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Stoichiometric response of dominant grasses to fire and mowing in a semi-arid grassland

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ABSTRACT

Prescribed burning and mowing are widely used grassland management strategies that potentially alter plant nutritional status, with consequent influences on community structure and ecosystem function. We evaluated the effects of annual burning and mowing on stoichiometric ratios (C:N, C:P, and N:P) of three dominant grasses (*Leymus chinensis*, *Stipa grandis*, and *Cleistogenes squarrosa*) in a semi-arid grassland in northern China. After treatments were applied for two years, both fire and mowing did not affect nutrient concentrations and stoichiometric ratios in green leaves. Fire reduced C:N and C:P in senesced leaves. There was no interaction between fire and mowing to affect stoichiometric ratios in green and senesced leaves. Averaged across the three grass species, fire reduced both N and P resorption efficiency. These results indicate that short-term (2-yr) annual burning and mowing would have limited effects on nutritional status of dominant grass species in this semi-arid grassland. Annual burning would lead to rapid nutrient cycling due to its positive effects on litter quality. These results suggest that prescribed burning may affect above- and below-ground processes of semi-arid grassland through changes in foliar stoichiometric ratios, and that the responses of green and senesced leaves to fire may differ greatly due to changes in nutrient resorption.

1. Introduction

Grassland ecosystems have been historically characterized by natural disturbances such as fire (Ojima et al., 1994) and grazing (Anderson et al., 2007; Cech et al., 2008). Both of these factors have influence on community structure and ecosystem function (Briggs et al., 2002; Collins and Smith, 2006). Prescribed burning and mowing are increasingly being used to mimic the natural processes of fire and grazing and manage and restore grassland ecosystems (Collins et al., 1998; Verrier and Kirkpatrick, 2005). Compared to their effects on plant species diversity and community composition (Contant et al., 2001; Van Dyke et al., 2004; Briggs et al., 2005), the effects of prescribed burning and mowing on plant tissue quality are not as well documented. This may limit our ability to predict ecosystem responses to these two disturbances because the quality of plant tissue has important implications for several ecosystem processes, e.g. herbivory and litter decomposition (Novotny et al., 2007). Furthermore, fewer studies have examined the nutritional quality of both green and senesced tissue. The nutritional response of green and senesced leaves to the same ecological factor may be different due to changes of plant internal nutrient restranslocation during tissue senescence (Billings et al., 2003). Such studies are necessary in order to examine whether the changes in nutrient status and stoichiometric ratios of green tissues in response to prescribed burning and mowing would be reflected in litter quality after senescence.

Prescribed burning clearly influences the availability of several kinds of resources, including light (Knapp and Seastedt, 1986), soil water and nutrients (Cui et al., 2010). Thus, fire can alter multiple plant physiological processes related to the acquisition of both energy and nutrients. Fire can be reasonably expected to alter the nutrient status and stoichiometric ratios of major elements in both green and senesced plant tissues. In a savanna ecosystem, macronutrient concentrations in live grass shoots are much higher in burned vegetation, although the effect is short-lived (Van de Vijver et al., 1999). However, long-term frequent burning may reduce tissue N concentrations (Kitchen et al., 2009; Schimel et al., 1991), increase C:N ratio of plant green tissues (Ojima et al., 1994), and enhance N use efficiency (Ojima et al., 1990). Changes in nutritional status of dominant plants in response to fire would have great

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implications for primary productivity. For example, Xu and Wan (2008) observed that short-term annual burning resulted in higher aboveground net primary productivity in a semi-arid grassland in northern China. Furthermore, while most studies focused on the changes of stoichiometric ratios only in green tissues, we know little about the stoichiometric responses of senesced tissues to fire. Fire can affect nutrient retraslocation during tissue senescence (Lü et al., 2011), implying that the responses of stochiometric ratios to fire between mature and senesced tissues may vary a lot.

Mowing and aboveground biomass removal, as an important grassland use strategy for hay harvesting at the end of the growing season, would remove a majority of the current year's standing aboveground biomass and consequently lead to the removal of substantial amounts of nutrients locked in plant tissues. However, Robson et al. (2007) suggested that positive feedback between mowing and dominant plant functional strategies maintained high N availability in subalpine grasslands. While C:N ratios have been used as indicators of plant tissue chemical responses to mowing (Pan et al., 2010), potential changes of other stoichiometric ratios are less well known. More attention should focus on C:P and N:P ratios not only because of the importance of P intake as an indicator of food quality for herbivores (Novotny et al., 2007) and microbes (Güsewell and Gessner, 2009), but also because leaf N:P ratio can be used as a reliable and simple index to predict the nature of nutrient limitation of particular plant communities (Güsewell et al., 2003; Koerselman and Meuleman, 1996). Furthermore, nutrient availability, partly governed by litter quality, is a critical factor potentially limited ecosystem responses to mowing. However, the potential effects of mowing on plant litter largely remained unknown.

