

Responses of nutrient concentrations and stoichiometry of senesced leaves in dominant plants to nitrogen addition and prescribed burning in a temperate steppe



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ABSTRACT

The quality of senesced leaves is a strong driver for litter decomposition and nutrient cycling in terrestrial ecosystems. The effects of global change factors and ecosystem management strategies on nutrients and stoichiometry of mature leaves have been well established. In contrast, we still know little about their effects on the quality of senesced leaves, which would be different from that of mature leaves due to the occurrence of nutrient resorption during leaf senescence. We examined the effects of nitrogen (N) addition ($5.25 \text{ g N m}^{-2} \text{ yr}^{-1}$), prescribed fire (with four frequencies, including no burning and burning every 1, 2, 4 years), and their interactions on N and phosphorus (P) concentrations and N:P ratios in senesced leaves of five dominant species in a temperate steppe of northern China. Nutrient concentrations and N:P ratios of senesced leaves varied substantially among the five species. Nitrogen addition increased N concentrations and N:P ratios but had no significant effect on P concentrations. Fire significantly increased N and P concentrations and N:P ratios in senesced leaves across all species. The effects of fire depended on its frequency. There was no interaction between N addition and fire in affecting nutrient concentrations and stoichiometry of senesced leaves. Our results suggested that N addition and fire can potentially alter litter quality by changing senesced leaves nutrient status and stoichiometric ratios, with an indirect effect on litter decomposition and ecosystem nutrient cycling in the grassland ecosystems.

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1. Introduction

Leaf senescence occurs with cellular disassembly and materials mobilization (Thomas and Stoddart, 1980; Aerts, 1996). Nutrient resorption is an important nutrient conservation mechanism through which plants would be less dependent on environmental nutrient availability (Aerts and Chapin, 2000; Lü et al., 2011; Jiang et al., 2012; Li et al., 2013). More than half of the nutrients in leaves can be resorbed during senescence (Vergutz et al., 2012). Nutrients remaining in senesced leaves, which are a fraction of nutrients that have not resorbed during leaf senescence, are important determinants for litter quality (Yuan and Chen, 2009). The quality of senesced leaves, together with soil properties and climate factors have been proposed as strong drivers for litter decomposition (Semmartin et al., 2004; Parton et al., 2007). Furthermore, nutrients in the senesced leaves can also affect soil nutrient availability

and carbon sequestration, with significant feedbacks on climate (Cornelissen et al., 2007; Dijkstra et al., 2012). Both natural and anthropogenic disturbances could influence plant nutrient status (van Heerwaarden et al., 2003; Lü and Han, 2010). Compared to what we know about the mature leaves, however, our knowledge about the responses of nutrients in senesced leaves to environmental changes is limited.

Currently, anthropogenic N inputs are 30–50% greater than that from natural sources (Galloway et al., 2008), as a consequence of globally increasing atmospheric N deposition (Galloway et al., 2004). Given the widespread N-limitation for primary production in most terrestrial ecosystems (Elser et al., 2007; LeBauer and Treseder, 2008), increased N availability may enhance primary production and ecosystem carbon (C) storage. The effects of increasing N availability on ecosystem functioning would be largely dependent on its effect on nutrient economy and stoichiometry of plants (Sardans and Penuelas, 2012). Furthermore, stoichiometric ratios of plant tissues exert strong controls on nutrient use efficiency (Vitousek, 1982), plant growth rate (Niklas et al., 2005), herbivory (Hall et al., 2007), litter decomposition (Güsewell and Gessner,

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2009; Song et al., 2011). The effects of N addition on plant stoichiometry are well established in diverse ecosystems (Henry et al., 2006; Esmeijer-Liu et al., 2009; Song et al., 2011; Han et al., 2013). It is notable that most of those studies emphasized the mature leaves and that the responses of senesced leaves to N enrichment (as well as other global change factors) may be different from that of mature leaves. For example, N addition had no effect on N:P ratios in green leaves but significantly increased N:P in senesced leaves of dominant plants in a temperate steppe (Lü et al., 2012). Elevated CO₂ significantly increased C:N ratios in green leaves but had no impacts on leaf litter stoichiometry of *Larrea tridentata* and *Lycium pallidum* in an intact Mojave desert ecosystem (Billings et al., 2003). Given the potential divergent responses of stoichiometry in mature and senesced leaves to the same environmental factors, more empirical evidence is needed for the effects of N enrichment on stoichiometry of senesced leaves.

