (Luo et al., 2013; Zhang et al., 2014; Gan et al., 2016). Other studies showed N fertilization decreased N resorption efficiency of six species in bogs (Van Heerwaarden et al., 2003), the fern *Athyrium distentifolium* (Holub and Tůma, 2010), and two grass species (Lü et al., 2013).

While many studies investigated the response of N or P resorption response to nutrient addition, few of them reported the P resorption response to N addition or N resorption response to P addition. Such interactions, however, are important to improve the understanding of nutrient conservation strategies in nutrient-poor environments. Previous results on P resorption efficiency to N additions are inconsistent. Van Heerwaarden et al. (2003) reported that 4 years of N fertilization increased or decreased or showed no effect on P resorption efficiency of six sub-arctic bog species, depending on the species. However, recent studies reported that foliar P resorption efficiency significantly decreased after N addition (Holub and Tůma, 2010; Lü et al., 2013). These inconsistent results indicate that more studies of the effect of nutrient supply on resorption efficiency are needed for a more general conclusion. To our knowledge, there is little information available for the nutrient efficiency of grass species on the Kunlun Mountain alpine grassland in northwestern China.

The alpine grassland of Kunlun Mountain, with an altitude varying from 2900 m to 3600 m, is one of the most important areas for livestock grazing in Xinjiang province of China. The sensitivity of this area to nutrient addition by global climate changes or human activities (Fang et al., 2013), however, is not well documented. *Stipa capillata* and *Seriphidium rhodanthum* are two dominant grass species in this area but received little attention in previous studies. Hence, field experiments with contrasting nutrients (N and P) addition rates are conducted with the objective to examine the intraspecific responses of nutrient resorption to N and P addition, the two dominant species *S. capillata* and *S. rhodanthum* are used to address the following questions: 1) How do short-term N and P additions affect nutrient resorption efficiencies of study species, as well as the N:P resorption ratio which is considered as a potential indicator for internal nutrient use by plants (Chen et al., 2015; Lü et al., 2013); 2) Are there differences between these two grass species in term of the N and P resorption response to nutrient additions?

2. Materials and methods

2.1. Study site and experimental design

This study was established at the alpine grassland of the Kunlun Mountain in northwest of China in 2013. The area has an elevation of 3100 m (81° 06′ 33″ E, 36° 08′ 03″ N). Long-term meteorological data for the study area were not available. In 2013, daily air temperature and precipitation were monitored by an onsite weather station. Mean annual air temperature was 3.7 °C, ranging from −8.7 °C in December to 14.5 °C in July. Total precipitation in 2013 was 330 mm with more than 90% occurred in the growing season from May to October. This study site has been fenced since 2009 to prevent grazing of large animals. The dominant grass species are *S. rhodanthum* and *S. capillata*, representing the total vegetation for 60% and 30%, respectively.