The main objective of this study was to examine the response of foliar stoichiometric ratios to annual burning and mowing. A second objective was to determine whether senesced leaves showed a similar pattern to green leaves in response to annual burning and mowing. To address these objectives, we examined stoichiometric quality of green and naturally senesced leaves from three dominant grasses in a semi-arid grassland in northern China that were exposed to different treatments of fire and mowing. Based on prior studies of plant and soil responses to annual burning and mowing, our hypotheses were that: (1) short-term (2-yr) annual burning would decrease C:N and C:P ratios in green leaves and affect N:P ratios; (2) mowing would increase C:N and C:P ratios in green leaves due to nutrient removal with mowing and consequently would have limited effects on green leaf N:P ratios; and (3) response patterns would be different between green leaves and senesced leaves with respect to all stoichiometric ratios.

2. Materials and methods

2.1. Study area

This study was conducted near the Inner Mongolia Grassland Ecosystem Research Station (IMGERS, 116°42′E, 43°38′N, 1250 m a.s.l), which is located in the middle reach of the Xilin River, northern China. Long-term (1970–2007) meteorological data indicated that the mean annual temperature in this area was 0.4 °C with mean monthly temperature ranging from −21.4 °C in January to 19.0 °C in July. Mean annual precipitation was 337 mm, with 51–89% occurring during the growing season (May–September). The sandy soil of this site is classified Haplic Calcisols according to the FAO (Food and Agricultural Organization of the United Nations) classification. Mean soil bulk density of the top 10 cm is 1.31 g cm^{-3} and pH is 7.5. The vegetation at the study area is dominated by *L. chinensis* (Trin.) Tzvel. (C3 perennial rhizome grass), *S. grandis* P. Smirn. (C3 perennial bunch grass), *C. squarrosa* (Trin.) Keng. (C4 perennial bunch grass), *Caragana microphylia* Lam. (shrub), and *Potentilla bifurca* L. (perennial forb).

2.2. Experimental design

The Grassland Fire Experiment (GFE) was established in 2005 with the general objectives to establish a grassland management regime that would maximize hay production. See the details of experimental design of GFE in Lü et al. (2011). The experiment is a randomized block (nine replicates) design. Plot sizes are 10 × 10 m. Plots were burned with a blast burner in early or late April each year before the start of the growing season since 2006, depending on snow melt. The fire removed almost all the aboveground plant material and soil surface litter. Except for the first year (2006), the fire intensity was not high because of relatively low aboveground biomass. Plots were mowed with a mower about 10 cm above the soil surface at the end of October each year. All the litter was removed to the edge of each plot. Only treatments of two burning frequencies (never burned and annual burning) and two mowing frequencies (never mowed and mowed once each year) in six blocks were used in this study. The six blocks were randomly selected from all the nine blocks.

2.3. Field sampling and chemical analysis

Representative green leaves of the three species, *L. chinensis*, *S. grandis*, *C. squarrosa*, were sampled in the plots on 20 August 2007, when the grassland reached its peak aboveground biomass production in this area (Cui et al., 2010). On average, these three species accounted 60–90% of the biomass and 50–80% of the coverage in each plot in the studied area. In each plot, we randomly selected and marked 20 individuals of each species. One green (fully expanded, usually the third or fourth one from the top of shoot) leaf was collected from each individual plant. The same number of senesced leaves for each marked species was collected on 25 October 2007, when the grasses were wholly senesced. We considered the leaves ready to abscise when they were completely dry and yellow without signs of deterioration (Wright and Westoby, 2003).