Nitrogen and P co-limitation of primary production is widespread in most of the terrestrial ecosystems (Vitousek et al., 2010; Harpole et al., 2011). It should be emphasized that, however, the response of P to elevated N inputs is much complex and less well understood (Lü et al., 2013). A combination of substrate composition and age, climate and vegetation controls the local availability of P (Schimel, 2004). Elevated N availability would increase P demand or limitation (Menge and Field, 2007). Perring et al. (2008) reported that enhanced plant growth following N enrichment would lead to increased P conservation. However, it has been found that elevated N deposition could stimulate the activity of soil phosphatase in an annual grassland (Menge and Field, 2007), and this process may increase soil P availability. For example, Lü et al. (2013) observed that plant available P and N concentrations in soil increased with increasing rates of N addition. The responses of P-related chemistry of plants to N inputs varied in different studies, both positive (Menge and Field, 2007) and neutral responses (Novotny et al., 2007) have been reported.

The effects of N addition on ecosystem characteristics and processes may be affected by natural and anthropogenic disturbances, such as fire (Britton et al., 2008). Fire can alter plant nutrient chemistry through its effects on soil physical and chemical characteristics (Certini, 2005; Henry et al., 2006). Long-term repeated burning would volatilize N from vegetation and litter and thus reduce soil N availability (Turner et al., 2007). On the other hand, fire can alter light availability (Knapp and Seastedt, 1986), soil water availability (Cui et al., 2010), soil pH (Certini, 2005), and soil temperature (Raison et al., 1986), with consequences on soil nutrient turnover. A single burning can enhance N and P concentrations in aboveground tissues of plants (Bennett et al., 2003). However, sustained and frequent fires could reduce N concentration and consequently lead to an increase of C:N ratio in vegetative tissues (Ojima et al., 1994; Kitchen et al., 2009). The major reason for the varied effects of fire on plant chemistry could reflect differences in fire frequency among different studies. It has been reported that soil N pools and inorganic N availability were higher at sites with lower fire frequency (Wan et al., 2001; Cech et al., 2008). Decreased leaf litter N content has been reported as well following repeated burning in a forest ecosystem (Williams et al., 2012). Beside its main effects, fire may interact with N deposition or addition to affect plant chemistry (Britton et al., 2008). However, the interactive effects of fire and N deposition on nutrient concentrations and stoichiometry of senesced leaves remain largely unknown.

In order to more clearly identify the interactive effects of fire and N deposition on the stoichiometry and nutrient concentrations in senesced leaves, we conducted a factorial experiment of N addition and fire frequency in a temperate steppe in northern China. Specifically, we identified the effects of N addition and prescribed burning on N and P concentrations and N:P ratios in senesced leaves of

dominant species. We hypothesized that: (1) N addition would increase N concentration, decrease P concentration, and thus enhance N:P ratio in senesced leaves; (2) the effects of fire on nutrient status of senesced leaves would vary among different fire frequencies; and (3) N addition and fire would not interact to affect N and P concentrations and stoichiometry in senesced leaves as we have observed that fire and N addition did not interact to affect nutrient concentrations and stoichiometry in mature leaves of dominant species in this ecosystem (Cui et al., 2010).

2. Materials and methods

2.1. Study site description

This study was carried out in a temperate steppe in northern China, near the Inner Mongolia Grassland Ecosystem Research Station (IMGERS, 43°38' N, 116°42' E, 1250 m a.s.l.). Long-term (1970–2007) mean annual precipitation is 337 mm, 80% of which occurs from May to September. The growing season lasts about 150 days. The mean annual temperature is 0.4 °C, with mean monthly temperature ranging from –21.4 °C in January to 19 °C in July. The sandy soil in this area is classified Haplic Calcisols (Food and Agricultural Organization of the United Nations) classification. Mean bulk density of soil is 1.3 g cm⁻³ and pH is 7.5 for the top 10 cm. The dominated plants of this ecosystem are C3 perennial rhizomatous grass *Leymus chinensis* (Trin.) Tzvel., C3 perennial bunch grass *Stipa grandis* P. Smirn., C4 perennial bunch grass *Cleistogenes squarrosa* (Trin.) Keng., shrub *Caragana microphylla* Lam., and perennial forb *Potentilla bifurca* L. Together, they accounted for more than 85% of the total aboveground biomass.

