Nutrient resorption of two dominant species in response to grazing intensity in desert grassland

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Research Article

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Abstract

Aims: Nutrition resorption in senescing leaves is critical mechanisms of nutrient preservation for the acclimatized plant especially in the barren desert steppe. As more frequent utilization of grassland resources in Inner Mongolia, the long-term grazing has a substantial impact on Nitrogen (N) and Phosphorus (P) cycling processes, and eventually disrupt the balance of nutrient supply and demand in desert grassland ecosystems.

Methods: A two-year field experiment for *Cleistogenes songorica* (*C. squarrosa*) and *Stipa breviflora* (*S. breviflora*) was explored to determine the effects of grazing intensity on nutrient resorption using a 15-year continuous grazing platform in desert grasslands in northern China.

Results: The N and P in mature leaves of *C. squarrosa* increased with moderate grazing and heavy grazing, while the P of mature leaves of *C. squarrosa* dropped with heavy grazing. *S. breviflora* showed a dissimilar response, as both moderate grazing and heavy grazing enhanced nitrogen and phosphorus resorption (N(P)RE) of *S. breviflora*, and the N(P)RE of *C. squarrosa* showed a trend consistent with it in moderate grazing but was reduced in heavy grazing. The variance in nutrient resorption was most strongly regulated by the N and P of mature and senescing leaves and soil moisture content.

Conclusions: Our findings reveal that grazing intensity has essential effects on plant nutrient resorption in desert grasslands. Nutrient resorption is basically regulated by soil moisture content and mature leaf nutrition concentration. The short-term extreme weather, such as frost, may potentially cause irreversible alterations in plant nutrient resorption.

Introduction

Nitrogen and phosphorus are the primary nutrients that could limit plant growth (Aerts and Chapin 1999). Nutrient resorption can help reduce plant dependence on environmental limited resources (Turner 1977; Lü et al. 2012b) by transport and reused of partially portable nutrients from the senescence tissues (Killingbeck 1984). Enhanced nutrient resorption improves the utilization rate of essential elements in plants (Zhao et al. 2020), which could help plants to adapt to low-nutrient environments (Aerts and Chapin 1999; Bai et al. 2012). Numerous studies have been carried out to understand plant leaf nutrient resorption in forest or shrub ecosystems, but little is known about grassland ecosystems, where are often severely N- and / or P-limited. However, due to the periodic apoptosis of herbaceous plant aboveground tissues every year, followed by large nutritional losses, the nutrient resorption in grassland ecosystems may play a more critical role in the balance of nutrient supply and demand than in forests. In particular, in desert grassland, the lack of precipitation will inhibits the mineralization of soil mineral nutrients (Zhou et al. 2012), leading to severe shortages of key soil nutrients (Del Grosso et al. 2008; Xia and Wan 2008; Huang et al. 2016). Furthermore, frequent windy weather in spring and autumn impedes plant litter returning to the soil in situ, which may further enhance the value of nutrient resorption to the maintenance of ecosystem productivity in desert grassland (Zhang

et al. 2018). Anthropogenic disturbances (e.g., grazing) also have a significant impact on the ecosystems functions in grassland (Liu et al. 2015), and alter plant nutrient utilization strategies and soil nutrient supply capacity (Steffens et al. 2008), which undoubtedly further affect plant nutrient resorption processes. Hence, it is crucial to understand variations in and mechanisms of plant N and P resorption under long-term grazing in order to better protect and utilize dessert grasslands (McSherry and Ritchie 2013).

Generally, the nutrient status of plant leaves (Kobe et al. 2005) and soil (Ren et al. 2018) are closely related to nutrient resorption. It is also widely accepted that anthropogenic disturbances and extreme climatic events could alter plant resorption processes through effecting plant tissue structure and physiology (Drenovsky et al. 2010). A study on the nutrient resorption efficiency of *Stipa krylovii* in a semiarid region found that the nutrient demand and resorption capacities of plants are governed by the nutrient status of leaves (Yuan et al., 2005). The resorption efficiency of four major tree species was predominantly driven by soil P content and soil moisture in the Loess Plateau (Xu et al. 2020). Nevertheless, we still lack a clear understanding of the mechanisms and pathways of governing nutrient resorption in grassland. As the frequency of anthropogenic and natural disturbances in desert grasslands changes, this makes it difficult to predict the potential effects on nutrient resorption.