The leaves were transported to the laboratory, oven dried at 70 °C for 48 h, and then weighed. Leaves of each species per plot were combined and ground to pass through a 40-mesh sieve using a mechanical mill (Retsch MM 400, Retsch GmbH & Co KG, Haan, Germany). Total C content was determined using a H_2SO_4–$K_2Cr_2O_7$ oxidation method (Zhou et al., 2009). Subsamples were digested in H_2SO_4–H_2O_2 (Bennett et al., 2002). Total N contents were analyzed with an Alpkem autoanalyzer (Kjektec System 1026 Distilling Unit, Sweden). Total P of the digest was measured colorimetrically at 880 nm after reaction with molybdenum blue. All stoichiometric ratios (C:N, C:P, and N:P) are reported as mass ratios.

2.4. Data analysis

Nutrient resorption efficiency (RE) was determined for the three species using the following equation (Billings et al., 2003):

$$([\text{N or P}]g - [\text{N or P}]s)/[\text{N or P}]g$$

where [N or P]g represents nutrient concentrations in green leaves, and [N or P]s represents nutrient concentrations in senesced leaves. This method of calculating nutrient RE may underestimate actual resorption since leaf mass changes during senescence are not considered (Lü et al., 2010; van Heerwaarden et al., 2003). However, the main aim of this study is not to give an accurate value of RE but to evaluate the changes of nutrient RE in response to fire and mowing.

The Kolmogorov–Smirnov test was used to test for data normality. When necessary, data were natural log transformed to meet the assumption of normal distribution of data and homogeneity of variances. Four-way ANOVAs with block, species identity, fire, and mowing as the main factors were performed to examine main and interactive effects on foliar nutrient concentrations, stoichiometric ratios, and nutrient RE. All analyses were conducted with SPSS V13.0 (SPSS, Chicago, Illinois, USA).

3. Results

Except for the significant effects of block on N RE ($P < 0.05$, Table 1), the effect of block and the interactive effects of block and fire or mowing on all measured variables were not statistically significant ($P > 0.05$). In contrast, species identity showed significant ($P < 0.05$) or marginally significant ($0.05 < P < 0.1$) effects on all the variables (Table 1). There was no significant interaction between species identity and fire or mowing to affect stoichiometric ratios in both green and senesced leaves (Table 1).

Fire showed no effects on N and P concentrations and all stoichiometric ratios in green leaves (Fig. 1a,b; Table 1). Fire enhanced N concentrations ($P < 0.05$) but did not affect P concentrations in senesced leaves (Fig. 1c,d; Table 1). Fire decreased C:N by 16% (Fig. 2) and C:P by 13% (Fig. 2) in senesced leaves. Fire and mowing interacted to affect N RE ($P < 0.05$), in that fire decreased N RE in unmowed plots and tended to increased N RE in mowed plots (Fig. 3a, Table 1). Only the N RE of *L. chinensis* showed significant responses to fire, as indicated by a significant interaction between fire and species identity ($P < 0.01$, Fig. 3a). Across the three grass species, fire reduced P RE by 17% ($P < 0.05$; Fig. 3b).

Mowing showed no effects on nutrient concentrations and stoichiometric ratios in both green and senesced leaves (all $P > 0.05$, Table 1). There was no statistically significant effect of mowing on nutrient resorption ($P > 0.05$).

4. Discussion

Our results show that nutrient concentrations and stoichiometric ratios in both mature and senesced leave varied among three dominant grasses in this semi-arid grassland. In the short-term (2-yr), both annual burning and mowing had no statistically significant effects on stoichiometric ration in green leave of grasses. In contrast, annual burning resulted in lower C:N and C:P ratios in senesced leaves. Mowing did not affect stoichiometric ratios in senesced leaves. In terms of nutrient quality in green and senesced leaves, all three grasses showed similar responses to fire and mowing. Considering the variation of nutrient quality among species found in this study, the changes of community composition in responses to fire and mowing as reported by others (Collins et al., 1998) may have greatly implications for several nutrient-related ecosystem processes, such as herbivory and litter decomposition. Bao et al. (2000) reported that annual burning increased the dominance of *L. chinensis* while had negative effects on *S. grandis* in this grassland. Given the higher leaf nutrient quality of *L. chinensis* compared to that of *S. grandis* (Figs. 1 and 2), it is reasonable to expect that annual burning would accelerate nutrient cycling through its effect on community composition.