2.2. Experimental design

This study was conducted as part of the Grassland Fire Experiment (GFE), which was established in 2005. The experiment applied prescribed fire at five frequencies that are no burning, burning every 1, 2, 4, 6 years, and N addition at four levels which are 0, 5.25, 17.5, 28 g N m⁻² yr⁻¹, and mowing at four frequencies (no mowing, mowing every year, mowing every other year, and mowing every year for 3 years followed by 1 year of no mowing). All the possible treatment combinations were conducted since 2006. In total, there are 80 treatment combinations, replicated 9 times (9 blocks). Each block was divided into 80 10 m × 10 m plots with 1 m buffers. All burnings were conducted in either April or May with a blast burner, depending on snow melt. The fire intensity was higher in the first year (2006) due to long-term (>20 year) accumulation of plant litter. The fire burned off almost all the senesced standing plant materials and the soil surface litter. The fire intensity was relatively lower in the following years due to lower plant litter accumulation.

Nitrogen was supplied as NH₄NO₃ in dry form in early July each year. Only the treatments of four burning frequencies and two N addition levels, ambient N (N0) and 5.25 g N m⁻² yr⁻¹ (+N), without mowing in 6 blocks (the 6 blocks were randomly selected among the 9 blocks) were used in this study. Our study was conducted in 2008, 3 years after the experiment began. The fire frequencies we used were no burning occurred in the three years (Burning 0/3 years), one burning within three years for the plots of burning every 4 years (Burning 1/3 years), two times of burning within three years for the plots of burning every 2 years (Burning 2/3 years) and 3 times of burning within three years for the plots of annually burned (Burning 3/3 years). We collected the plant samples in October 2008. For the treatment 'Burning 1/3 years', it had been 29 months since the last fire (May 2006). For the treatments 'Burning

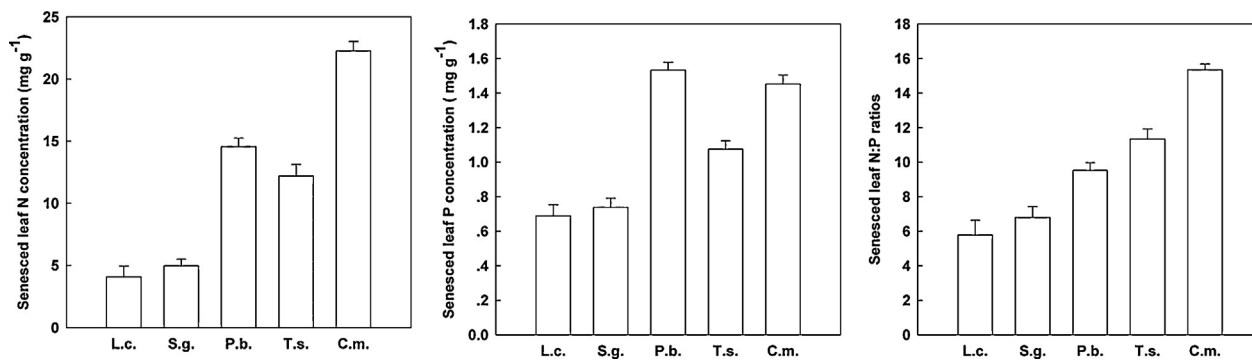


Fig. 1. The variation of foliar N and P concentrations and N:P ratios of senesced leaves among five dominant plant species in the control plots. Values are means and 1 SE. L.c., *Leymus chinensis*; S.g., *Stipa grandis*; P.b., *Potentilla bifurca*; T.s., *Thalictrum squarrosom*; C.m., *Caragana microphylla*.

2/3 years' and 'Burning 3/3 years', it has been five months since the last fire (May 2008).

2.3. Sample collection and chemical analysis

Representative senesced leaves of the five dominant plant species, including two perennial grasses (*L. chinensis* and *S. grandis*), two non-legume forbs (*P. bifurca* and *T. squarrosom*) and one legume shrub (*C. microphylla*), were sampled from the plots on 25 October 2008, when the leaves of all plants were totally senesced. We considered that the senesced leaves were ready to be abscised when they were wholly dry and yellow without signs of deterioration (Wright and Westoby, 2003). Together, the five species contributed >70% of the aboveground biomass in this ecosystem. Individually, *L. chinensis* accounted for 20%–30%, *S. grandis* accounted for 15%–25%, *P. bifurca* accounted for 10%–15%, *T. squarrosom* accounted for 5%–10%, and *C. microphylla* accounted for 15%–20% of the total aboveground biomass in this community.

The collected leaves were transported to the laboratory, oven dried for 48 h at 70 °C. Leaves of each species from each plot were combined and ground with a ball mill (Retsch MM 400, Retsch GmbH & Co KG, Haan, Germany). Plant materials were digested in H₂SO₄–H₂O₂ (Bennett et al., 2003). Total N concentrations were analyzed by an Alpkem autoanalyzer (Kjektec System 1026 Distilling Unit, Sweden). Total P concentrations of the digest were measured colorimetrically at 880 nm after reaction with molybdenum blue. The stoichiometric N:P ratios were reported as mass ratios.