Two experiments as N addition (experiment 1) and P addition (experiment 2) were established in early May. In experiment 1, five N rates as 0, 0.4, 0.8, 1.6, and 3.2 M N m^{-2} yr^{-1} of urea were applied. In experiment 2, five P rates as 0, 0.05, 0.1, 0.2, and 0.4 M P m^{-2} yr^{-1} of KH_2PO_4 were applied. Determination of these application rates was based on a previous study in grassland from Inner Mongolia of China (Yu et al., 2010). No deficiency symptoms of N or P deficiencies in plants were observed during the experiment, even for the non-fertilized treatment, suggesting the soil available N and P were sufficient for growth and development of the study species during the treatment period. Appropriate quantities of KCl were applied in both experiments to ensure adequate supply of soil K. All fertilizers were used in solid form and thoroughly mixed with in-situ soil, and applied to the plot surfaces during rainy days in early May to ensure that fertilization was effective. For both experiments, treatments were laid out in a randomized block design with four replicate plots of 4 × 4 m each. All plots were separated from each other by a 1 m buffer area.
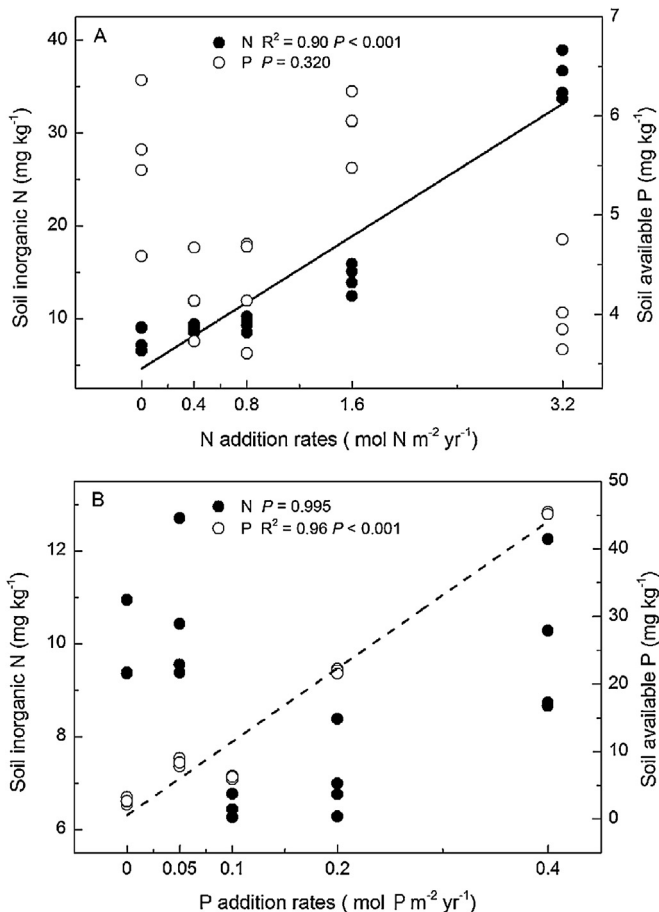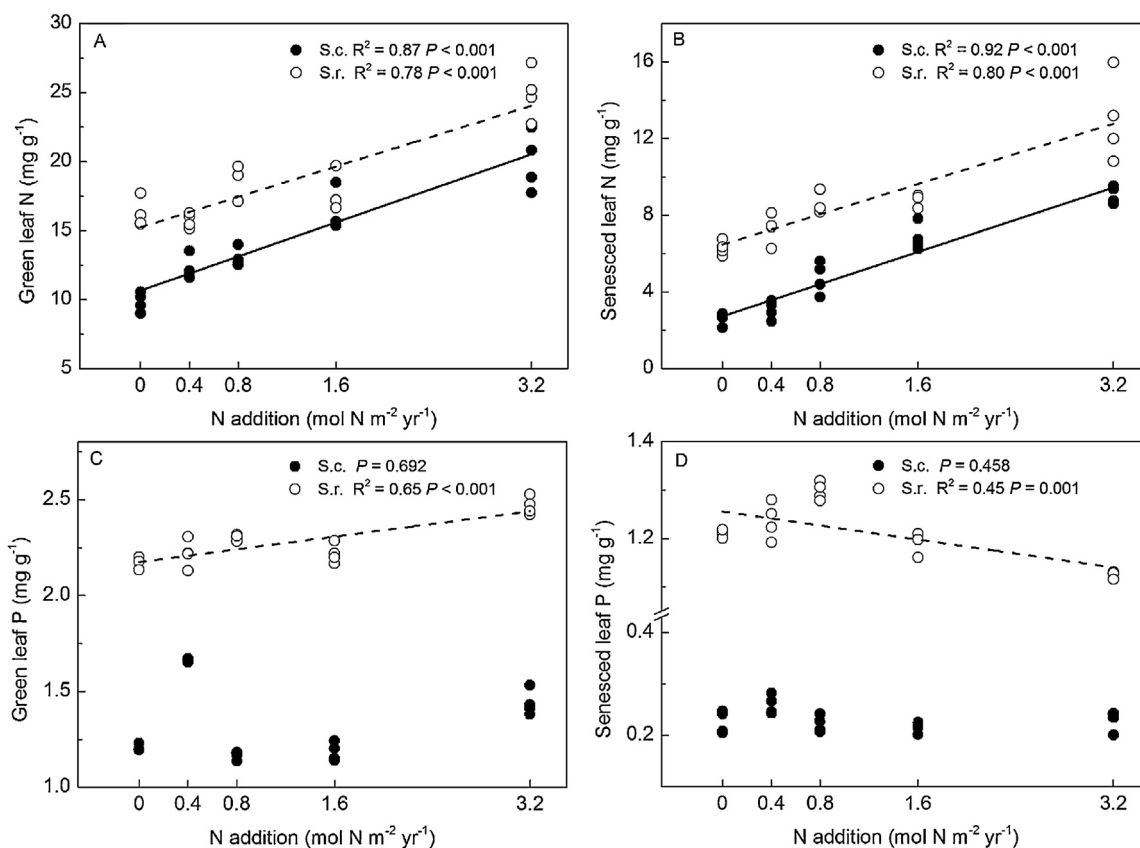

Fig. 1. Relationships between N (a) or P (b) addition rates and available N and P concentrations in soil.

Table 1
Results of the two-way ANOVAS for leaf nutrient concentrations and nutrient resorption efficiencies as dependent on nitrogen addition (N), grass species (S), and their interactions. The F-value with level of significance were presented. [N]g and [P]g represent N and P concentrations in green leaves, respectively; [N]s and [P]s represent N and P concentration in senesced leaves, respectively; NRE and PRE represent N resorption efficiency and P resorption efficiency, respectively.

Factors	d.f.	Ng	Pg	Ns	Ps	NRE	PRE	NRE:PRE	$\mathrm{Log_e}$ (NRE:PRE)
N	4	67.3***	76.5***	69.2***	22.7***	13.0***	45.5***	23.2***	22.3***
S	1	107.5***	481.4***	165.9***	2845.0***	52.7***	974.0***	178.4***	165.9***
N × S	4	5.2**	55.8***	2.2 ns	20.9***	2.4 ns	22.9***	2.17 ns	0.82 ns

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ns, not significant.

