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Increased precipitation modulates the influence of nitrogen and litter inputs on the nutrient resorption proficiency rather than efficiency of *Leymus chinensis*

Yue Shen · Xin Yang · Xiao Sun · Wenqing Chen · Gaowen Yang · Nan Liu · Jishan Chen · Yingjun Zhang

Abstract Resorption of nutrients from senescing organs is an important conservation mechanism that is usually influenced by the supply of soil nutrients and plant growth requirements. Therefore, it is likely that increases in nitrogen (N), precipitation, and litter could lead to changes in nutrient resorption because of changes in nutrients in the soil and accelerated plant growth in response to the alleviation of water limitations in arid and semiarid environments. In the current study, we investigated the effects of water, N, and litter addition on the nutrient resorption efficiency and proficiency of N and phosphorus (P) in leaves and stems of *Leymus chinensis* in Inner Mongolia, China. Our results showed that N addition significantly decreased the N resorption efficiency in leaves under water addition, and increased P resorption efficiency under ambient precipitation conditions. There was no apparent influence of either litter or water addition on N and P resorption efficiencies. However, N and litter addition significantly altered N and P resorption proficiencies, and these effects were modulated by water availability. Furthermore, changes in resorption proficiencies were mainly associated with alterations in the nutritional status of green organs in response to water, N and litter addition, except for leaf P. Our findings highlight the importance of increased precipitation in modulating the nutrient resorption proficiency of plants under potentially increased nutrient availability in semiarid grasslands. Therefore, global changes in precipitation and N, and corresponding litter changes could result in complex effects on plant nutrient economies and, in turn, could influence the return of nutrients to the soil.

Keywords Precipitation · Nitrogen · Litter · Nutrient resorption · Stem

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Introduction

Environmental changes induced by anthropogenic activities, such as increased precipitation, nitrogen (N), and litter inputs, have significantly influenced ecosystem nutrient cycles (Dukes et al. 2005; Harpole et al. 2007; Huanng et al. 2009; Lü et al. 2011). Precipitation at mid latitudes is predicted to increase over this century (Weltzin et al. 2003), which could directly improve soil available water, and indirectly enhance soil-available nutrients by accelerating N mineralization and the activities of mycorrhiza fungi (Burke et al. 1997; Ma et al. 2012; Wang et al. 2006), or decrease soil-available nutrients by leaching (Lehmann and Schroth 2003). Meanwhile, increasing N deposition can also elevate available N in the soil, and alter other properties, such as pH (Lan and Bai 2012). The alleviation of soil nutrient and water limitation to plants would result in an increase in plant biomass and, thus, litter production, which would then feed back to the soil nutrient cycle (Huang and Spohn 2015; Vincent et al. 2010; Xiao et al. 2014; Xu et al. 2013). Changes in soil nutrient and water levels, which are both important limiting factors in arid and semiarid grasslands (Shen et al. 2016), are likely to influence nutrient resorption. Nutrient resorption is a crucial physiological process for plant nutrient conservation, which would then lead to changes in the nutrient cycle. In Inner Mongolia, it was reported that both N and phosphorus (P) are limiting, and that P will become more limited under enriched N conditions (Bai et al. 2014). Meanwhile, under increased precipitation conditions, soil available P and plant P uptake are likely to increase (Schachtman et al. 1998; Aerts and Chapin 2000; Passioura 2002; Peuke and Rennenberg 2004), which could alleviate P limitation. However, the nutrient resorption responses under increased precipitation and N deposition conditions are unclear. Therefore, exploring the effects of these factors, both individually and in combination, on nutrient resorption would help improve understanding of the influence of anthropogenic activities on nutrient cycling in grassland ecosystems.

Many studies have explored the influence of N deposition on plant nutritional status (Cui et al. 2010; Han et al. 2014; Xia and Wan 2008). The changes in the nutritional status of leaves, together with increases in soil-available N, and reduced availability of soil-available phosphorus (P) induced by N inputs

(Peñuelas et al. 2013) influence nutrient resorption. Several studies have shown that, in response to N deposition, N resorption is generally reduced, whereas P resorption is either increased or shows no response (Lü and Han 2010; van Heerwaarden et al. 2003; Yan et al. 2015; Zhang et al. 2015); these responses mainly depend on available P in soil and the physiological demands of the plant, such as its growth rate. In arid and semiarid grasslands, increased precipitation enhances plant P demand resulting from an increased growth rate, and N inputs are likely to exacerbate P limitation (Li et al. 2015b). Previous studies showed that plant phosphate uptake is strongly limited because of very low P movement in soil under drought conditions (Schachtman et al. 1998; Aerts and Chapin 2000; Passioura 2002; Peuke and Rennenberg 2004), i.e., soil available P and plant P uptake could increase under more precipitation conditions. Therefore, we speculate that increased precipitation would enhance P resorption under N input conditions. Compared with the many studies of leaf nutrient resorption, fewer published studies have investigated how increased N inputs affect nutrient resorption from the stem, which also has an important role in nutrient cycling (Lü et al. 2012a; Mao et al. 2013). Two studies reported that N and P resorption in stems showed either a positive or no response to N addition, and the responses were different from that in leaves (Li et al. 2015a; Mao et al. 2013).

Increased precipitation influences N and P resorption not only by improving the physiological demands of plants, but also by altering nutrient availability in the soil. Some studies investigated the effect of water addition on N and P resorption, although the results were inconsistent. For example, Lü and Han (2010) reported that the addition of water reduced N resorption and enhanced P resorption, whereas Huang et al. (2009) found that both N and P resorption increased in response to a reduced supply of water, but showed no response when the supply was increased. These inconsistent results might result from the interaction of the water supply with other factors, especially with available N and P in the soil. Another study reported that N inputs enhanced the effect of water addition on P resorption (Lü and Han 2010). Moreover, water addition might also alter nutrient resorption in stems, although few studies have examined this in detail.