2.4. Statistical analysis

Data were tested using Levene's test for normality. The main and interactive effects of species identity, fire and N fertilization on plant senesced leaves N and P concentrations and stoichiometric N:P ratios were determined by three-way analysis of variances (ANOVAs). Post hoc Tukey's multiple comparison test was used to analyze the significant differences among treatment means. We further analyzed the effects of fire and N addition on each species individually because there were significant interactions between species identity and fire or N addition for multiple variables. Statistical significance was determined at $p=0.05$. All analyses were conducted with SPSS V13.0 (SPSS, Chicago, IL, USA).

3. Results

3.1. Interspecific differences of five species

In the control plots, the five species varied greatly in N and P concentrations and N:P ratios in senesced leaves (Table 1; Fig. 1).

Nutrient concentrations and N:P ratios of the senesced leaves were lowest in *L. chinensis*, and highest in *C. microphylla* (Fig. 1). Nutrient concentrations of grasses were lower than that of forbs and the legume shrub. The N:P ratios for all the species were less than 14 in the control plots, except for *C. microphylla*.

3.2. Responses of N and P chemistry in senesced leaves to N addition and fire

Across all the species, N addition significantly enhanced N concentration by 17.6% (Fig. 2) and N:P ratio by 21.8% (Fig. 3), but had no effect on the P concentration in senesced leaves (Table 1, Fig. 4). When the five species were analyzed individually, N addition significantly increased N concentrations and N:P ratios of four non-legume species (*L. chinensis*, *S. grandis*, *P. bifurca* and *T. squarrosom*), but had no effect on N:P ratio of the legume *C. microphylla* (Figs. 2 and 3; Table 2).

The five species responded differently to the fire treatments. When the species were analyzed individually, fire only significantly increased N concentration of *S. grandis*, P concentration of *T. squarrosom*, and N:P ratios of both species (Table 2). The effects of fire varied among different frequencies. For example, N concentrations of *S. grandis* were higher in plots with higher fire frequencies (Fig. 2). P concentrations of *T. squarrosom* were significantly influenced by fire frequencies under N addition conditions (Fig. 4). P concentrations of *C. microphylla* were gradually increased with increasing of fire frequency under ambient N conditions (Fig. 4). Under ambient N conditions, N:P ratios of *S. grandis* were higher in plots with higher fire frequencies (Fig. 3). N:P ratios of *T. squarrosom* were significantly differed among the four fire frequencies under N addition conditions (Fig. 3).

Table 1

Results (F -values) of three-way ANOVAs on the effects of species identity (S), N addition (N), fire (F) and their interactions on N and P concentrations and N:P ratios in senesced leaves.

	d.f.	N	P	N:P
S	4	338.8***	440.1***	53.8***
N	1	45.5***	0.7	72.9***
F	3	7.8***	5.2**	9.9***
S × N	4	1.6	0.4	7.1***
S × F	12	0.9	1.0	1.8
N × F	3	1.5	2.1	0.5
S × N × F	12	0.6	1.4	1.2

The F -values are presented, together with their level of significance. For all variables error d.f. = 227.

* 0.05 < p < 0.1.