Fig. 2. Relationships between N addition rates and green and senesced leaf N (a, b) and P (c, d) concentrations in *Stipa capillata* (S.c.) and *Seriphidium rhodanthum* (S.r.) by general linear regression analysis.

Table 2
Results of the two-way ANOVAS for leaf nutrient concentrations and nutrient resorption efficiencies as dependent on phosphorus addition (P), grass species (S), and their interactions. The F-value with level of significance were presented. [N]g and [P]g represent N and P concentrations in green leaves, respectively; [N]s and [P]s represent N and P concentration in senesced leaves, respectively; NRE and P PRE represent N resorption efficiency and P resorption efficiency, respectively.

| Factors	d.f.	Ng	Pg	Ns	Ps	NRE	PRE	NRE:PRE	$\mathrm{Log_e}$ (NRE:PRE)
P	4	37.6***	172.8***	33.0***	408.8***	9.9***	16.4***	5.1**	5.5**
S	1	28.4***	772.9***	154.8***	1022.0***	81.7***	295.5***	44.4***	46.5***
P × S	4	14.6**	211.7***	11.4 ns	87.3***	2.4 ns	14.2***	0.7 ns	0.6 ns

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ns, not significant.

2.2. Plant and soil sampling and measurements

Plant and soil samples were collected as outlined by (Lü et al., 2013) with minor modifications. In early August, 100 fully expanded leaves of S. capillata and S. rhodanthum with similar sizes were randomly selected in the subplot (1 × 1 m) in the center of each plot, and marked with a red thread. Half of the 100 marked leaves were sampled as a green leaf group on

20 August 2013 and the rest were monitored weekly from mid-September to mid-October, and sampled as a group at full senescence.

The leaves were oven-dried at 75 °C for 48 h, ground and mixed evenly for elemental analysis. Total N concentrations (DW, dry weight; mg N g⁻¹) were determined colorimetrically using the Kjeldahl acid-digestion method with an Alpkem autoanalyzer (Kjeldahl System 1026 distilling unit, Hilleød, Sweden). The total P concentration (DW, mg P g⁻¹) was determined colorimetrically
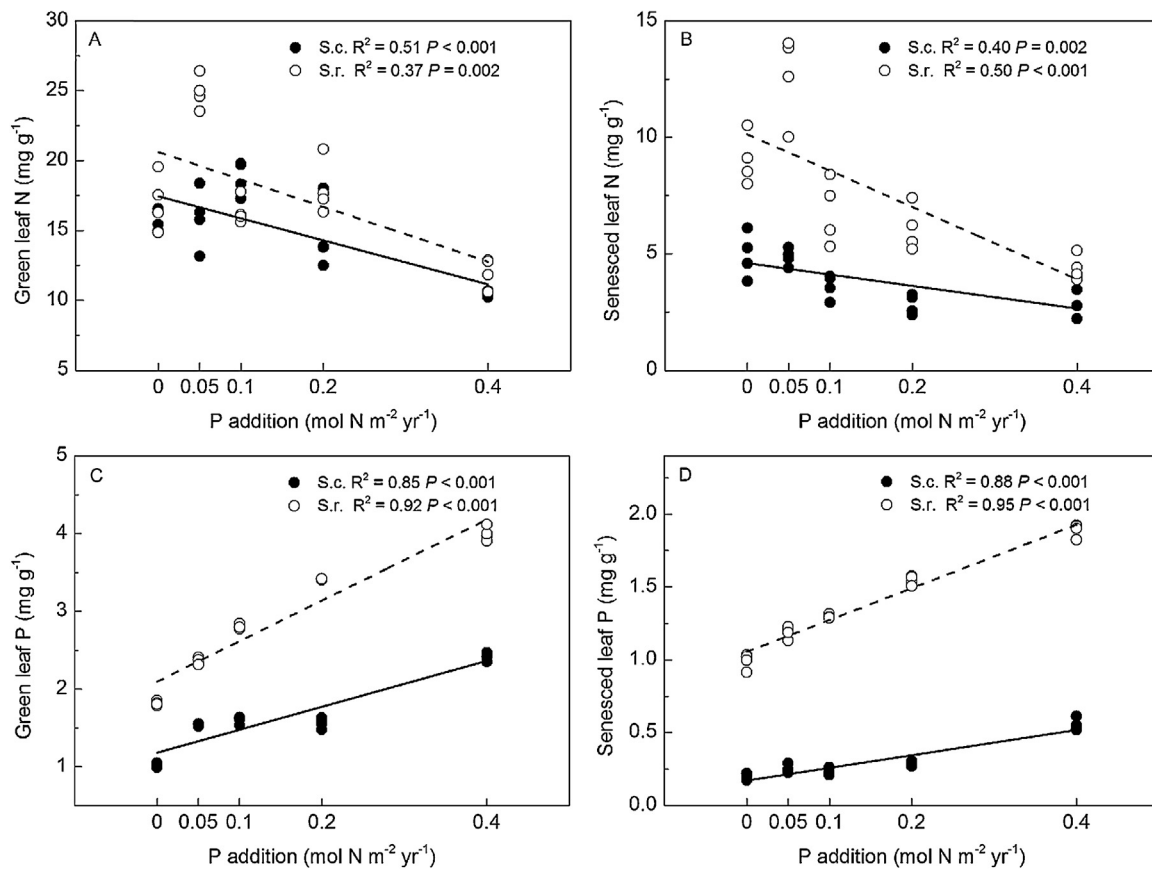
Fig. 3. Relationships between P addition rates and green and senesced leaf N (a, b) and P (c, d) concentrations in *Stipa capillata* (S.c.) and *Seriphidium rhodanthum* (S.r.) by general linear regression analysis.