Litter covers the soil surface in many terrestrial ecosystems and originates from the deposition of dead

plant material (Facelli and Pickett 1991). It has a key role in nutrient cycling between plants and the soil (Huang and Spohn 2015; Sayer 2006), and the amount of litter might increase as a result of global change, just as N deposition and increased precipitation are expected to alleviate plant growth limited by soil-available N and water (Fang et al. 2012; Zhou et al. 2009). An increase in litter would be expected to improve soil fertility. Previous studies showed that available P in soil increased with an increase in litter input (Huang and Spohn 2015; Rinnan et al. 2008). This might result from enhanced microbial P mineralization stimulated by litter carbon (C) inputs (Spohn and Kuzyakov 2013) and decreased P leaching (Schreeg et al. 2013). A meta-analysis showed that litter inputs have a positive influence on soil-available N, but the effect could be weakened by other factors, such as leaching (Xu et al. 2013). Therefore, we suggest that soil N and P would increase in arid and semiarid regions, but that increased precipitation would weaken this positive effect. The change in soil nutrients caused by litter addition might also alter nutrient resorption. To our knowledge, only one study has investigated the effects of an increase in litter on leaf and stem N and P resorption, reporting a reduction in both (Li et al. 2015a). Moreover, a change in the amount of litter might interact with other factors to affect plant nutrient resorption; for example, the effect of litter inputs on N resorption can be enhanced by N deposition (Li et al. 2015a). Only a few studies have investigated the effects on plant nutrient conservation of an increase in litter in combination with other climatic factors.

Nutrient resorption can be measured in terms of its efficiency or proficiency. Nutrient resorption efficiency is defined as the ability of a plant to resorb nutrients with respect to green organs, expressed as a percentage value (Aerts 1996). Nutrient resorption proficiency is the absolute level to which a nutrient is reduced during leaf senescence, and can be measured as the nutrient concentrations in senesced leaves (Killingbeck 1996); that is, low nutrient concentrations in senesced leaves indicate high nutrient proficiencies. In the current study, a field experiment was conducted to investigate the effects of increased precipitation, and N and litter addition on N and P resorption (measured as both resorption efficiency and proficiency) in the leaves and stems of *Leymus chinensis,* a dominant species on the grasslands of

Inner Mongolia that has important ecological and economic value. We hypothesized that (i) N resorption would increase with an increase in precipitation, because of increased plant growth, but would decrease with N and litter inputs because of an increase in available N in the soil; (ii) P resorption would increase to balance the P limitation induced by N addition or the need for plant growth induced by water addition; (iii) the effect of N and litter inputs would be modulated by the increase in precipitation, because of alleviation of water limitations on plant growth in this area and changes in available nutrients in the soil. We also expected that nutrient resorption in leaves and stems in response to treatments would be different.

Materials and methods

Site description

The study was conducted in a fenced temperate steppe located in the Maodeng area of the city of Xilinhaote, Inner Mongolian, China (44°10′00.2″N 116°28′53.9″E). The mean annual temperature in this area (1982–2003) is 0.7 °C and the mean monthly temperature ranges from −21 °C in January to 19 °C in July. The mean annual precipitation is 343 mm, 80% of which falls between May and August. Soil is characterized as Calcic Chernozem according to the ISSS Working Group RB (1998). Mean soil bulk density is 1.32 g cm^{-3}, and its pH is approximately 8.46. Total N, total carbon (C), total P, and Olsen-P in the 0 to 10 cm soil layer were 1.2 and 10.2 mg g^{-1}, 350 and 2.2 mg kg^{-1}, respectively. This site was dominated by *L. chinensis*, has been fenced since 2013, and has not received any grassland management.

Experimental design

The experiment used a three-factorial split-plot design with four replicates. During late April 2013, four 26 m × 14 m blocks were established. Each block was split into two main plots, one for the increased precipitation treatments and the other for the ambient precipitation treatments. Each main plot was divided into four 4 × 4 m^2 subplots. N treatments (N addition versus ambient N) and litter treatments (litter addition versus control without litter addition) were randomly assigned to each subplot within each main plot. The C, N, and P concentrations in litter were 42.56, 0.27, and

0.021%, respectively. There was a 2-m buffer zone between any two subplots.

During the middle of the growing season (July–August) in each study year, each increased precipitation plot was irrigated with 15 mm of precipitation per week by spray irrigation. In total, 120 mm of precipitation was applied to the precipitation plots during the growing season, which was equal to 30% of the mean annual rainfall of this region. At the beginning of the growing season (May) each year from 2013 to 2015, 10 g N m^{-2} in the form of urea was added to the N addition plots and 200 g m^{-2} plant litter was applied to the surface of the soil in the litter addition plots (corresponding to increases in ecosystem productivity of 60%.). The plant litter had been collected from the adjacent mature *L. chinensis* grassland and air-dried. To prevent the litter on the soil surface from blowing away, a 2.5-cm net was laid over the surface of the soil and left in place until the plants had reached 15 cm in height (early June). To ensure that the plots were exposed to the same amount of soil disturbance, the plots with no litter addition were also covered with a net, which was removed at the same time as for the litter addition plots.

Field sampling and measurements

During mid-August 2015 (the peak of the growing season), 60 *L. chinensis* shoots that were similar in height were randomly selected within each plot; from 30 of these plants, the third and fourth fully expanded leaves from the top of each shoot and one basal stem per shoot were collected, so that the concentration of nutrients in these organs could be determined. The remaining 30 shoots were marked with labels, and the third and fourth fully expanded leaves on each shoot were tagged with a red thread. All tagged leaves and the corresponding stems were collected in late October following their senescence.

All plant samples (including the green and senescent leaves and stems) were oven dried at 65 °C for 48 h, and then weighed separately. To determine the N and P concentrations, only labeled organs (including green and senescent leaves and stems) were used. These materials were ground down to a size that enabled them to be passed through a 40-mesh sieve using a mechanical mill. Each sample was extracted with sulfuric acid, and total N concentration was determined colorimetrically using the Kjeldahl acid-digestion method with a 2300 Kjeltec Analyzer Unit (FOSS, Hillerød, Sweden). P concentration (mg g^{-1}) was measured using persulfate oxidation followed by colorimetric analysis (Carter and Gregorich 2008). The total N and P pools of an individual organ (for both green and senesced organs) were calculated from the individual organ weight and its N or P concentration.