** p < 0.01.

*** p < 0.001.

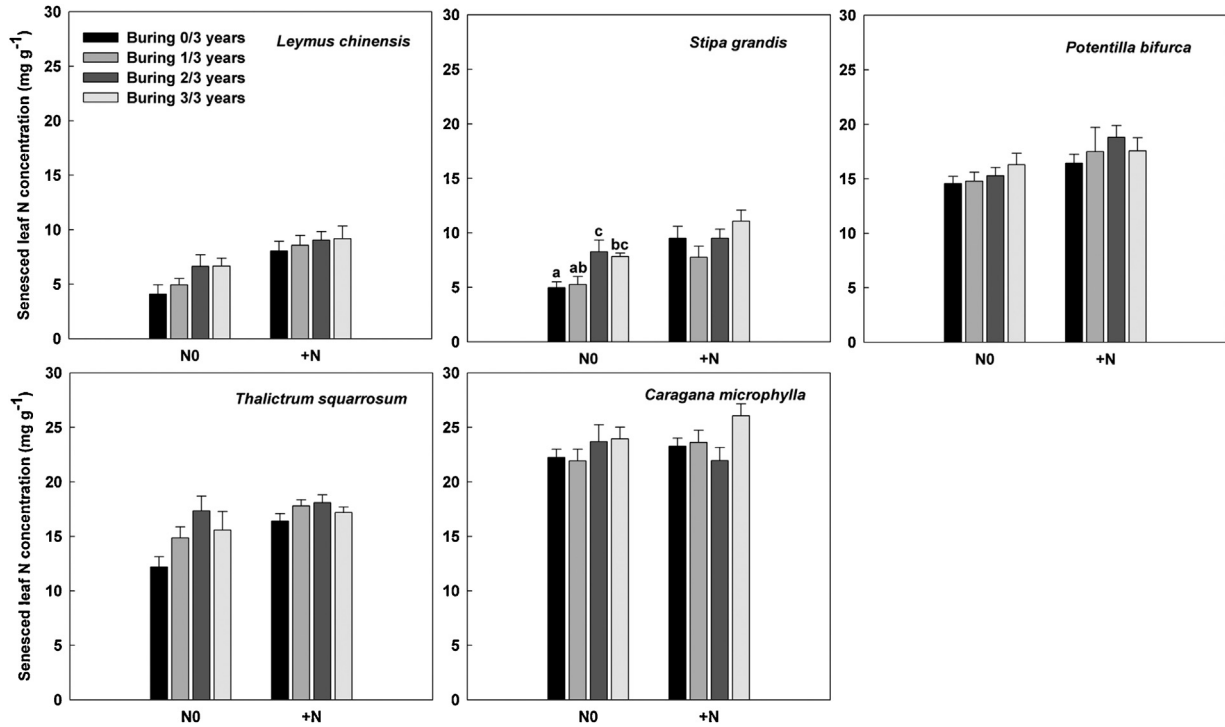


Fig. 2. Senesced leaf N concentrations of five dominant plants in response to N addition and fire. Values are means and 1 SE.

When the five species were analyzed individually, none of the variables were impacted by the interactions between N addition and fire for *L. chinensis*, *S. grandis*, *P. bifurca* and *T. squarrosum* (Table 2). However, P concentration and N:P ratio of *C. microphylla* were significantly affected by the interaction between fire and N

addition (Table 2). In no burning plots, N addition increased P concentration and declined N:P ratio of *C. microphylla* by 16.3% and 10.0%, respectively. In the burning plots, P concentration of *C. microphylla* was reduced by 2.6% and N:P ratio was enhanced by 6.2% after N addition.