after wet digestion with $H_2SO_4 + HClO_4$ (Parkinson and Allen, 1975).

On 20 August 2013, four soil samples (0–15 cm) were randomly collected from each plot using a 2 cm-diameter soil auger, and combined as a single composite sample. All soil samples were sieved through a 2 mm mesh to remove roots and impurities. The inorganic N (NH_4^+-N + NO_3^--N) in the soil was measured using a flow injection autoanalyzer (FIAstar 5000, Foss Tecator, Denmark) after being extracted 1 h with 2 M KCl. The Olsen's P of the air-dried soil was determined after extracting with 0.5 M $NaHCO_3$. The concentrations of inorganic N and available P were reported based on dry soil mass

2.3. Calculation of nutrient resorption

Nutrient resorption efficiency (NuRE) was defined as the proportion of the mature leaf nutrient pool that was resorbed (Lü et al., 2013):

$$NuRE = (1 - Nutrient_{senesced}/Nutrient_{green}) \times 100\%,$$

where $Nutrient_{senesced}$ and $Nutrient_{green}$ are N or P concentrations of the senesced and green leaves, respectively. Nitrogen and P concentrations were expressed on a dry mass basis. Nutrient resorption proficiency was expressed as N or P concentrations in senesced leaves, and low concentrations correspond to high resorption proficiency (Killingbeck, 1996).

### 2.4. Statistical analysis

All of statistical analyses were performed in SPSS version 16.0 (SPSS Inc., Chicago, IL, USA). Data were tested for normality using the

Kolmogorov–Smirnov test and for equality of error variance using Levene's test. For NRE:PRE ratio, we log transformed our data to meet requirements whereas for all other analyses we used untransformed data. Two-way ANOVA was performed to examine the grass species and the nutrient (N or P) addition effects, as well as their interaction effect on leaf nutrient (N or P) concentration and resorption. Regression analyses were conducted to determine the relationships between N or P addition rate, soil available nutrient concentrations, and leaf nutrient concentrations or resorption efficiencies.

3. Results

There were significant positive relationships between nutrient addition rate and soil available nutrient concentrations for N and P, with R^2 being 0.90 and 0.96, respectively (Fig. 1). Inorganic N (NH_4^+ and NO_3^-) concentration ranged from 8.0 ± 1.3 mg kg^{-1} in the no N addition treatment to 36.0 ± 2.4 mg kg^{-1} in the highest addition treatment (Fig. 1a). Soil available P concentration with highest inputs of P (45.2 ± 0.5 mg kg^{-1}) was sixteen times higher than that without P addition (2.7 ± 0.4 mg kg^{-1}) (Fig. 1b).