During mid-August, three soil cores were sampled from the top 10 cm of soil from each plot using a soil corer (5 cm in diameter) and combined into one sample for each plot. Roots and stones were removed by sieving the soil samples through a 2-mm mesh, and the fresh soil samples were brought immediately to the laboratory for analysis. The concentrations of inorganic N (NO_3^--N and NH_4^+-N) in the soil were analyzed with a flow injection auto analyzer (AutoAnalyser 3; Seal Analytical, Norderstedt, Germany). Soil inorganic N is presented as mg kg^{-1}. The soil available P (mg kg^{-1}) was analyzed using the Olsen methods (Carter and Gregorich 2008).

Calculation of leaf resorption efficiency and proficiency

The nutrient resorption efficiency was calculated as the ratio of the difference in the nutrient pool between the green and senesced organs using the following equation:

$$\text{Resorption efficiency} = (1 - X_{sen}/X_{gr}) \times 100\%$$
(1)

Here, we used the nutrient pool rather than nutrient concentration (mg g^{-1} or mg cm^{-2}), because leaf mass loss caused by leaching or leaf area shrinkage during senescence can lead to underestimation of leaf resorption efficiency (van Heerwaarden et al. 2003; Vergutz et al. 2012). X_{gr} and X_{sen} are pools of N or P in green and senesced organs, respectively. The nutrient resorption proficiency was measured as the nutrient concentration in senesced organs according to Killingbeck (1996).

Statistical analysis

We used the response ratio (ln RR) usually employed in meta-analysis or medical studies to quantify the response of resorption efficiency of leaves and stems to treatments using the following equation:

$$\ln X_t/X_c = \ln X_t - \ln X_c \qquad (2)$$

where X_t and X_c are values of resorption efficiency in the experimental treatment and in the control.

The main and interactive effects of increasing precipitation, and N and litter addition on available N and P in the soil, N and P concentrations in green organs, N:P ratios in green leaves and the N and P resorption (efficiencies and proficiencies) were analyzed using a split-plot analysis of variance (ANOVA). Increased precipitation was applied to the main plots and N and litter addition treatments were applied to the subplots, which meant that we could test the increased precipitation effect against the plot mean square error. We used a paired t test to evaluate whether water addition influenced these response variables. The variables among treatments at the same water treatment levels were tested by Least Significant Difference tests (LSD). All statistical analyses were performed using SAS Version 9.0 (SAS Institute, Cary, NC, USA).

Results

Effects of increased precipitation, N and litter addition on soil-available nutrients

Increased precipitation had no significant effects on inorganic N and available P concentrations in the soil (Table 1). N and litter addition significantly increased soil inorganic N by 63.4 and 20.0%, and soil available P by 34.5 and 39.0%, respectively, compared with the controls (Table 1; Fig. 1a, b).

Effects of increased precipitation, N and litter addition on N and P concentrations in green organs and N:P ratio in green leaves

Increased precipitation significantly reduced the N concentration in green leaves and stems and P concentration in green stems (Table 2; Fig. 2a, b, d). By contrast, N addition significantly increased the N concentration in green leaves and stems and the P concentration in green leaves (Table 2; Fig. 2a, b, c), and litter addition also significantly enhanced the N concentration in green leaves and the P concentration in green leaves and stems (Table 2; Fig. 2a, c, d). There was no significant interaction among

Table 1 Results from split-plot ANOVA testing the effects of block (B), water (W), nitrogen (N), litter addition (L), and their interactions on soil inorganic nitrogen concentration, and soil available P concentration

	df	Soil inorganic N		Soil available P	
		F	P	F	P
B	3	0.92	0.53	2.31	0.26
W	1	0.02	0.89	0.14	0.73
N	1	53.54	**< 0.0001**	12.35	**0.0025**
L	1	7.67	**0.013**	15.19	**0.0011**
B × W	3	1.18	0.35	0.45	0.72
W × N	1	3.33	0.085	0.00	0.99
W × L	1	0	0.95	0.66	0.43
N × L	1	0.35	0.56	0.04	0.84
W × N × L	1	0.00	0.90	0.93	0.34

P values below 0.05 are in bold

precipitation, N and litter addition in terms of their effects on nutrient levels in green leaves and stems (Table 2), but water treatment significantly decreased the effect of N plus litter addition on stem N concentration, and N addition on P concentration. None of the treatments had a significant effect on the N:P ratio in green leaves (Table 2).

There were significant positive relationships between N concentrations in green and senesced organs (leaves and stems) (Fig. 3a, c) and between P concentrations in green and senesced stems (Fig. 3d).

Effects of increased precipitation, N and litter addition on N and P resorption efficiency and proficiency

N addition significantly decreased N resorption efficiency under water addition conditions, but increased P resorption efficiency in leaves under ambient conditions (Table 3; Fig. 4a, c). However, none of the individual or combination treatments had a significant effect on the N or P resorption efficiency in the stems (Table 3), except for a positive effect of water addition on the P resorption efficiency of the control (Fig. 4d).

Increased precipitation significantly reduced the N concentration in senescent stems (i.e., high proficiency) (Table 3; Fig. 5b), whereas N and litter addition significantly decreased the N resorption
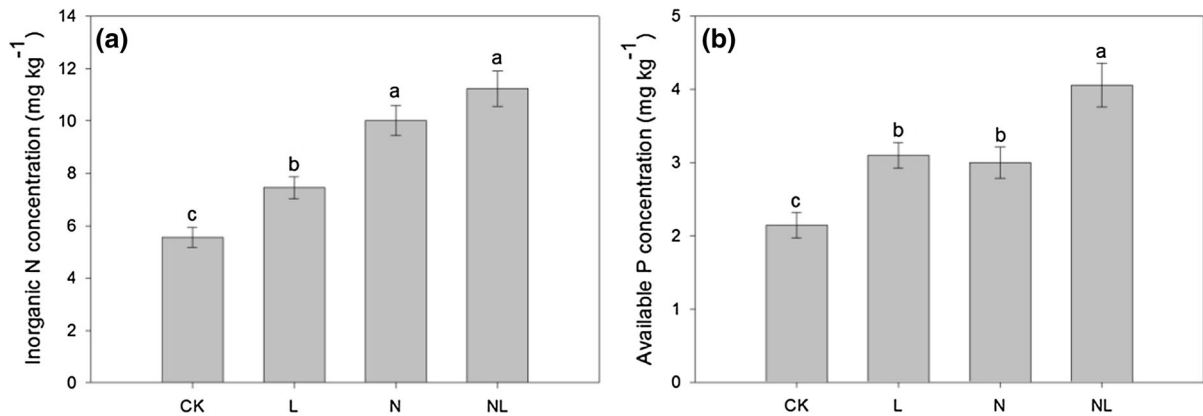
Fig. 1 Variations in inorganic N (**a**) and available P concentration (**b**) in soils. Values are mean ± SE ($n = 4$). *CK* control, *L* litter addition, *N* nitrogen addition, *NL* both nitrogen and litter addition. The same lowercase letters indicate that the treatments are not significantly different at $P \leq 0.05$