4.1. Responses of stoichiometric ratios in mature leaves to fire and mowing

Contrary to our first hypothesis, fire had no effects on stoichiometric ratios of green leaves in all the three grasses. In our previous studies, we found that annual burning did not significantly affect soil inorganic N availability in the growing seasons during the first three years (2006–2008) of treatments in this ecosystem (Cui et al., 2010; Zhou et al., 2009). The unchanged soil inorganic N availability in response to annual burning may account for the limited responses of green leaf N status and C:N ratio. Given that foliar N concentrations can greatly influence photosynthesis, results from this study imply that foliar nutrient changes following annual burning will not be a major factor for the potential changes of primary productivity in this semi-arid grassland. Previous studies suggested that frequent burning would promote a shortage of N in the grassland (Ojima et al., 1994). Results from our present work and previous ones indicate that short-term (2–3 yr) annual burning would not reduce N quality of the dominant species in this semi-arid grassland ecosystem.

There was no effects of annual burning on green leaf C:P ratios because fire did not influence foliar C or P concentration in any of the three grass species. Though we have previously observed that fire would enhance plant available P concentrations in soils of this ecosystem (Cui et al., 2010), results from the present work indicate that plant available P concentrations would not be a main factor accounting for the variation of mature leaf P concentrations and C:P ratios in dominant grasses. As suggested by van de Vijver et al. (1999), several factors, such as P uptake ability, canopy light penetration, and relocation of nutrients from roots to shoots, can all contribute to the variation of foliar C:P in response to prescribed burning. The result that no changes of mature leaf N:P in response to annual burning in this study is similar with results from grassland (Cui et al., 2010), mixed oak forest (Huang and Boerner, 2007), and alpine heathland (Britton et al., 2008), but is different from result from an annual grassland where fire decreased N:P ratio of annual

Table 1
Results (*P*-values) of four-way ANOVAs for foliar nutrient concentrations, stoichiometric ratios, nitrogen resorption efficiency (N RE) and phosphorus resorption efficiency (P RE) as dependent on blocks (B), species (S), fire (F), mowing (M), and their interactions. Ng, Pg = N and P in green leaves; Ns, Ps = N and P in senesced leaves; C:Ng, C:Pg, N:Pg = stoichiometric ratios in green leaves; C:Ns, C:Ps, N:Ps = stoichiometric ratios in senesced leaves ($n = 6$).

	Ng	Pg	C:Ng	C:Pg	N:Pg	Ns	Ps	C:Ns	C:Ps	N:Ps	NRE	PRE
B	0.862	0.650	0.983	0.905	0.954	0.821	0.594	0.521	0.206	0.402	0.031	0.117
S	0.087	0.053	0.076	0.048	0.098	0.031	0.022	0.013	0.005	0.063	0.002	0.011
F	0.075	0.853	0.106	0.882	0.134	0.043	0.124	0.024	0.045	0.471	0.017	0.021
M	0.220	0.312	0.326	0.246	0.707	0.285	0.548	0.179	0.589	0.703	0.183	0.072
F × M	0.973	0.344	0.920	0.205	0.248	0.515	0.880	0.277	0.672	0.679	0.018	0.063
B × F	0.921	0.647	0.955	0.668	0.529	0.550	0.675	0.359	0.275	0.612	0.15	0.106
B × M	0.907	0.845	0.947	0.687	0.899	0.711	0.402	0.397	0.141	0.431	0.014	0.059
B × M × F	0.952	0.442	0.966	0.438	0.491	0.934	0.548	0.680	0.184	0.485	0.028	0.181
S × F	0.289	0.750	0.256	0.713	0.604	0.931	0.243	0.283	0.157	0.262	0.008	0.081
S × M	0.934	0.409	0.960	0.362	0.365	0.974	0.680	0.928	0.204	0.396	0.175	0.116
S × M × F	0.798	0.352	0.811	0.325	0.279	0.603	0.587	0.663	0.211	0.595	0.104	0.032