Both N addition rates and grass species had significant ($P < 0.001$) effects on N and P concentrations in green and senesced leaves (Table 1). There were significant interactions between N rates and grass species on N concentrations in green leaves and P concentrations in both green and senesced leaves. Nitrogen concentrations in green and senesced leaves of the two species were positively correlated with N addition rate (Fig. 2a and b). Nitrogen concentrations in green leaves were consistently lower in *S. capillata* than in *S. rhodanthum* but the difference was more evident at low than high N rates, resulting in an interaction effect between N rates and grass species. Phosphorus concentrations in both green and senesced
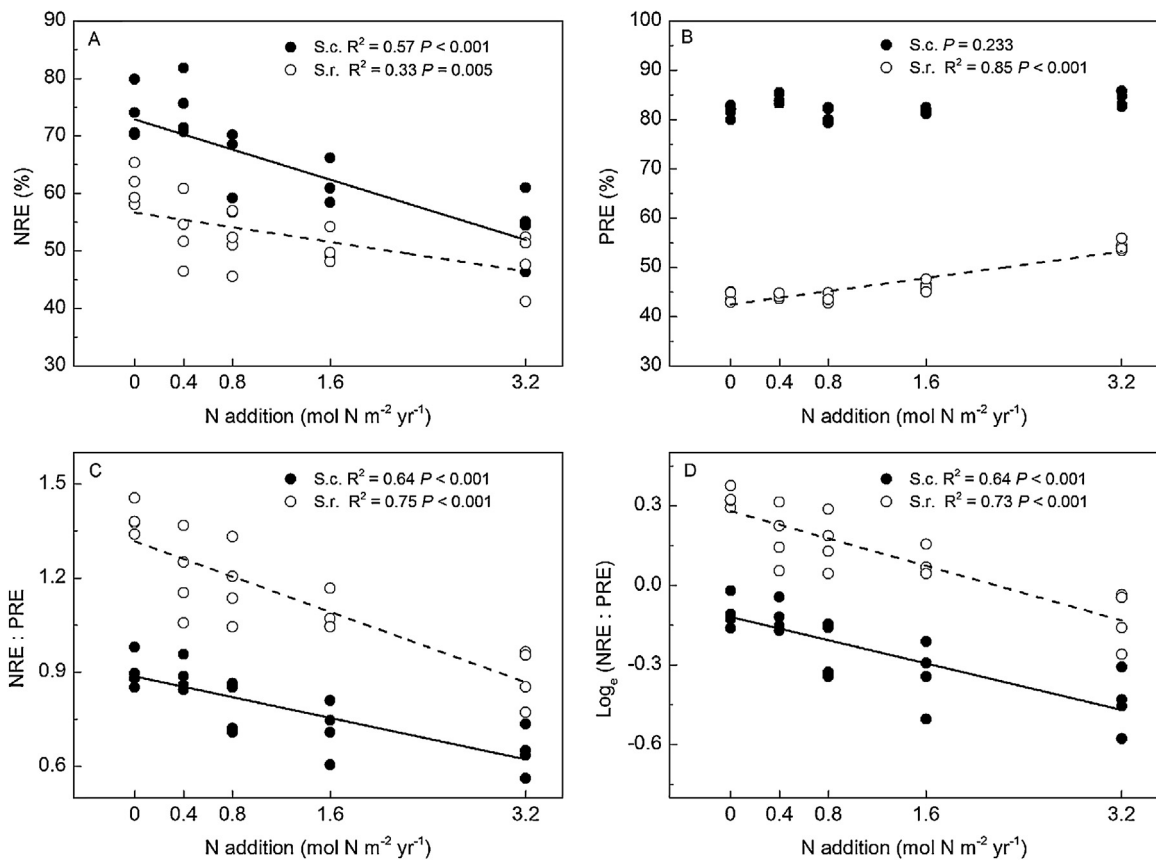
Fig. 4. General linear regression analysis between N addition rates and N resorption efficiency (NRE, a) and P resorption efficiency (PRE, b), N resorption efficiency to P resorption efficiency ratio (NRE:PRE, c) and their log transform ($\log_e$ (NRE:PRE), d) in *Stipa capillata* (S.c.) and *Seriphidium rhodanthum* (S.r.).

leaves of *S. capillata* did not change across the N input gradient (Fig. 2c and d). In contrast, P concentrations in green leaves of *S. rhodanthum* significantly increased, while those for senesced leaves decreased, with increasing N addition rate (Fig. 2c and d). Similar to N, P concentrations of *S. capillata* were consistently lower than those for *S. rhodanthum* in all treatments.

Similar to the N addition experiment, both P addition rates and grass species had significant effects ($P < 0.001$) on N and P concentrations in green and senesced leaves (Table 2). Also, there were significant interactions between P rates and grass species on N concentrations in green leaves and P concentrations in both green and senesced leaves. Phosphorus addition reduced N concentrations in green and senesced leaves of two species, resulting in negative relationships between leaf N concentrations and P addition (Fig. 3a and b). In contrast, P addition increased P concentrations in green and senesced leaves of the two species, resulting in positive relationships between P concentrations and P addition (Fig. 3c and d). Similar to N, P concentrations of *S. capillata* were consistently lower than those for *S. rhodanthum* at all P addition rates while the differences were more evident at high P rates than low P rates, resulting in significant interactions between P rates and grass species.

Both N addition rates and grass species had significant ($P < 0.001$) effects on resorption efficiency for N and P (Table 1). There was a significant N rates by grass species interaction effect on PRE but not on NRE. Nitrogen addition reduced NRE of both grass species, resulting in a negative relationship between N rate and NRE (Fig. 4a). Nitrogen addition did not affect PRE of *S. capillata*, but increased that of *S. rhodanthum*, resulting in a significant N rates by grass species interaction effect (Fig. 4b). Both NRE:PRE and $\log_e$ (NRE:PRE) in *S. capillata* and *S. rhodanthum* decreased with N

addition rate (Fig. 4c and d). Response of nutrient resorption efficiencies to P addition varied between grass species. For *S. rhodanthum*, NRE and PRE were positively correlated with P addition rate (Fig. 5a–d). However, NRE in *S. capillata* was not affected by P addition, but PRE decreased with P addition (Fig. 5). For both grass species, N or P concentrations in senesced leaf were positively correlated with their available concentrations in soil (Fig. 6a and c). For both species, there were negative relationships between soil inorganic N concentration and NRE (Fig. 6b). The PRE of *S. capillata* decreased, while that of *S. rhodanthum* increased with increasing soil available P concentration (Fig. 6d).