Table 2 Results from split-plot ANOVA testing the effects of block (B), water (W), nitrogen (N), litter addition (L), and their interactions on N and P concentration in green leaf and stems, and N:P ratio in green leaves

	df	Green leaf N		Green stem N		Green leaf P		Green stem P		N:P ratio in leaves	
		F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
B	3	3	0.2	3.95	0.14	2.57	0.23	0.03	0.99	4.58	0.1217
W	1	30.86	**0.011**	53.7	**0.0052**	5.19	0.11	11.76	**0.04**	0.18	0.6993
N	1	39.09	**< 0.0001**	23.24	**0.0001**	11.83	**0.0029**	0.01	0.91	2.51	0.1308
L	1	13.21	**0.0019**	3.9	0.06	32.87	**< 0.0001**	20.93	**0.0002**	4.14	0.0568
B × W	3	0.39	0.76	0.28	0.84	1.06	0.39	1.87	0.17	0.85	0.4868
W × N	1	0.2	0.66	0.54	0.47	0.01	0.93	0.7	0.41	0	0.9453
W × L	1	0.03	0.86	0.04	0.84	0.38	0.54	0.02	0.89	0.35	0.5611
N × L	1	0.38	0.54	0.33	0.57	0.03	0.88	1.11	0.31	0.02	0.888
W × N×L	1	0.38	0.54	0.97	0.33	0.47	0.5	0	0.96	0.73	0.4029

P values below 0.05 are in bold

proficiency of leaves and stems (Table 3; Fig. 5a and b). Water and N addition significantly enhanced P proficiency in senescent leaves and stems, respectively, whereas litter addition significantly reduced P proficiency in senescent leaves and stems (Table 3; Fig. 5c, d). There were significant interactive effects between water and N addition on N proficiency in senescent stems and P proficiency in senescent leaves and stems (Table 3; Fig. 5b, c, d). However, only a significant interactive effect was found between water and litter addition on P proficiency in senescent leaves (Table 3; Fig. 5c).

The response of nutrient resorption efficiency in leaves and stems to treatments

N and P resorption efficiencies in leaves were significantly higher than that in stems under each treatment and control condition ($P < 0.0001$–0.039). Under ambient conditions, the N responses in stems for litter and N addition were 20.58 and 1.46 times that in leaves, respectively, but the response in stems for combined treatments of N and litter was 0.75 times that in leaves. Water addition decreased the N response in stems for litter and N inputs by 0.30 and 0.90 times, respectively, whereas it increased the N response in leaves for litter and N inputs by 0.57 and
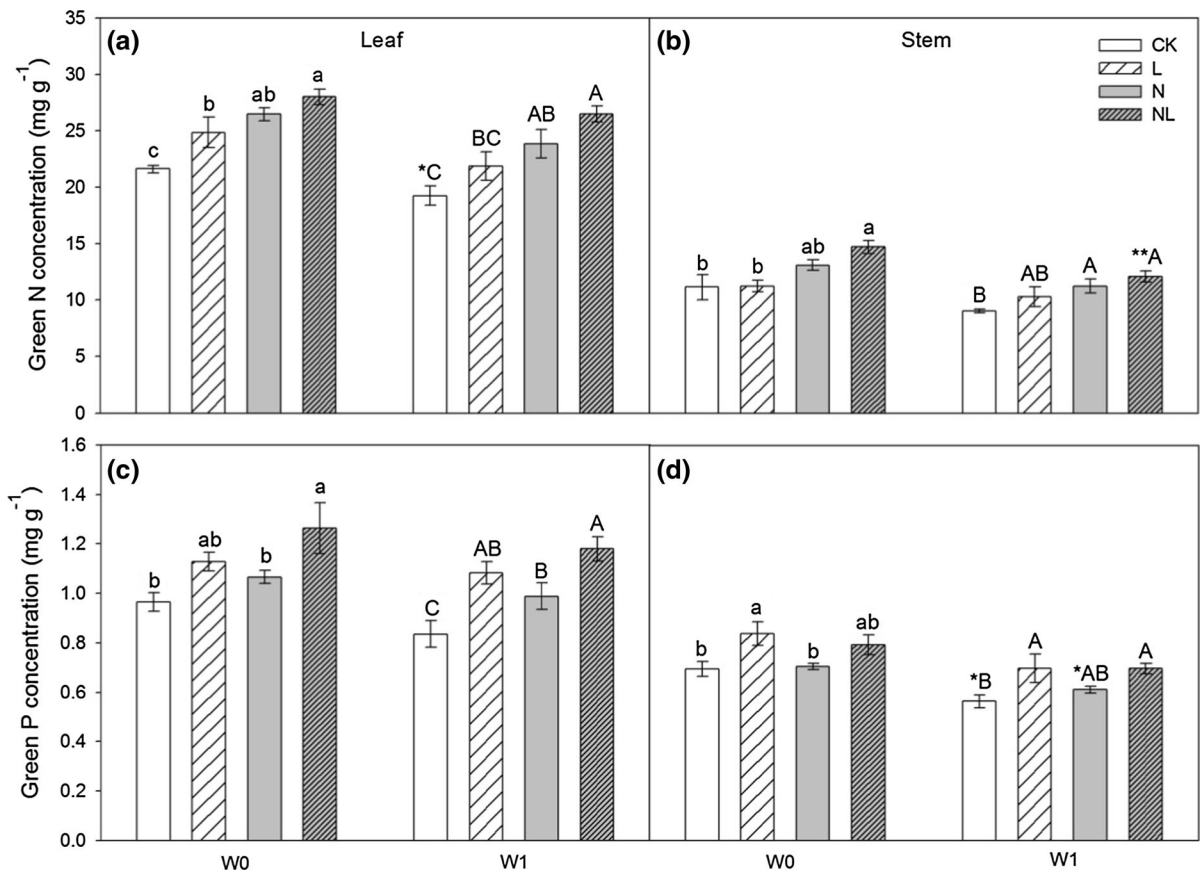
Fig. 2 Variations in N and P concentration in green leaves (**a**, **c**) and stems (**b**, **d**). Values are mean ± SE ($n = 4$). *W0* ambient precipitation, *W1* water addition, *CK* control, *L* litter addition, *N* nitrogen addition, *NL* both nitrogen and litter addition. Asterisks above the bars indicate where the means of the water addition treatments are significantly different from the means of