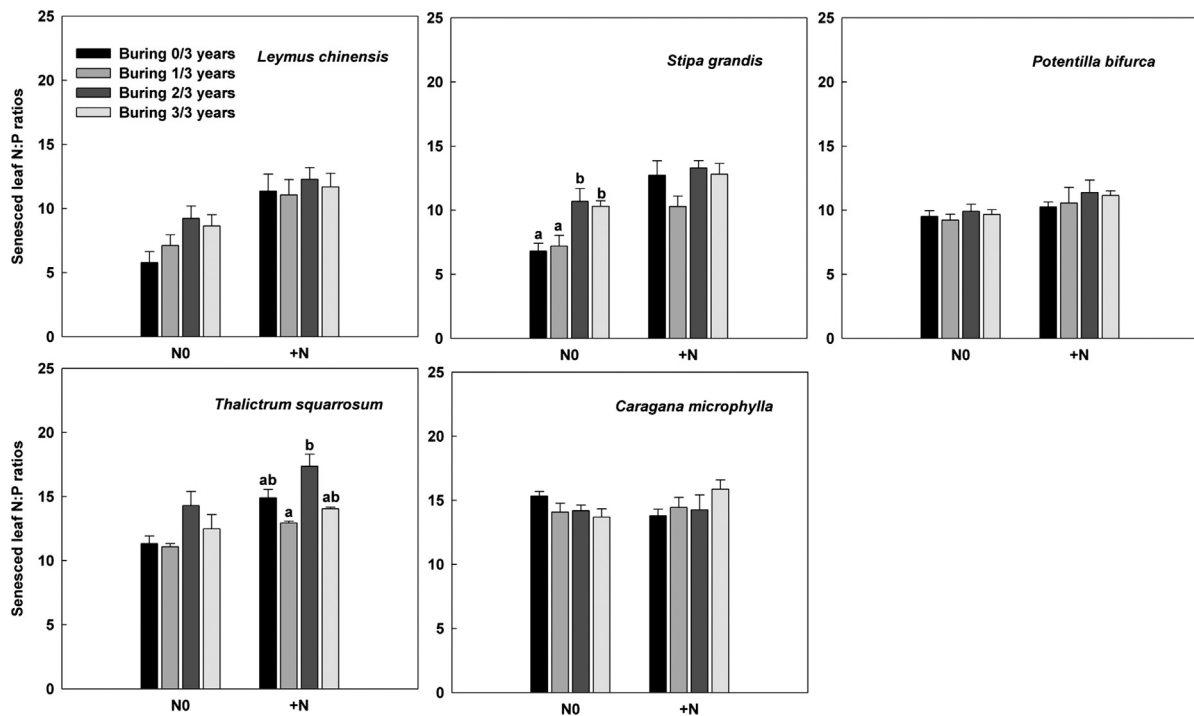


Fig. 3. Senesced leaf N:P ratios of five dominant plants in response to N addition and fire. Values are means and 1 SE.

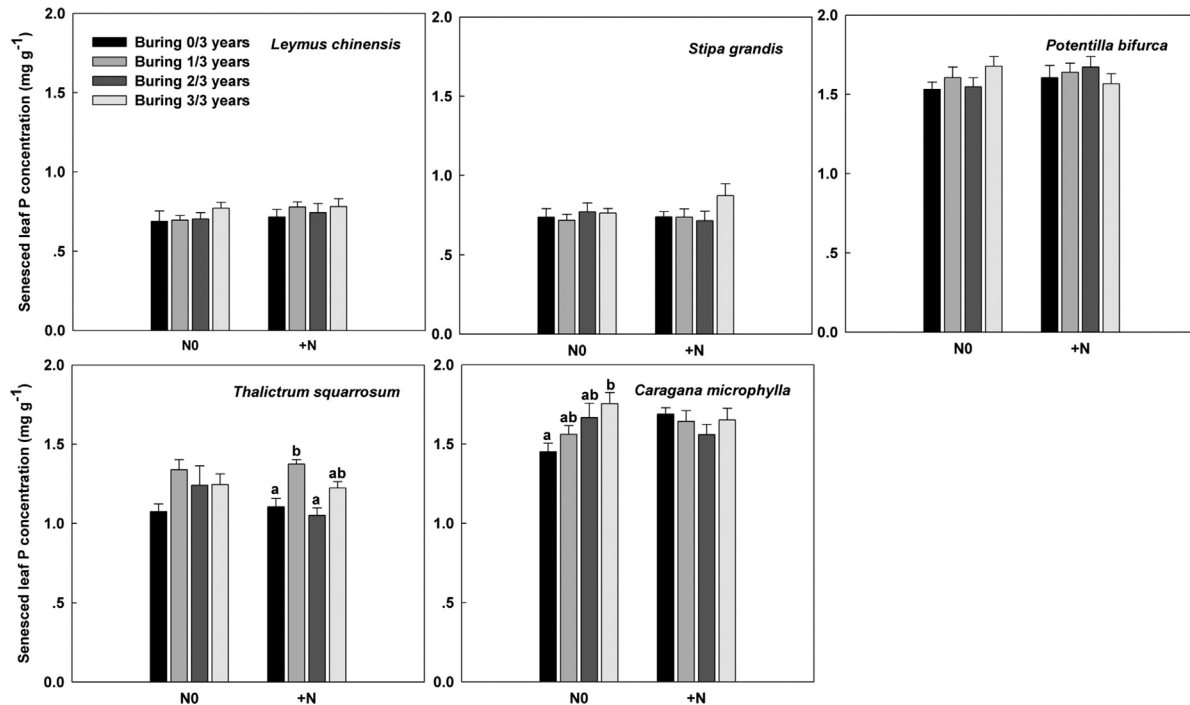


Fig. 4. Senesced leaf P concentrations of five dominant plants in response to N addition and fire. Values are means and 1 SE.

4. Discussion

Our findings suggested that N addition significantly increased N concentration and N:P ratios but had no effects on P concentration of senescent leaves. We found that nutrient concentrations and N:P stoichiometric ratios of plant litter were significantly influenced by prescribed burning. In accordance with our hypothesis, the effects of fire were dependent on its frequency. Generally, N and P concentrations and N:P ratios following low fire frequencies were relatively lower than that following high fire frequencies. Consistent with our expectation, across all the five species (when the five species were considered as a whole), there was no interaction

between fire and N fertilization to affect nutrient concentrations and stoichiometry of senesced leaves in this study (Table 1).