4. Discussion

Our results clearly showed that nutrient resorption efficiency for the two dominant alpine grass species on the Kunlun Mountain were significantly affected by short-term addition of N and P. While previous studies mainly focused on the N addition on NRE or P addition on PRE solely, the present study also investigated the interactions between N addition and P resorption or P addition and N resorption. The resorption efficiency and proficiency of the two grass species showed different responses to nutrient addition with *S. rhodanthum* being more sensitive than *S. capillata*. Given the high percent cover of *S. rhodanthum* (approximately 60%), our data suggest that this ecosystem is sensitive to nutrient addition, with potential implications for more rapid soil N cycling with N deposition (Aerts and de Caluwe, 1997). We also observed that P resorption proficiency was generally more sensitive than P resorption efficiency. Such knowledge would increase our understanding of internal N or P use of alpine grasses in response to the nutrient addition by climate change or human activities, and thus
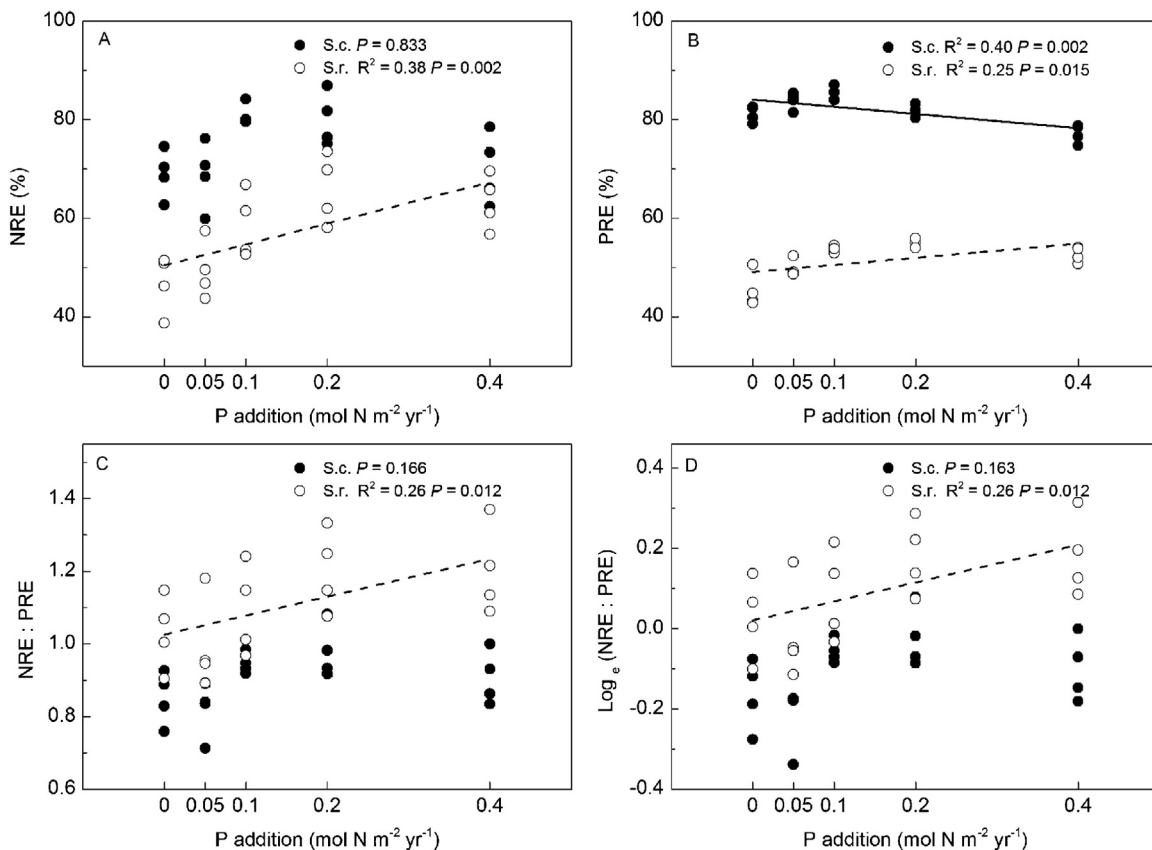
Fig. 5. General linear regression analysis between P addition rates and N resorption efficiency (NRE, a) and P resorption efficiency (PRE, b), N resorption efficiency to P resorption efficiency ratio (NRE:PRE, c) and their log transform (log$_e$ (NRE:PRE), d) in *Stipa capillata* (S.c.) and *Seriphidium rhodanthum* (S.r.).

provide a theoretical base for the ecological preservation of the grassland on the Kunlun Mountain. It is also important to be aware of that only one single year data from the current study is available. The interannual variability of plants' nutrient resorption capacity was reported previously (Freschet et al., 2010; Drenovsky et al., 2013) and needs further investigations in this aspect.