the corresponding ambient precipitation treatments: **$P \leq 0.01$, *$P \leq 0.05$. The same lowercase letters indicate that the treatments in the ambient precipitation plots are not significantly different at $P \leq 0.05$. The same capital letters indicate that the treatments in the water addition plots are not significantly different at $P \leq 0.05$

6.40 times, respectively, resulting in responses in leaves that were 0.56 and 9.70 times that in stems, respectively (Fig. 6a). The P resorption efficiency in both organs showed positive responses to all treatments, and the different response strengths between the two organs were modulated by water addition, with the RR of stems being higher (0.061 vs 1.79 times, respectively) than that in leaves under water addition conditions, whereas the RR was similar to or lower than (0.35–0.41 times, respectively) that of leaves under ambient precipitation conditions (Fig. 6b).

Discussion

Effects of precipitation, N and litter manipulation on green organ nutrient concentrations and N:P ratio in green leaves

The negative influences of increased precipitation on N concentration in green organs of *L. chinensis* were also reported by Lü and Han (2010). Given that increased precipitation increased the aboveground biomass by 37.7% (Fig. 1Sa), it is reasonable to expect that these negative effects of increased precipitation resulted from a biomass dilution effect (van Heerwaarden et al. 2003). In line with other studies (Lü et al. 2012b), N addition significantly increased N concentration in green organs regardless of water
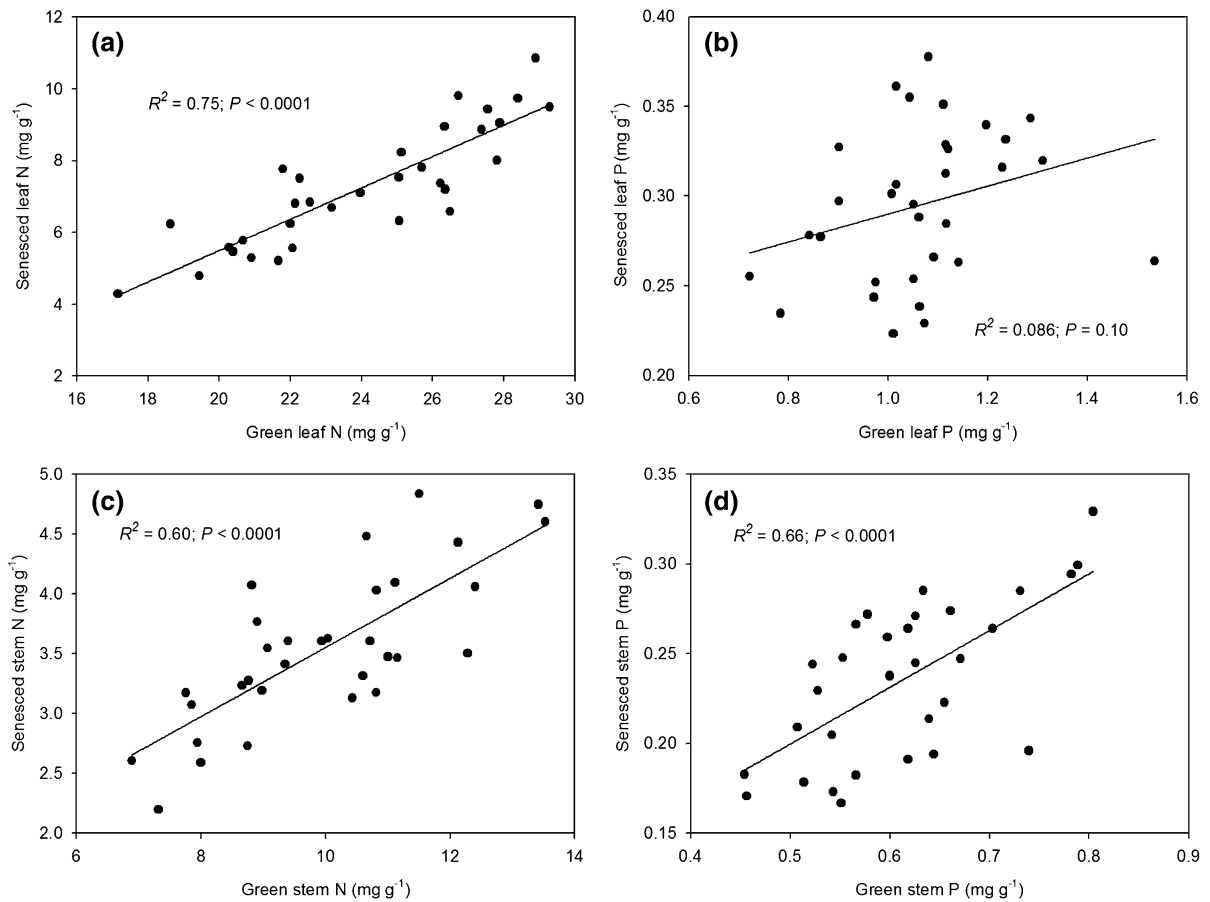
Fig. 3 The relationships between N in green and senesced leaves (**a**), P in green and senesced leaves (**b**), N in green and senesced stems (**c**), P in green and senesced stems (**d**) of *Leymus chinensis*

available in the soil. Furthermore, N addition also increased the P concentration in green leaves, which probably resulted from the increase of soil available P induced by N addition via a reduction in soil pH, or by enhancing P mineralization and uptake by roots (Figs. 1Sb, 2S) (Stevens et al. 2010; Wang et al. 2015). N addition decreased the P concentration in senesced leaves only under ambient conditions, likely caused by an increase in P resorption, which indicated an increase in P limitation under individual N addition conditions. Litter addition significantly increased N in green leaves and P in both green organs because of the increase in soil available nutrients (Fig. 3S), which was in accordance with results of Li et al. (2015a, b). Thus, our results suggested that long-term mowing (which can reduce litter biomass) could decrease grass quality, and we need apply N and P fertilizer to the grasslands in Inner Mongolia.