The effects of grazing on plants' nutrient resorption are complex and multifaceted (Tonn et al. 2019). Trampling and excretion caused by large herbivores can change soil nutrient cycle processes (Barthelemy et al. 2018; Hargreaves et al. 2019), while selective feeding by sheep can also influence the nutrient acquisition strategies of specific plants on account of plant compensatory growth and self-protection mechanisms (Han et al. 2008). Furthermore, changes in soil and community structure caused by long-term grazing can also indirectly affect plant nutrient resorption by altering soil moisture (Leriche et al. 2001) and nutrient retention and supply capacity (Wang et al. 2020). However, further research is required to deepen our understanding of factors and mechanisms affecting plant nutrient resorption in grazing grassland. According to Wang et al. (2020), overgrazing raised NRE of *L. chinensis* and *S. grandis*, but lowered N(P)RE in *C. squarrosa*. Moreover, occasional climatic extremes may also play a key role in nutrient resorption processes, which could have a disproportionate impact on grassland ecosystem functions that exceeds our expectations. Many studies, for example, have discovered that plants without particular cold tolerance can barely withstand temperatures below 0 °C (Marcellos and Single 1984; Fuller et al. 2007; Al-Issawi et al. 2013; Wang et al. 2011). Extreme cold may lead to varying degrees of freezing damage to plants, which could cause irreversible damage, defoliation or even death of plant tissues, resulting in interrupted and reduced nutrient resorption (Wang et al. 2011). Undoubtedly, it makes our precise study on plant nutrient resorption even more challenging in desert grassland.

The desert steppe habitat is the most arid in the Eurasian steppe (Gong Li et al. 2000) and grazing significantly impacts its plant and soil ecosystem processes (Lin et al. 2010). However, due to the complexity of the influencing factors and the scarcity of relevant data, the response of nutrient resorption to grazing intensity in desert grasslands is difficult to predict. This study was carried out on a 15-year

grazing platform to investigate the effect of grazing on the leaf nutrient status and resorption of two major species in desert grasslands. It fills a knowledge gap by providing more detailed information on the interaction of plant, soil, and meteorological factors with nutrient resorption than previous studies. Here, we hypothesized that: (1) in desert grasslands, long-term sheep grazing affects plant nutrient resorption via regulating soil and plant nutrient availability; and (2) moderate grazing may increase resorption, whereas the effect of heavy grazing on nutrient resorption may vary by species and the nutrient requirements.

Materials And Method

Site description

The research was carried out in Siziwang Banner, central Inner Mongolia, northern China (41°47'17"N, 111°53'46"E, elevation 1450 m). With an average annual precipitation of 220 mm (average from 2002 to 2019; 264 mm in 2018 and 279 mm in 2019), the region has a typical semiarid climate, with 86 to 89% of precipitation falling during the growing season (May to September). The average annual temperature is 3.7 °C, with a 175-day frost-free season. The soil is a Kastanozem (as classified by the FAO) with a sandy loam in texture and a pH of 8.3. In the top 10 cm of soil, total C, N, and P concentrations are 17.23 g kg^{-1}, 1.61 g kg^{-1}, and 0.33 g kg^{-1}, respectively. The diversity and coverage of plants in desert steppe are both relatively low, with less than 25 species of plants (including shrubs and herbage) and 20% coverage. *Stipa breviflora* (C3 grass) and *Cleistogenes songorica* (C4 grass) are the dominant perennial grasses in the desert steppe, accounting for more than 62% of total aboveground biomass.

Table 1 Soil (0-10 cm) and plant characteristics in desert grassland

Soil					Plant		
pH	SM (%)	STC (mg g^{-1})	STN (mg g^{-1})	STP (mg g^{-1})		TC (mg g^{-1})	N/P
8.3	10.50	17.23	1.61	0.33	Sb	464.52	24.65
					Cs	444.79	17.49

Notes: SM, soil moisture; STN, soil total nitrogen content; STP, soil total phosphorus content; AGB, aboveground biomass; N/P, mature leaf nitrogen / phosphorus ratio; TC, leaf total carbon content; Sb, *S. breviflora*; Cs, *C. squarrosa*.

Experimental design

A long-term controlled experiment site was established in June 2004 as a randomized complete block design with three treatments: no grazing (CK) (fenced to exclude animal grazing), moderate grazing (MG) 1.82 sheep (ha half yr)$^{-1}$, and heavy grazing (HG) 2.71 sheep (ha half yr)$^{-1}$. These stocking rate treatments took into account the appropriate carrying capacity for livestock at the experimental site and the balance of grass supply and livestock demand in the desert steppe. Each treatment was replicated three times.

The sheep used in the experiment were all 2 years old wethers (30 kg weight), which were replaced every three years. From June through November, they were released into the experimental area at 6 am for free grazing in each treatment plot and returned to the corral at 6 pm for water and salt supplements.

Sampling and measurements

In May 2017, two 20 mÍ20 m subplots (with the same elevation and slope) were set up in each plot (18 subplots in total). Within each subplot, at least 30 shoots of plants of each species with similar growth and height and showing no signs of herbivory or disease were randomly selected and marked. In mid-August, when aboveground biomass achieves its peak value in this ecosystem, the fully unfolded upper third and fourth leaves of each shoot were sampled and mixed together to generate mature leaf samples. From mid-September to mid-October, the remaining leaves on each branch were monitored weekly for senescence, and leaves were gently flicked off and collected to constitute the senesced leaf sample when they were totally dry and yellowed but still attached. For chemical analysis, all samples were oven-dried for 48 hours at 65°C and pulverized in a ball mill (Retsch MM 400; Retsch, Haan, Germany) to pass through a 1-mm screen. Total leaf N concentrations were determined by CN analyzer (Vario TOC Elemental Inc, Donaustra, Hanau, Deutschland). Total leaf P concentrations were measured by perchloric acid oxidation followed by colorimetric analysis. Data is presented as percent macronutrient concentration per unit of plant dry matter in all analyses.