Being consistent with several previous studies (Killingbeck, 1996; Huang et al., 2008; Lü et al., 2013), our study found that increased N addition leads to a decrease in both N resorption efficiencies and proficiencies. For two dominant grass species in a semi-arid grassland similar to our environment, Lü et al. (2013) also reported that N addition decreased both N resorption efficiencies and proficiencies. It is worth noting that, one of the dominant grass species, *Stipa grandis*, from Lu et al.'s work belongs to same genus as *S. capillata* in our study. Similarly, Distel et al. (2003) reported that the nutrient use efficiency of two *Stipa* species grown on natural grasslands of central Argentina were lower under high than low fertile conditions. These results suggested that N additions enhanced plant N uptake from soil, and thus decreased plant internal N recycling (Lü et al., 2013). In addition, decreased N resorption efficiencies and proficiencies with increasing N addition rates would increase the rates of N returned from senesced leaf to soil by litter decomposition.

Similar to the response of N resorption to N addition, P fertilizer addition decreased P resorption proficiency for both grass species. Such results were similar to previous studies which reported negative effects of nutrient availability on nutrient resorption (Lü et al., 2013). The increase of P concentration in green and senesced leaves by P addition lead to low efficiency of internal P use. While the two grass species had similar trends of resorption, the more dominant species, *S. rhodanthum*, is more sensitive than *S. capillata*,

suggesting a decline of nutrient resorption for the alpine grassland ecosystem with potentially increase nutrient availability by climate change or human activities. It is interesting to note the P resorption proficiency was generally more sensitive than P resorption efficiency, confirming previous suggestions that resorption proficiency is more sensitive than efficiency to increased nutrient availability and is a good indicator for nutrient internal use (Rejmánková, 2005).

While previous studies suggested a negative response of NRE to N addition and PRE to P addition (Huang et al., 2008; Lü et al., 2013), few of them investigated the interactive effects of PRE in response to N addition and NRE in response to P addition. Our results showed that short-term N fertilizer additions increased P resorption efficiency and proficiency in *S. rhodanthum* but not in *S. capillata*. Similarly, P fertilizer additions increased NRE of only *S. rhodanthum*. These results suggest the response of nutrient resorption to fertilizer input differs between grass species. The PRE of *S. capillata* was greater than 80%, which could be due to a "complete resorption" effect (Killingbeck, 1996). Our results differed from a previous study in which 4-yr N fertilizer application decreased P resorption efficiencies and proficiencies of perennial grass (Lü et al., 2013). However, it should be noted that the above-mentioned results were found with 4 years' N addition. Such high N input might increase P-limitation of plants, and then stimulate soil phosphatase activity leading to high soil available P (Menge and Field, 2007). In addition, in a previous study, Van Heerwaarden et al. (2003) found 4 years of N fertilization significantly increased P repsorption efficiencies and proficiencies in two of six sub-arctic bog species, indicating that N addition increased P-limitation and thus an increase in P resorption to use the potentially available P. Enzyme play a role in energizing nutrient resorption, and these
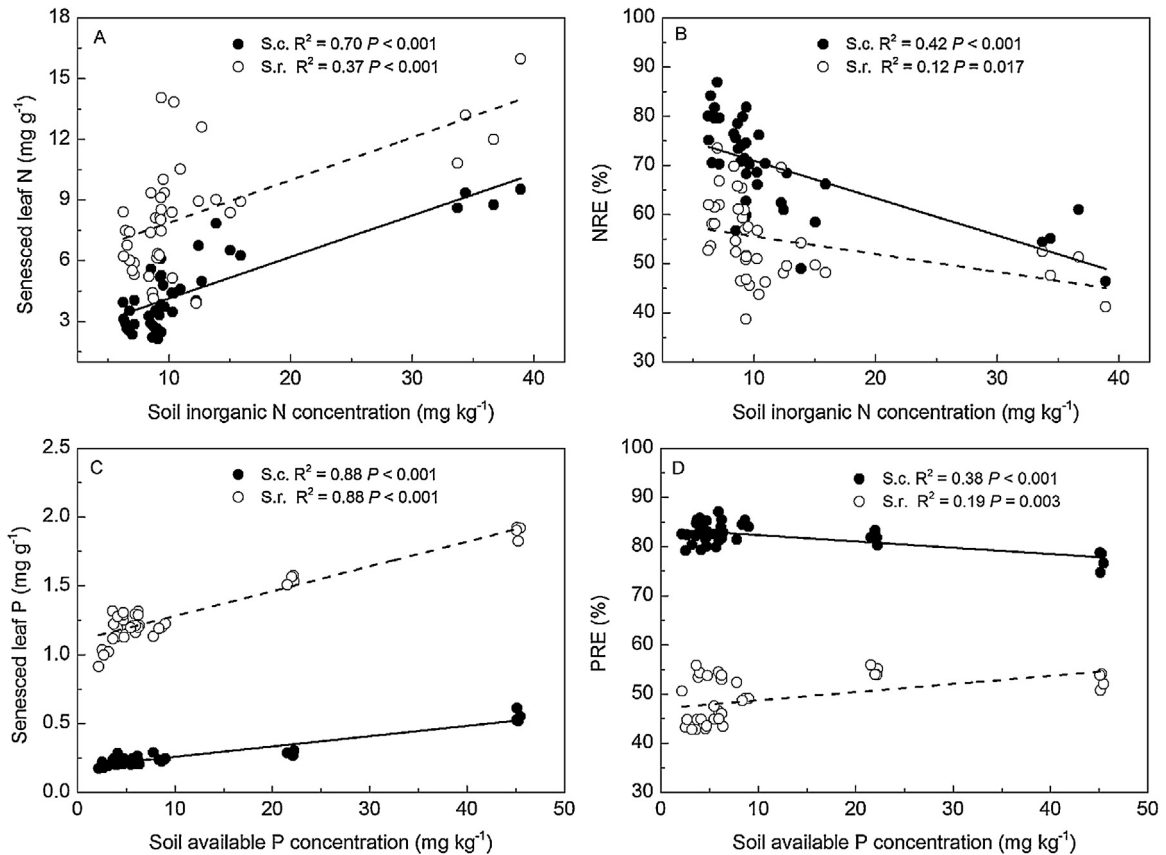
Fig. 6. Nitrogen or P concentration in senesced leaves and resorption efficiencies (NRE and PRE) in relation to soil concentrations of available N and P in *Stipa capillata* (S.c.) and *Seriphidium rhodanthum* (S.r.).