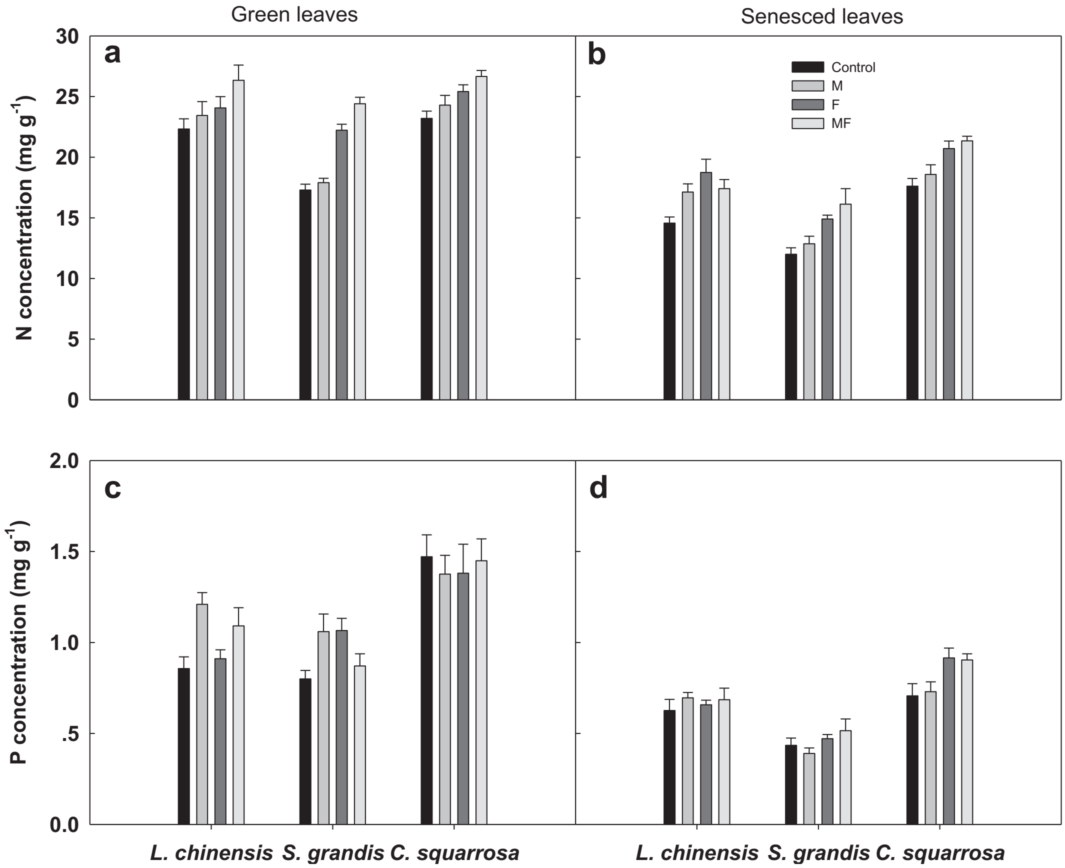

Fig. 1. Responses of nitrogen (a,b) and phosphorus contents (c,d) in green and senesced leaves in three dominant grass species to fire (F) and mowing (M). Error bars are SE ($n = 6$).

grasses (Henry et al., 2006). The inconsistent results among different studies may be attributed to fire type, time after fire, and species sensitivity to fire. Foliar N:P can be a useful indicator for nutrient limitation status of plant growth (Koerselman and Meuleman, 1996). In the control plots, N:P ratios of all the three species were >16 (Fig. 2c), indicating their growth were more P- than N-limited. Results from this study indicate that short-term annual burning would not alter the original status of nutrient limitation of dominant grasses in this semi-arid grassland. In all, our results suggest that short-term prescribed fire would not have negative effects on forage quality when it is used as a management strategy to constrain the establishment and expansion of woody vegetation.

Averaged across the three grasses, mowing and biomass removal did not significantly alter nutrient status and stoichiometric ratios in green leaves. It has been reported that shoot nutrient concentrations often increase in grasses following defoliation as a result of higher relative allocation of nutrient to shoots or increased plant nutrient uptake after defoliation (Green and Detling, 2000; Leriche et al., 2003). However, decreased soil nutrient availability in response to biomass removal following mowing is also common in grassland ecosystems (Turner et al., 1993). Consequently, we suspect that the unaltered nutrient status of mature leaves may be a balance between the positive effects of clipping and the negative effects of biomass removal. It is notable that results in this work are from a short-term experiment. In the long-term, the negative effects of biomass removal on plant tissue quality may be more important than the positive effects of defoliation. For example, in a long-term (13-yr) experiment in the tallgrass prairie, Kitchen et al. (2009) reported that mowing and biomass removal significantly reduced the N content in roots. Though frequent biomass removal with mowing would result in obvious nutrient loss, results from this study suggest that mowing and aboveground biomass removal would not alter forage quality of this semi-arid grassland in the short-term. In many grassland ecosystems, mowing is used to mimic grazing by large mammals. However, it is notable that the ecological effects of mowing may be different from those of grazing.