Samples of topsoil (0-10 cm depth) were collected from each subplot in mid-August. Three soil cores were collected randomly using a 5 cm diameter soil auger and mixed into a single composite sample for each plot. All soil samples were air-dried and sieved through a 2 mm mesh sieve to remove roots and tiny rocks. Total soil N was determined on a CN analyzer (Vario TOC Elemental Inc, Donaustra, Hanau, Deutschland). Soil total P was measured using the alkali-molybdenum antimony colorimetric method (Parkinson and Allen 1975). Soil pH was measured using the soil-water ratio of 1:5 (w: v) and a glass electrode pH-meter (Model 9107 BN, Orion, America). The correlations between nutrient resorption and soil characteristics were then fully assessed using these soil samples.

Data analyses

Nutrient resorption efficiency (RE), defined as the proportion of the senesced leaf nutrient pool that is resorbed, was calculated as the nutrient (N or P) concentrations in the mature and senesced leaves for corresponding species and plots, with the following formula:

$RE\ (\%) = [1 - (Nutrient_{senesced} / Nutrient_{mature})] \times 100\%$ (Boerner 1984)

where $Nutrient_{mature}$ and $Nutrient_{senesced}$ are the N or P concentrations in mature and senesced leaves, respectively.

Analysis of variance (ANOVA) was used to examine the differences in nutrient contents of mature and senesced leaves and nutrient resorption efficiency in the different grazing intensity treatments for each

species. Duncan's multiple comparison test followed significant ANOVAs (p<0.05) to differentiate between means. We regressed nutrient resorption against plant (leaf total N and P concentrations) and soil (soil moisture, soil total N and P concentrations) factors to examine whether changes in nutrient resorption were dependent on those possible factors. RandomForest was also utilized to evaluate and identify the elements that influence N (P) nutrient resorption. All statistical analyses were carried out in R 3.6.0 (Team RC 2019, R Core Team 2019; Vienna, Austria).

Results

The concentrations of N and P in mature leaves were higher than in senesced leaves, while the concentrations of N and P in mature *S. breviflora* leaves were lower by 11.25% and 45.97% than in *C. songorica* leaves (Fig. 1; p 0.05). For both species, grazing had similar effects on nutrient content. MG significantly enhanced mature leaf N by 10.15% for *S. breviflora* (p 0.05) in 2018, although this was not consistent across years. Grazing raised leaf N by up to 33.91% (p 0.05) in mature and senescent *C. songorica* leaves; however, but HG significantly reduced N in mature and senescent *S. breviflora* leaves by 10.83% and 9.18%, respectively. MG enhanced mature leaf P content in *C. squarrosa* by more than 13.59% and senescent leaf P content by up to 31.21%, but had no effect on mature leaf P content in *S. breviflora*. MG reduced senescent leaf P of *S. breviflora* by 32.00% (p < 0.05) in 2019, but not in 2018. Senescent leaf P of *S. breviflora* was reduced by more than 21.34% by HG, but elevated by 27.43% for *C. songorica*.

In general, *C. songorica*'s N(P)RE was substantially higher than that of *S. breviflora* (p<0.05). *S. breviflora*'s NRE rose by up to 26.2% (p<0.05) when it was grazed. Furthermore, MG increased the NRE of *C. songorica* by up to 9.29%, while HG decreased it by up to 33.72% (p<0.05). In 2019, grazing increased the PRE of *S. breviflora* by up to 16.20% (p<0.05), but showed a distinctly pattern in 2018. On the other hand, HG reduced *C. songorica*'s PRE by 11.2% (p<0.05), but MG had no effect.

Notably, the comprehensive analysis of nutrient resorption revealed that soil nutrients (STN and STP) and moisture (SM), leaf nutrients ($TN(P)_m$ and $TN(P)_s$) and growing season meteorological variation (GSP and ATG) could explain 66.9%-82.73% of the variation in nutrient resorption (Fig. 4). The nutrient content of mature and senescing leaves, as well as soil moisture, had the greatest impact on nutrient resorption, with the contributions of each element varying by species.