Our results showed that nutrient concentrations and N:P ratios in senesced leaves varied significantly among five dominant species in the temperate steppe. Interspecific variation of nutrient concentrations has previously been observed in the mature leaves of dominant plants in this area (Cui et al., 2010). Although nutrient resorption efficiency varied greatly among different species (Lü et al., 2011), results from this study and those from Cui et al. (2010) indicate that the interspecific variation of nutrient concentrations and stoichiometry would be consistent in mature and senesced leaves. Generally, grasses had lower foliar N and P concentrations in senesced leaves than other plant functional groups. According to a study based on analysis of mature leaf samples from 213 species in Chinese grasslands, grasses had lower leaf N and P than herbs while legumes had higher N and N:P ratios than non-legumes (He et al., 2006, 2008). In this study, the legume shrub, *C. microphylla* showed the highest N and P concentrations in senesced leaves. We suspect that the specific variation of root phosphomonoesterase activity would account for the specific differences of foliar P concentrations. Recently, Venterink (2011) reported that leguminous species generally had higher root phosphomonoesterase activity than non-legume species. The legume *C. microphylla* and the forb *T. squarrosus* showed higher N:P ratios in senesced leaves than those of other species, indicating that the litter decomposition of these two species would be vulnerable to P-limitation (Güsewell and Freeman, 2005). Given the fact that global change factors exert strong control on community composition (Kardol et al., 2010), the interspecific variation of litter quality as observed in this study has great implications for ecosystem nutrient cycling under global change scenarios.

For all the non-legume species, senesced leaf N concentration and N:P ratios showed positive responses to N addition, which is consistent with the response of mature leaves (Cui et al., 2010). Similarly, Huang et al. (2008) also found that N concentration in senescent and mature leaves of five species increased with increasing N availability in the grassland ecosystem. With increasing

Table 2

Results (*F*-values) of two-way ANOVAs on the effects of fire (F), N addition (N) and their interaction on N and P concentrations and N:P ratios in senesced leaves.

		[N]	[P]	N:P
<i>L. chinensis</i>	N	25.1***	1.5	29.6***
	F	2.1	0.9	1.9
	N × F	0.4	0.2	0.7
<i>S. grandis</i>	N	21.9***	0.3	38.6***
	F	5.1*	1.3	7.2***
	N × F	1.3	0.9	2.0
<i>P. bifurca</i>	N	7.4**	0.5	6.7**
	F	0.7	0.3	0.6
	N × F	0.3	1.4	0.1
<i>T. squarrosus</i>	N	6.8**	0.4	13.2***
	F	3.3	3.4*	6.1**
	N × F	0.9	1.1	0.5
<i>C. microphylla</i>	N	1.3	0.5	0.4
	F	2.5	2.1	0.4
	N × F	1.4	5.3**	3.8*

The *F*-values are presented, together with their level of significance. For all variables error d.f. = 227.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

soil N availability, plants may become relatively more dependent on soil N resources rather than resorbing N from senescing tissues (Aerts and Chapin, 2000). Thus, more N would be expected to remain in senesced leaves after N addition. For example, Lü et al. (2011) reported that N addition reduced foliar N resorption, resulting in a higher N concentration in senesced leaves. Although we found a positive response of P in mature leaves to N addition in a previous study (Cui et al., 2010), there was no effect of N addition on P concentrations in senesced leaves as observed in this study. It is well documented that more P is resorbed during leaf senescing after N addition (Lü and Han, 2010). The unchanged P concentrations in senesced leaves in response to N addition would be a balance between enhanced P concentrations in mature leaves and higher P resorption during senescence. Menge and Field (2007) reported that N deposition decreased P concentration in senescent leaves of the dominant grass by 44% in an annual grassland. They considered that the reduction of P concentration indicated P stress to plants under elevated N deposition. Considering the inconsistencies between results from this study and those from Menge and Field (2007), more empirical evidence is needed to clarify the divergent effects of N addition on P concentrations in senesced leaves. Irrespective of the divergent responses of senesced leaf P to N addition, related studies generally found positive responses of N:P stoichiometry to N addition (Lü and Han, 2010). N:P ratios of plant litter are important for litter decomposition as they exert strong control on microbial composition and activity (Güsewell and Gessner, 2009). Given the globally increasing reactive N availability in terrestrial ecosystems, our results has great implications for understanding litter decomposition and ecosystem nutrient cycling under the global change scenarios.