improved P resorption could be due to more enzymes for the resorption process (Sondergaard et al., 2004). Similar to response of P resorption to N addition, P addition can likely increase plant growth and thus the N demand, leading to increased N resorption proficiencies to use internal N. Such speculation are supported by lower N concentrations in senesced leaf at high P addition. However, inconsistent results of nutrient resorption also were reported in recent years (Holub and Tůma, 2010; Ostertag, 2010). These results, in combined with ours, suggest that the interactive effects of N and P on plant resorption processes are complex and further studies with plants under specific environments are required to draw a more general conclusion.

Nitrogen and P are tightly coupled at a variety of organizational levels from the cell to the ecosystem and their dynamics interact with one another (Ågren et al., 2012). Our results showed that N fertilizer additions reduced NRE:PRE ratio of both species but P fertilization increased NRE:PRE ratio of one species. Obviously, nutrient fertilization would increase soil nutrient availability and further alter N:P ratios which are strongly linked with NRE:PRE, and have direct and indirect effects on plant internal nutrient cycling (Lü et al., 2013). Nevertheless, *S. capillata* and *S. rhodanthum* showed different responses of nutrient concentrations and resorptions to nutrient addition. For instance, nutrient concentrations in *S. rhodanthum* were higher than in *S. capillata*, while nutrient resorption efficiencies showed opposite tendency between them. Our data suggest that N or P fertilization would alter nutrient status of different plant species, and dominant alpine perennial grass species-specific responses of nutrient resorption to nutrient addition. Many reports have indicated that nutrient

addition would change the plant diversity in different ecosystems (Reich et al., 2001; Bobbink et al., 2010; Yang et al., 2011). Therefore, N or P fertilization could alter the plant community composition by the indirect influences on nutrient cycling in ecosystems.

In conclusion, we showed that nutrient additions altered the nutrient cycling and storage in plants. These two dominant alpine perennial grass species-specific responses of nutrient resorption to nutrient addition, and resorption proficiency is more sensitive than efficiency to increased nutrient availability and is a good indicator for nutrient internal use. While the response of N or P resorption to N or P addtion were generally negative, the interactive effects of nutrient addition on nutrient resorption were complex and differed between two dominant grass species on the alpine grassland of Kunlun Mountain. In addition, soil available N:P ratio affected the plant internal nutrient cycling by altering N and P resorptions. Our study provides detailed insights about the nutrient resorption sensitivity to short-term nutrient additions and suggests the grassland ecosystem on Kunlun Mountain is sensitive to nutrient additions by climate change or human activities. As nutrient resorption is an important mechanism for plants conservation, the nutrient additions would potentially alter plant community composition, and have an indirect effect on nutrient cycling in ecosystems. Future research should focus on the mechanisms and the controls of variation in nutrient resorption, and its effect on plant community composition and ecosystem stability. Thus, long-term data of plant and soil are needed to measure to understand the responses of ecosystem to nutrient addition.

Author contribution

Lei Li is responsible for conception and design, analysis and interpretation and critical revision of the article, and overall responsibility. Xiaopeng Gao is responsible for revise manuscript. Xiangyi Li Fanjiang Zeng, Lisha Lin are responsible for data analysis. Yan Lu, Dongwei Gui are responsible for data collection.

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