For *S. breviflora*, we observed a substantial negative relationship between N(P)RE and soil moisture (p 0.05; Fig. 3 a, c), but not in *C. songorica* (Fig. 3 b, d). Plant NRE was found to be positively linked with mature leaf N concentration, notably in *S. breviflora* (p 0.05; Fig. 3 e). Similarly, a significant positive correlation was found between PRE and mature leaf P content in both species (p 0.05; Fig. 3 g, h). By contrast, plant NRE was negatively linked with soil total N, particularly in *S. breviflora* (p 0.05; Fig. 3 i). PRE had a similar relationship with total P in the soil, which was especially strong for *S. breviflora* in 2018 and for *C. songorica* in 2019 (p 0.05; Fig. 3 k, j).

Discussion

Effects of grazing intensity on leaf nutrient concentration

The N and P contents in mature leaves are critical drivers of plant physiological processes (Kobe et al. 2005) that strongly reflecting plant growth and internal nutrient circulation (Michaels 2003). While the general patterns of plant nutrient response to grazing are still inconclusive, our study showed that MG and HG may both enhance nutrient content (N and P) in plants, notably in the mature leaves of *C. squarrosa* (p 0.05) (Fig. 1). This is in line with the results from investigations conducted in other grassland types. Wang *et al.* (2020) suggested that overgrazing increased N and P concentrations in mature leaves of *L. chinensis* and *S. grandis* in a typical steppe in Inner Mongolia. In the meadow steppe, grazing significantly enhanced the N content of eight non-legume dominant species (Han et al. 2008). This response could be caused by herbivory, which triggered the plants' overcompensation mechanism (Yang et al. 2018) and photosynthetic and plant growth rate (He et al. 2020). Appropriate grazing intensities also alter the physicochemical properties of the soil, promoting soil nutrient availability (Bardgett et al. 2001), and improving plant N access and use efficiency (de Mazancourt et al. 1999). On the other hand, overgrazing may disrupt the process of nutrient cycling, and inhibit N and P uptake and accumulation by plants in grassland ecosystems (Fernández et al. 2010; Li et al. 2017). This may become more visible during drought, which often leads to a stronger inhibiting effect on soil mineralization processes (Zhou et al. 2012). In fact, compared with either the CK or MG plots, HG reduced the leaf P content at least partly in both *C. squarrosa* and *S. breviflora* in 2018, which was a dry year (Fig. 1). In addition, some studies have found that there was negligible sensitivity of leaf nutrient content to grazing intensity, which may be attributed to severe water limitation masking other disturbance factors in some particular ecosystems (Ye et al. 2020).

Response of nutrient resorption to grazing intensity

Nutrient resorption helps plants adapt to nutrient-limited situations such as is found in desert steppe by reducing nutrient loss and soil dependency (Aerts and Chapin 1999). The impact of anthropogenic disturbances, particularly in grazing, on nutrient resorption in grasslands cannot be ignored (Wen et al. 2013), but their magnitude and mechanisms remain unclear (Ngatia et al. 2015). The N(P)RE of *S. breviflora* and *C. squarrosa* were essentially raised by grazing, especially under MG (Fig. 2). This is in agreement with extensive studies in semiarid grasslands, such as Zhang et al. (2022), who found an increase in both NRE and PRE of herbs after 34 years of grazing. Similarly, MG increased the NRE of *L. chinensis* and *C. squarrosa* (Zhang et al. 2020). Although numerous studies have indicated that grazing promotes nutrient resorption, this has not been widely validated (Ngatia et al. 2015; Millett and Edmondson 2015). Lü *et al.* (2015), for example, revealed interspecific variations in nutrient resorption among dominant species after 30 years of grazing. HG lowered the N(P)RE of *C. squarrosa* in this study (Fig. 2), which is consistent with findings on overgrazing in semiarid grasslands (Wang et al. 2020). This could be linked to the species' genetic features (Mikola et al. 2018) as well as to soil nutrient availability (He et al. 2011).

Previous studies have shown that plant nutrient resorption is generally dependent on plant nutrient content (Kobe et al. 2005) and soil resource availability (Li et al. 2011). In a meta-analysis, nutrient resorption was found to be adversely linked with mature leaf nutrients (Vergutz et al. 2012). However, this association has not been uniformly supported. It was reported that NRE was significantly and positively related to mature leaf N concentration of 28 common species in the arid regions of northern China (Yuan et al., 2005). Our study also found a similar relationship between N(P)RE and leaf N(P) content (Fig. 3). This could be because the higher the nutrient content of mature leaves, the more nutrients will be required to meet their growth and metabolic needs (Cruz et al. 2010). Meanwhile, higher N content tends to mean more protein in mature leaves, which could be considered as removeable N, and resulting in higher NRE (Yuan et al., 2005). Apart from the mature leaves' nutrient content, the correlation between soil nutrient availability and nutrient resorption has been broadly accepted (Yan et al. 2018; Xu et al. 2020). Our results showed that N(P)RE was negatively correlated with soil N(P) (Fig. 3), which is in accordance with the findings of Wang (2020), suggesting that soil nutrient shortage enhances the dependence on nutrient resorption. The variance in N(P)RE is less well explained by total soil N(P) content (Fig. 4), which is likely due to the hydrological conditions in the dry regions, which influences soil nutrient availability and plant nutrient resorption.