4.2. Responses of stoichiometric ratios in senesced leaves to fire and mowing

In consistent with our third hypothesis, results from this study showed that annual burning significantly reduced C:N ratios in senesced leaves whereas had no influence on these ratios in green leaves. The differential response patterns between green and senesced leaves in response to fire can be attributed to decreased N RE in response to fire. Higher N concentrations and lower C:N ratios in the litter would induce higher litter decomposition rates (Aerts and Chapin, 2000) and more rapid nutrient cycling (Liu et al., 2010). Thus, results from this study indicate a positive relationship between annual burning and leaf litter C:N ratios in this semi-arid grassland. In the long-term, however, this correlation may not exist because frequent burning leads to nitrogen loss through volatilization (Blair, 1997; Ojima et al., 1994).

We found that annual burning resulted in lower C:P ratios in senesced leaves but had no effect on green leaf C:P ratios. This is likely due to the lower P RE in response to annual burning. These changes in P-related parameters may be a result of the alteration of soil P in response to fire. Compared with N, the losses of P through volatilization or leaching are much smaller in response to fire. Fire

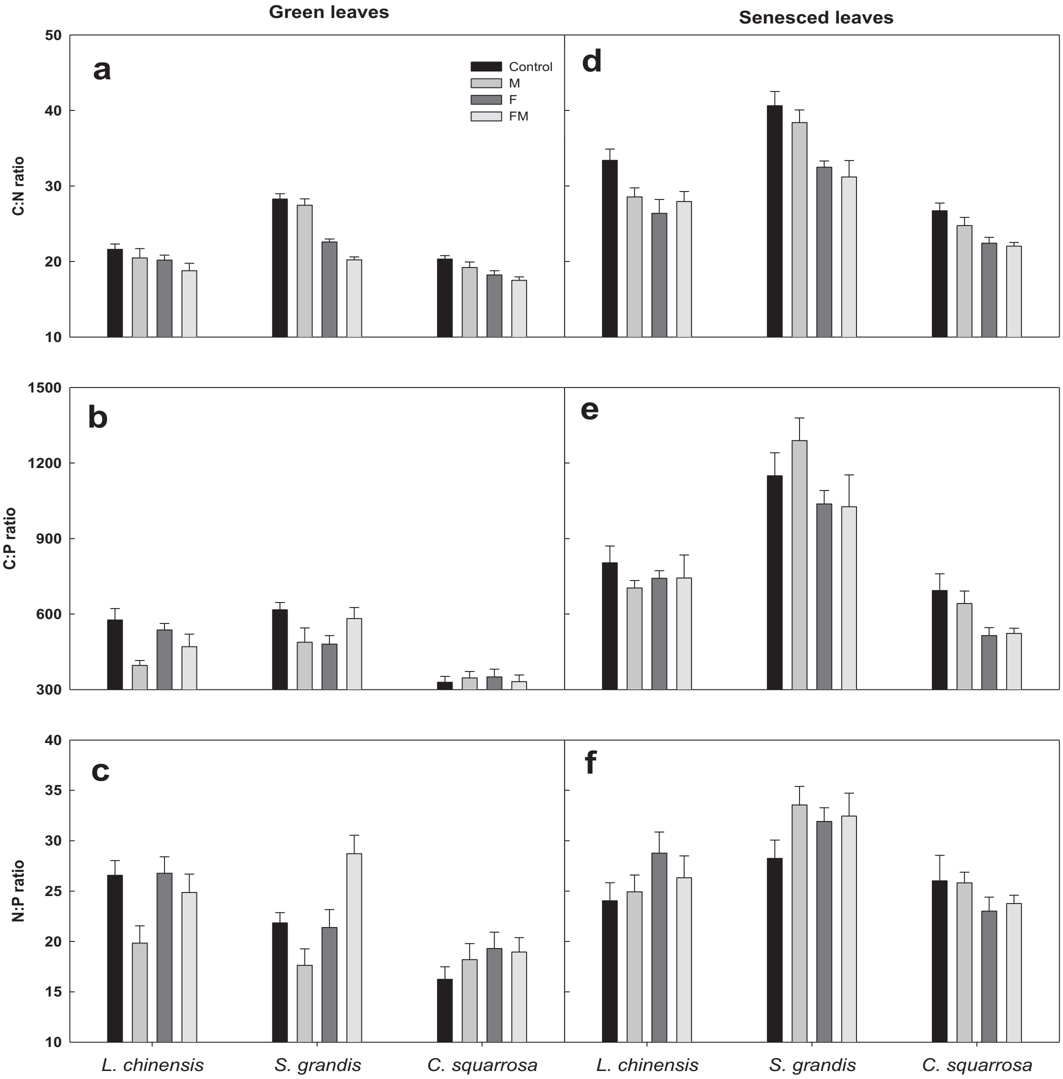

Fig. 2. Responses of stoichiometric ratios of green (a,b,c) and senesced leaves (d,e,f) in three dominant grass species to fire (F) and mowing (M). Error bars are SE ($n = 6$).