N:P ratios in green leaves have been suggested as good tools to detect nutrient limitation for plants in terrestrial ecosystems (Koerselman and Meuleman 1996). In our study, the N:P ratio in green leaves was higher than 20 (Fig. 4S), indicating that the study area was P limited (Koerselman and Meuleman 1996; Aerts and Chapin 2000). As also reported by Yu et al. (2010, 2015), none of the treatments had an effect on the N:P ratio in green leaves, which suggested that *L. chinensis* can maintain stoichiometric homeostasis in leaves in response to changes in available resources in the soil caused by N, water and litter inputs.

Effects of precipitation, N, and litter manipulation on leaf nutrient resorption

N addition significantly reduced the N resorption in leaves under water addition conditions, resulting in

Table 3 Results from split-plot ANOVA testing the effects of block (B), water (W), nitrogen (N), litter addition (L), and their interactions on N resorption efficiency (NRE) and P resorption efficiency (PRE), and N resorption proficiency (NRP) and P resorption proficiency (PRP) in leaf and stems

		B 3	W 1	N 1	L 1	B × W 3	W × N 1	W × L 1	N × L 1	W × N × L 1
Leaf NRE	F	0.85	0.04	20.69	0.04	2.06	0.58	0.5	0.69	0.09
	P	0.55	0.85	**0.0002**	0.85	0.14	0.46	0.49	0.42	0.77
Stem NRE	F	0.55	1.24	0.01	0.47	0.76	0.53	0.07	0.96	0.01
	P	0.68	0.35	0.93	0.51	0.53	0.47	0.8	0.34	0.93
Leaf PRE	F	0.38	0.48	22.67	0.26	2.55	4.65	4.31	2.57	0.01
	P	0.78	0.54	**0.0002**	0.61	0.088	**0.045**	0.053	0.12	0.94
Stem PRE	F	1.13	4.38	0.07	0.08	0.79	1.21	0.34	0.20	0.14
	P	0.46	0.13	0.8	0.78	0.52	0.29	0.57	0.66	0.71
Leaf NRP	F	1.1	1.98	63	7.16	2.23	0.33	0.18	0.26	0.02
	P	0.47	0.25	**< 0.0001**	**0.015**	0.12	0.58	0.68	0.62	0.89
Stem NRP	F	0.64	20.63	53.47	15.91	2.67	7.47	0.12	0.37	1.41
	P	0.64	**0.02**	**< 0.0001**	**0.0009**	0.08	**0.01**	0.73	0.55	0.25
Leaf PRP	F	0.71	0.18	6.8	27.9	0.62	11.63	14.53	1.61	0.04
	P	0.61	0.7	**0.018**	**< 0.0001**	0.61	**0.0031**	**0.0013**	0.22	0.84
Stem PRP	F	0.93	36.48	0.04	15.96	1.58	6.54	0.11	0.07	0.07
	P	0.52	**0.0091**	0.85	**0.0008**	0.23	**0.02**	0.75	0.79	0.79

P values below 0.05 are in bold

low resorption efficiency and proficiency, which is in agreement with global patterns observed across species and in other field studies (Lü et al. 2015; van Heerwaarden et al. 2003; Yuan and Chen 2015). Under ambient precipitation conditions, N addition also decreased N resorption proficiency, i.e., increased N concentration in senescent leaves, which largely resulted from the high N concentration in green leaves, and the significant positive relationship between N concentration in green and senescent leaves (Fig. 3a). The results showed that N addition significantly increased P resorption in leaves only under ambient precipitation conditions, which was reflected in the high resorption efficiency and proficiency in these leaves. The increase in P resorption proficiency with N addition without water possibly resulted from increased plant growth and limited P uptake by roots caused by low soil phosphate movement and transpiration (Peuke and Rennenberg 2004). The significant positive influence of N addition on P resorption efficiency disappeared under water addition conditions, which was mainly caused by the alleviation of water limitation in this site, resulting in more P movement in the soil and more P uptake by plants

(Peuke and Rennenberg 2004). Li et al. (2015a) reported no clear effect of N addition on P resorption efficiency without water treatment. These results suggest that the effects of N inputs on N and P resorption are modulated by increased precipitation. As with the results of Li et al. (2015a) and Lü and Han (2010), no significant influence of litter and water addition was found on leaf N or P resorption efficiencies, respectively. However, there was a significant effect of N and litter addition on leaf P proficiency. Although N and litter addition significantly increased green leaf P concentration, there was no significant positive relationship between P in green and senesced leaves. This lack of relationship confirmed that P is limiting for plant growth, i.e., that the pattern of P resorption proficiency is independent of P in green leaves.

Effects of increased precipitation, N, and litter manipulation on stem nutrient resorption