Water is one of the most important limiting factors for nutrient availability, and it plays a critical regulatory function in nutrient cycling in water-stressed ecosystems (Wang et al. 2018). In this study, the C3 species *S. breviflora* showed a significant negative correlation between soil moisture and N(P)RE (Fig. 3, Fig. 4). Studies on semi-arid grasses (Yuan et al. 2005a; Ren et al. 2018), such as *S. krylovii*, are in line with the findings of our study. Research on four major tree species in the Loess Plateau (Xu et al. 2020) came to the same conclusion. Plants can obtain more N and P from the soil for growth in arid regions because higher soil moisture alleviates the limitation of soil nutrient efficiency caused by water deficit (Sala et al. 1989). Increased soil nutrient availability has been shown in numerous studies to reduce plant nutrient resorption (Lü et al. 2012a; Ren et al. 2015). Water-limitation elicited a stronger response in the C3 species *S. breviflora* than grazing. The N(P)RE of *C. squarrosa*, on the other hand, displayed no significant relationship with soil moisture (Fig. 3). This is similar to results on NRE and soil moisture of *Juniperus oxycedrus* in a Mediterranean climate zone (Kutbay and Ok 2003). This could be attributed to the C4 species' high water use strategy (Liang et al. 2002, 2009), which minimizes nutrient cycling restrictions (Wang and Wang 2001) while meeting nutritional requirements. In addition to the aforementioned factors, the impact of abrupt temperature fluctuations on nutrient resorption should not be underestimated (Kobe et al. 2005; Tong et al. 2021).

Response of leaf senescence and N (P) resorption to climate change

Average daily minimum temperature shows a substantial increasing tendency (0.4 °C/decade) (Wang et al. 2021) in the context of global warming. However, the damage caused by frost to plants cannot be overlooked. Inconsistent with our expectations, the contribution of the senescent leaves nutrition content to variation in resorption was very significant in both *C. squarrosa* and *S. breviflora* during our study. This may imply that the plant nutrition reabsorption may be incomplete before the senescent leaves naturally

undergo abscission. In fact, our measured levels of nutrient resorption were still lower than those of Ren (2018), which was obtained with same species in a nearly identical desert grasslands. This may be related to the premature frost damage occurring at the end of the growing season. The meteorological data indicate that frost appeared earlier in our study (2018 and 2019) than in Ren's (2017) (Fig. S1). Resulting damage to living leaf tissue and even premature abscission, may inhibit or interrupt the resorption process, and eventually appearing as incomplete NRE (senescent leaf N content 10 mg/g, Fig. 1) (Killingbeck 1996; Li et al. 2013; Drenovsky et al. 2019). In a study on *Kandelia obovate*, NRE and PRE were 61% and 42%, respectively, in normal conditions, but decreased to 13% and 10% after frost damage (Wang et al. 2011). Similar to the results of this experiment (Fig. 4), *Laguncularia racemosa* had greater C and N content in senescing leaves following frost (Ellis et al. 2006), which was one of the key reasons for reduced nutrient resorption. It appears that the earlier frost occurs during leaf senescence, the higher the comparable nutrient loss it may cause. However, due to the unpredictability of frost damage and the absence of experimental data on its effects, this assumption needs to be verified further. Furthermore, since this experiment was conducted in a semiarid zone, drought may also be a non-negligible factor leading to poor nutrient resorption (Yuan et al., 2005; Khasanova et al., 2013), which may be exacerbated as a result of global climate change (Allison and Treseder 2008).

Conclusion

We assessed the response of leaf nutritional status and resorption of two dominant plants to a grazing intensity gradient in a desert grassland. The sensitivity of nutrient resorption in response to grazing and the environment varied between C3 (*S. breviflora*) and C4 (*C. squarrosa*) plant species as examined. Moderate and heavy grazing enhanced nutrient contents in the mature leaves for *C. squarrosa*, but did not occur for *S. breviflora* because of water scarcity in dessert grassland. For both species, moderate grazing promoted nutrient resorption (N and P), while the effect of heavy grazing varied with the plant adaptation strategies. The soil moisture content and mature leaf nutrient may be the key factors regulating plant leaf nutrient resorption besides plant species in the desert steppe. Meanwhile, after further analysis of data, it indicated that extreme low temperature at the end of the growing season may play an irreplaceable role for nutrient resorption in desert grassland, but it needs to be much deeper research by targeted experiment. Overall, our findings revealed the substantial effects of grazing intensity on plant resorption as well as the environmental regulatory mechanisms in this process in dessert grassland. Our study provides a basis for a better understanding of plant grazing-adaptive nutrient use strategies and ecosystem nutrient cycling processes in dry region.

Statements & Dclarations

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author’s contributions

Guodong Han and Yunbo Wang designed and oversaw the long-term experiment. Qingge Zhao and Chen Liu collected the samples, analysed the data, and wrote the first draft of manuscript. All authors discussed and revised the manuscript together.