may enhance plant available P in the soil (Ojima et al., 1994; Rau et al., 2007), which is also the case in this ecosystem (Cui et al., 2010). Increased soil P availability would lead to lower P RE. It has been found that nutrient resorption efficiency of dominant grasses would be much lower in environments with high nutrient availability in this semi-arid grassland (Lü and Han, 2010). Results from this study indicate that nutrient resorption may play an important role in determining the differential response patterns between green and senesced leaves to annual burning. Because the quality of senesced leaves, rather than that of green leaves is more directly related to litter decomposition, we suggest that senesced leaves should be given more attention in future studies.

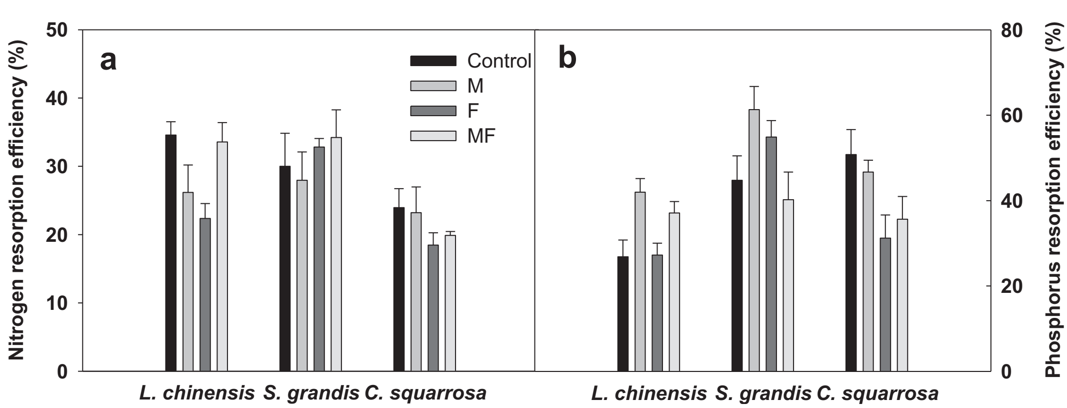

Fig. 3. Effects of fire (F) and mowing (M) on nitrogen (a) and phosphorus (b) resorption efficiency of three dominant grass species in a semi-arid grassland in northern China. Error bars are SE ($n = 6$).

Given that mowing showed no effects on leaf litter quality and that biomass removal did reduce the quantity of litter, frequent mowing and biomass removal would lead to a negative effect on nutrient retention in this grassland. Furthermore, mowing had no effects on nutrient resorption efficiency of the three grass species, indicating that the short-term effects of mowing on plant nutrient conservation strategies would be limited. From a nutritional perspective, short-term frequent mowing would be an appropriate management strategy for maintaining the condition of grassland without resorting to the use of stock in this semi-arid area. The limited effects of mowing on plant nutrition status and nutrient resorption parameters may be resulted from the mowing season. In this study, the grassland was mown at the end of each growing season to mimic the hay harvesting by the local people. It is well known that nutrient concentrations in senesced plants are much lower than nutrients in mature plants with green tissues (Aerts and Chapin, 2000). Consequently, mowing and biomass removal at the end of growing season would lead to less nutrient loss than that at the middle of growing season. Considering the role mowing played in maintaining community composition and its potential effects on nutrient loss, our results indicate that mowing and biomass removal at the end of growing season would be a better grassland management strategy in this semi-arid grassland.

5. Conclusions

This study demonstrated that short-term annual burning and mowing treatments have no effects on the quality of green and senesced leaves whereas annual burning enhanced nutrient quality of senesced leaves. Importantly, the stoichiometric responses of green and senesced leaves greatly differed due to changes in nutrient resorption. Results from this study may help illustrate some of the mechanisms by which these ecosystem management strategies will affect plant-mediated ecosystem processes, both above- and below-ground.

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