It was unexpected that none of the treatments had significant effects on nutrient resorption efficiency in stems, but there were significant effects of water, N,
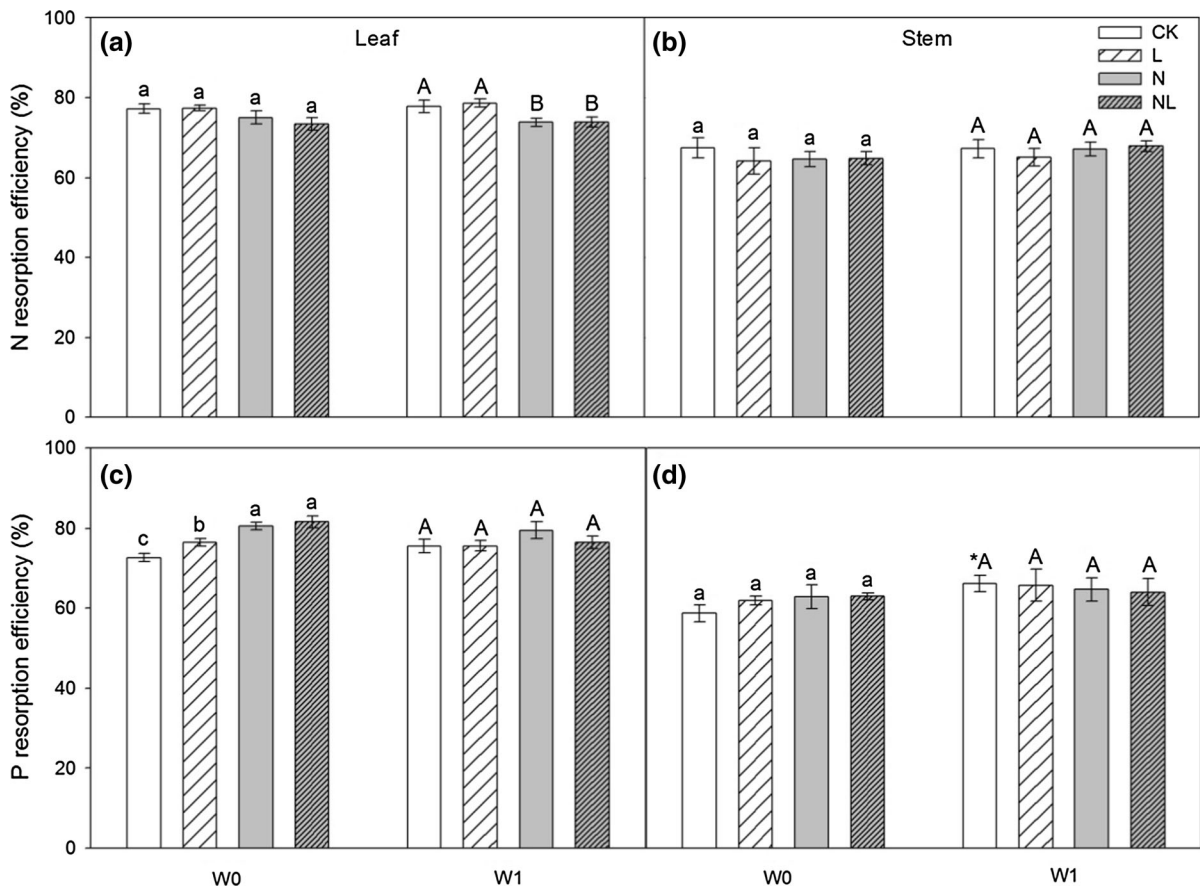
Fig. 4 Variations in N and P resorption efficiencies in senesced leaves (**a, c**) and stems (**b, d**). Values are mean ± SE ($n = 4$). *W0* ambient precipitation, *W1* water addition, *CK* control, *L* litter addition, *N* nitrogen addition, *NL* both nitrogen and litter addition. Asterisks above the bars indicate where the means of the water addition treatments are significantly different from the means of the corresponding ambient precipitation treatments: **$P \leq 0.01$, *$P \leq 0.05$. The same lowercase letters indicate the treatments in the ambient precipitation plots are not significantly different at $P \leq 0.05$. The same capital letters indicate the treatments in the water addition plots are not significantly different at $P \leq 0.05$

and litter addition on N and P proficiency. The different responses of the two indexes (resorption efficiency versus proficiency) were largely because resorption proficiency has a close relation with the amount of nutrients in green stems, which were significantly affected by the treatments. Furthermore, the negative effects of N addition on N resorption proficiency were weakened by water addition. This likely resulted from the increase in physiological requirements needed to support plant growth in response to the alleviation of water limitation (Fig. 1S). In contrast to the positive effect of N addition on leaf P resorption, there was no significant influence of N addition on stem P resorption. One possible explanation for the different responses in both

organs is that leaves are metabolic organs, which often exhibit high stoichiometric homeostasis and a high demand for nutrients associated with photosynthesis compared with structural organs (e.g., stems), which contain low P, and some of which cannot be resorbed (Kerkhoff et al. 2006). Litter addition or N plus litter had significant effects on P resorption proficiency only under water addition conditions. This was mainly ascribed to (i) water addition significantly decreasing P allocation to green stems in the control, which has a close positive relationship with the P concentration in senescent stems; and (ii) water addition also increasing the P resorption efficiency of the control, resulting in a low P content in senescent stems.
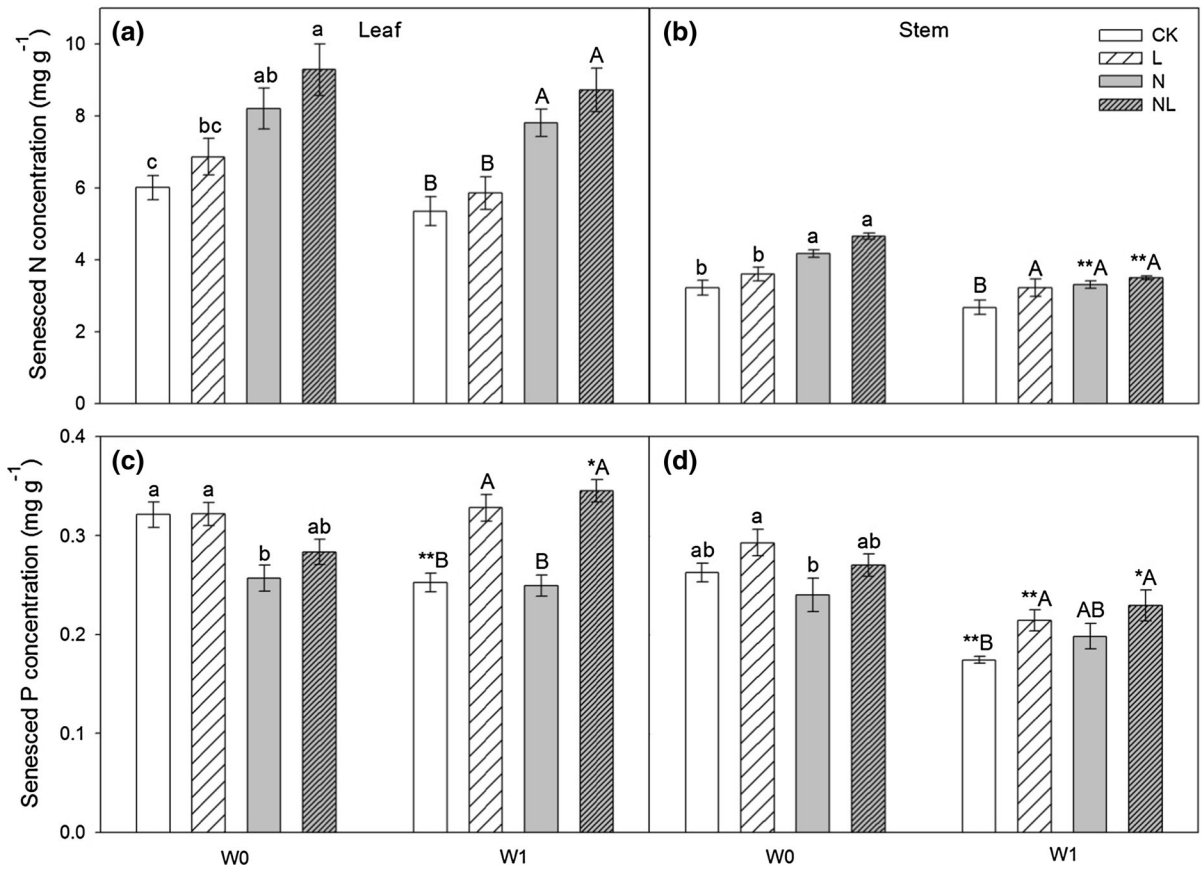
Fig. 5 Variations in N and P proficiencies in leaves (**a**, **c**) and stems (**b**, **d**). Values are mean ± SE (*n* = 4). *W0* ambient precipitation, *W1* water addition, *CK* control, *L* litter addition, *N* nitrogen addition, *NL* both nitrogen and litter addition. Asterisks above the bars indicate where the means of the water addition treatments are significantly different from the means of the corresponding ambient precipitation treatments: **$P \leq 0.01$, *$P \leq 0.05$. The same lowercase letters indicate the treatments in the ambient precipitation plots are not significantly different at $P \leq 0.05$. The same capital letters indicate that the treatments in the water addition plots are not significantly different at $P \leq 0.05$