Together with our results from a previous study (Cui et al., 2010), we found both convergence and divergence in the responses of nutrient concentrations and stoichiometry in mature and senesced leaves to prescribed burning. Fire significantly enhanced N and P concentrations in mature leaves (Cui et al., 2010). It is notable, however, that when the five species were analyzed individually, the effects of fire were only significant on N concentration in *S. grandis* and P concentration in *T. squarrosus*. The mineralization of N and P from plant residues, such as senesced leaves, is a major input of inorganic nutrients to the soil, which can be directly taken up by plants (Manzoni et al., 2010). Higher nutrient concentrations in litter generally lead to a higher decomposition rate (Cornelissen et al., 2007; Güsewell and Gessner, 2009). Consequently, our results suggest that fire would accelerate litter decomposition rate and stimulate nutrient cycling through its effects on the quality of plant litters of some species in this temperate steppe. The responses of N:P ratios in mature and senesced leaves to fire were different. While we found that fire significantly enhanced N:P ratios in senesced leaves in this study, Cui et al. (2010) reported no effects on N:P ratios in mature leaves for the same five plant species. While the relative enhancement of N and P in mature leaves by fire was similar following prescribed burning (Cui et al., 2010), the enhancement of N in senesced leaves (10.40%) was much higher than that of P (5.99%). The resorption processes during leaf senescence would be the major reason accounting for the divergent responses of N:P ratios in mature and senesced leaves to fire. It has been found that fire had no effect on N resorption but increased P resorption in the same ecosystem (Lü et al., 2011). Together, our results gave strong evidence for the important role of nutrient resorption in structuring the stoichiometric responses of mature and senesced leaves to fire disturbance. Furthermore, our results showed that stoichiometric responses of senesced leaves (at least to fire) would not mirror those of mature leaves.

The effects of fire on ecosystem functioning and community composition are dependent on its frequency (Tester, 1996; Peterson and Reich, 2001). In the short-term, fire may enhance microbial activity (Ojima et al., 1994), stimulate net photosynthesis (Reich et al., 1990), and promote N availability (Wan et al., 2001). Long-term repeated burning would result in greater inputs of plant residues with lower quality, which caused a significant reduction in soil microbial biomass and N availability (Ojima et al., 1994). In the present study, high fire frequencies generally resulted in higher N and P concentrations and N:P ratios of senesced leaves. It has been reported that the frequency of past fires had no effect on C and N contents of mature leaves in an Australian eucalypt forest (Christie and York, 2009) and increases in fire frequency would decrease the amount of nutrients in aboveground biomass in a savanna ecosystem (Oliveras et al., 2013). Given the divergent effects of different fire frequencies on plant nutrient status as observed in this study and others, more attention should be paid on when comparing the results about fire from different studies. As the prescribed burning only lasted for three years in this study, it remains unclear whether the results we observed would exist under longer term burning. It should be noted that the effects of fire on plant chemistry would be dependent not only on fire frequency, but also on the time since fire. We cannot separate such effects on the present study. The relative effects of both fire frequency and the time since fire deserve more attention in the further studies.

For four out of the five species, we observed no interaction between N addition and fire to affect nutrient chemistry of senesced leaves, which is consistent with the results from green leaves in this ecosystem (Cui et al., 2010). These results indicate that N addition and fire independently affected plant N:P stoichiometry in both mature and senesced tissues in the temperate steppe. Consistently, plant N:P ratios were not affected by interaction between fire and N deposition in a California annual grassland (Henry et al., 2006) and in an alpine heathland (Britton et al., 2008). However, we found that fire and N addition did interact to affect senesced leaves P concentration and N:P ratio of the legume shrub *C. microphylla*. Given the changes of community composition after N addition and fire observed in other grasslands (Tester, 1996; Boyer and Zedler, 1999; Peterson and Reich, 2001; Clark et al., 2007), the interspecific responses of plant tissue chemistry to N addition and fire deserve further attention.

5. Conclusions

This study demonstrates that both of N addition and prescribed burning directly affect nutrient concentrations and stoichiometry of senesced leaves of the five dominant species, which accounted for more than 70% of the total aboveground biomass in this ecosystem. Consequently, the stoichiometric influence of N addition and burning of senesced leaves can have a direct affect on litter decomposition. There were both convergence and divergence in the responses of nutrient concentrations and stoichiometry of mature and senesced leaves to N addition and fire. It would be inappropriate to assess the effects of natural and anthropogenic disturbances on the quality of plant litter based on our current knowledge from mature leaves. Considering the facts that we still know less about the senesced leaves than mature ones and that senesced leaves play an important role in several key ecological processes, more attention should be paid to the responses of senesced leaves to both global change factors and ecosystem management strategies in future studies. Findings from this study will improve our understanding of senesced leaves characteristics under the effects of fire and N addition and thereby contribute to grassland management.

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