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Figures

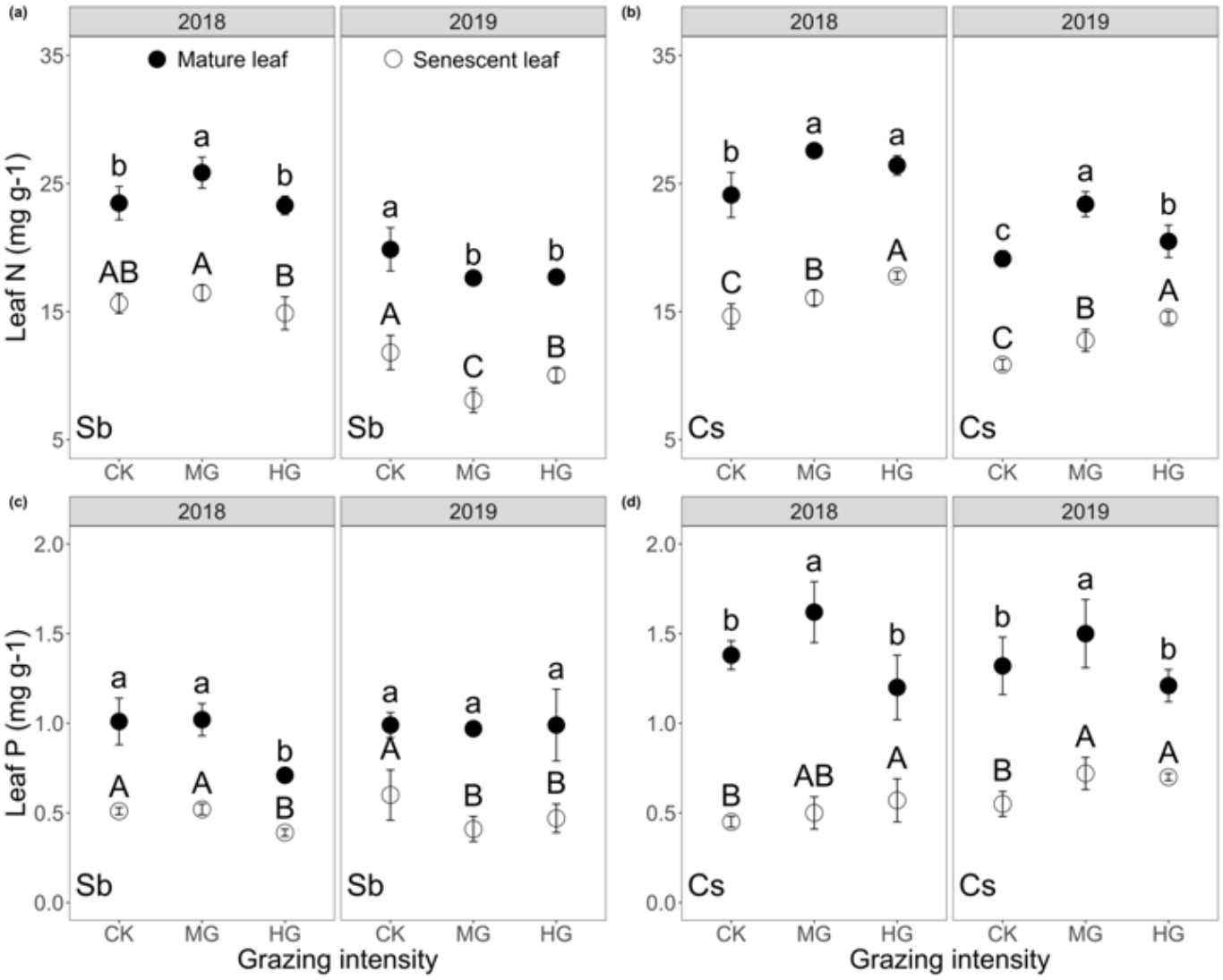

Figure 1

Effects of grazing intensity on N and P concentrations in mature and senesced leaves for two dominant species during two years in the desert steppe. Significant differences in the nutritional content of mature (senescent) leaves of the same species are indicated by different lowercase (uppercase) characters (p< 0.05). Error bars show one standard error of the mean. Abbreviations: Sb, *S. breviflora*; Cs, *C. songorica*; CK, no grazing; MG, moderate grazing; HG, heavy grazing.