Fig. 6 Natural logarithm of the values of N (**a**) and P (**b**) resorption efficiency (RR) for treatments. *L* litter addition, *N* nitrogen addition, *NL* both nitrogen and litter addition, *W* water addition, *WL* both water and litter addition, *WN* both water and nitrogen addition, *WNL* water, nitrogen and litter addition
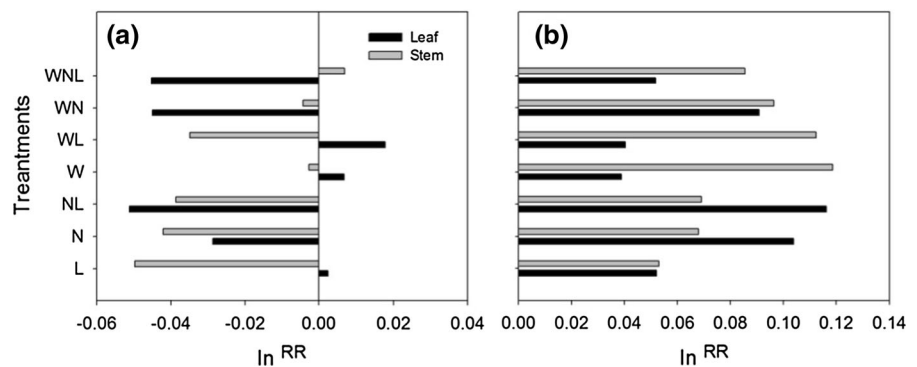
The difference in leaf and stem resorption traits and response to treatments

Although stem N and P resorption efficiencies were lower than in leaves, the resorption efficiencies of stems should not be ignored (Freschet et al. 2010). The N and P resorption efficiencies of *L. chinensis* stems (66.05% for N and 63.4% for P) were higher relative to the values recorded for *L. chinensis* by Lü et al. (2012b) and Li et al. (2015a), and almost twice as high as other N resorption efficiencies reported for other plants, such as *Stipa grandis* (Lü et al. 2012b). Moreover, the N and P resorption efficiencies in stems contributed 16.0 and 19.6%, respectively, to the total aboveground N resorbed from the aboveground senescing parts. The contribution of N was 5–56% lower than that reported by Lü et al. (2012b) (varying from 17 to 36%); this discrepancy might be due to the increase in leaf biomass resulting from the treatments used in the current study.

According to the conclusions of a previous study (Kobe et al. 2005), the resorption proficiency is largely controlled by nutrients in green organs exposed to treatments. Therefore, we compared the response of the resorption efficiency of leaves and stems to all treatments. Under ambient conditions, the N in stems generally showed a strong response to individual litter or individual N addition compared with that in leaves, whereas the P resorption efficiency of stems showed a weak response to individual N or individual litter treatments. As described previously, the function and structure of both organs determine the different responses to N and litter addition (Kerkhoff et al. 2006).

Conclusions

In the current study, for *L. chinensis*, changes in precipitation, N, and litter had significant effects on nutrient levels in green organs and nutrient resorption proficiency rather than resorption efficiency, which was only sensitive to N addition. As hypothesized, we showed that water modulated the response of leaf and stem nutrient resorption to N and litter addition. Our results highlight a strategy of adaptation to climate change-related alterations in the nutrient and water content of soil by a dominant species of the eastern Eurasian steppes and, in turn, how this feeds back to

ecosystem nutrient cycling. These results have important implications for both understanding the influence of N deposition, precipitation, and litter changes on nutrient cycling, and our ability to predict and mitigate these influences in an increasingly anthropogenically altered environment. In addition, N and P resorption in stems of *L. chinensis* contributed 16.0 and 19.0% to the total aboveground N and P resorbed from aboveground senescing parts, respectively, whereas N and P in senesced stems accounted for 32.8 and 44.4% of aboveground litter N and P, respectively. Thus, we should not ignore the importance of non-leaf organs to the plant nutrient economy and ecosystem nutrient cycling.

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