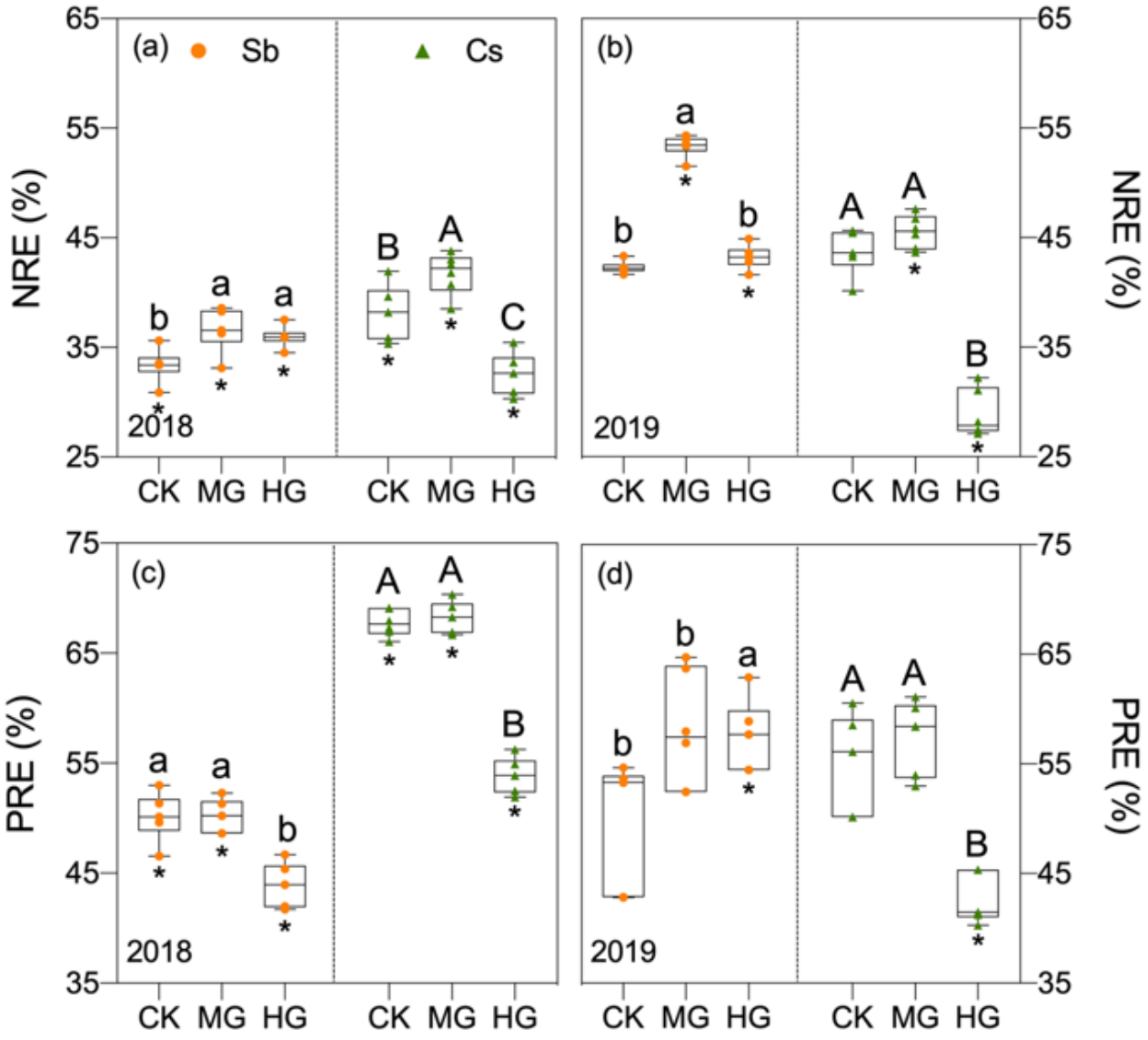

Figure 2

Effects of grazing intensity on NRE and PRE for two dominant species in a desert grassland. Error bars show one standard error of the mean. Upper (lower) case letters indicate a significant difference within a species ($p < 0.05$). * below the box represents significant interspecific variation ($p < 0.05$).

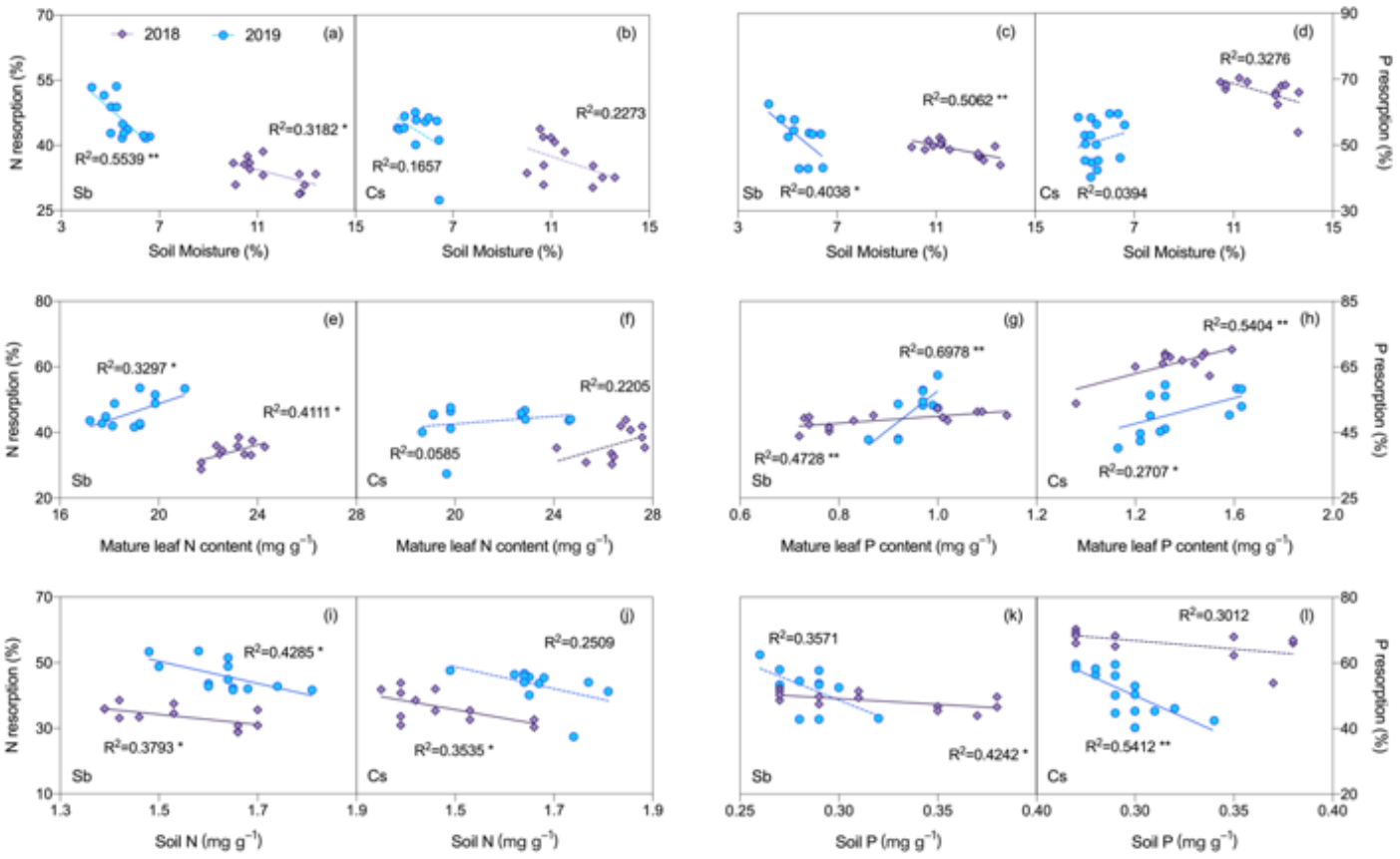

Figure 3

Regression relationships between N (P) resorption and soil moisture, soil N (P), mature leaf N (P). Sb: *S. breviflora*; Cs: *C. songorica*. '**' indicates p 0.01, '*' indicates 0.01 p 0.05.

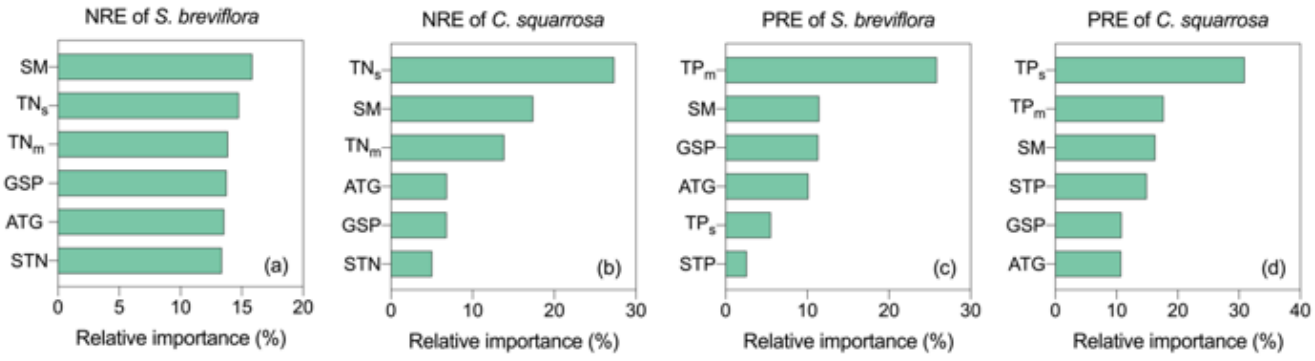

Figure 4

Effects of soil and plant nutrients, precipitation, average growing season temperature, and soil moisture on leaf nutrient resorption. Soil N(P) content - STN(P); average temperature of growing season - ATG;

growing season precipitation - GSP; mature leaf N(P) - $TN(P)_m$; senesced leaf N(P) - $TN(P)_s$; soil moisture content - SM.

Supplementary Files

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