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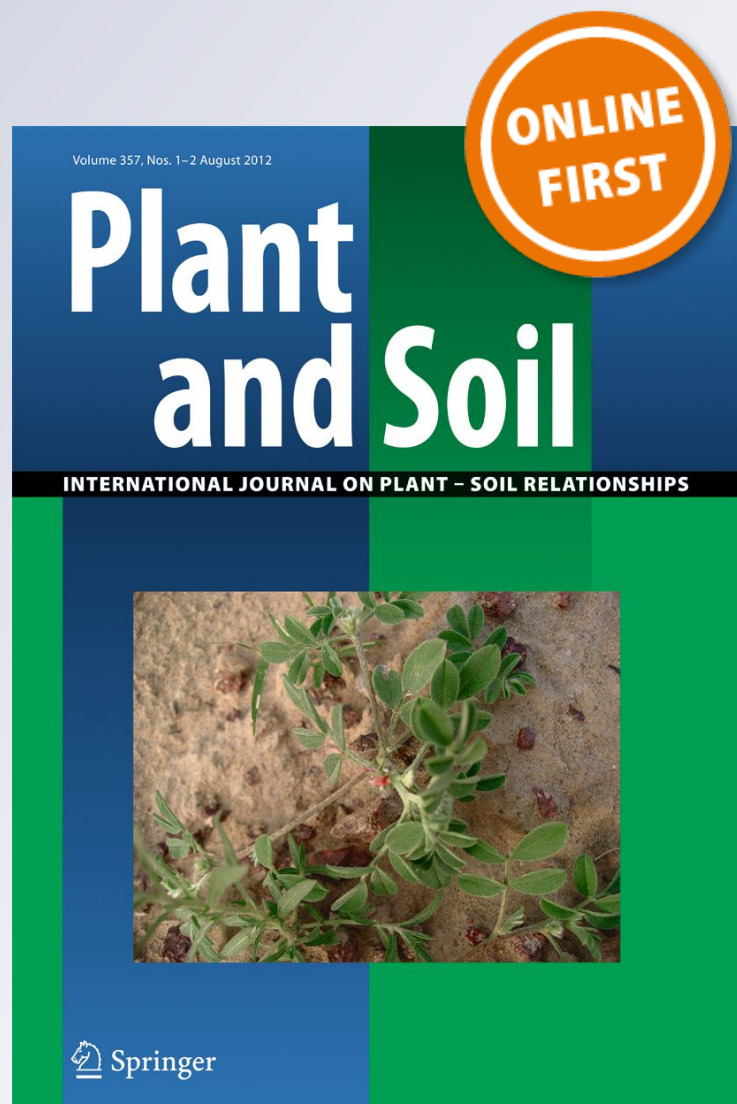
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# Response of leaf, sheath and stem nutrient resorption to 7 years of N addition in freshwater wetland of Northeast China

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## Abstract

**Background and Aims** Increased N availability induced by agricultural fertilization applications and atmospheric N deposition may affect plant nutrient resorption in temperate wetlands. However, the relationship between nutrient resorption and N availability is still unclear, and most studies have focused on leaf nutrient resorption only. The aim of our study was to examine the response of leaf and non-leaf organ nutrient resorption to N enrichment in a temperate freshwater wetland.

**Methods** We conducted a 7-year N addition experiment to investigate the effects of increased N loading on leaf, sheath and stem nutrient (N and P) resorption of two dominant species (*Deyeuxia angustifolia* and *Glyceria spiculosa*) in a freshwater marsh in the Sanjiang Plain, Northeast China.

**Results** Our results showed that, for both leaf and non-leaf organs (sheath and stem), N addition decreased N resorption proficiency and hence increased litter N concentration. Moreover, the magnitude of N addition effect on N resorption proficiency varied with fertilization rates for *D. angustifolia* sheaths and stems, and *G. spiculosa* leaves. However, increased N loading produced inconsistent impacts on N and P resorption efficiencies and P resorption proficiency, and the effects only varied with species and plant organs. In addition, N enrichment increased litter mass and altered litter allocation among leaf, sheath and stem.

**Conclusions** Our results highlight that leaf and non-leaf organs respond differentially to N addition regarding N and P resorption efficiencies and P resorption proficiency, and also suggest that N enrichment in temperate freshwater wetlands would alter plant internal nutrient cycles and increase litter quality and quantity, and thus substantially influence ecosystem carbon and nutrient cycles.

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**Keywords** Fertilization · Litter quality · Litter quantity · Marsh · Resorption efficiency · Resorption proficiency

## Introduction

Resorption of nutrients from senescing tissue, one of the most important mechanisms of nutrient conservation, is a key control of productivity and elemental

cycling in terrestrial ecosystems (Aerts and Chapin 2000; Vergutz et al. 2012). Nutrient resorption can be characterized by nutrient resorption efficiency (the percentage of the difference in nutrient pool between mature and senesced organs to mature organ nutrient pool) (van Heerwaarden et al. 2003a) and nutrient resorption proficiency (the level to which nutrient concentration is reduced in senesced organs) (Killingbeck 1996). High nutrient resorption efficiency makes plants less dependent on current nutrient uptake and increases plant fitness, especially in nutrient-poor ecosystems (Aerts 1996; Eckstein et al. 1999). Moreover, nutrient resorption proficiency directly influences litter quality and thus litter decomposition rate and soil nutrient availability (Killingbeck 1996; Vitousek 1998).

Because of the important role of nutrient resorption in plant nutrient conservation (Aerts and Chapin 2000; Eckstein et al. 1999), it is predicted that species growing in low-nutrient habitats have high nutrient resorption efficiency and proficiency. Recent studies have indicated that nutrient resorption proficiency is highly dependent on soil nutrient status, and decreases with increasing nutrient availability (Kozovits et al. 2007; Norris and Reich 2009; Rejmánková 2005; Richardson et al. 2005; Wright and Westoby 2003). However, the response of resorption efficiency to soil nutrient availability is inconsistent, and there is no clear nutritional control on nutrient resorption efficiency (Güsewell 2005; van Heerwaarden et al. 2003b; Lü and Han 2009; Soudzilovskaia et al. 2007; Vitousek 1998). Moreover, in contrast to the intensive research on leaf nutrient resorption response to soil nutrient availability, no study has so far investigated the effect of soil nutrient availability on nutrient resorption of non-leaf organs. Plant non-leaf organs, especially culms of grasses, have high nutrient resorption efficiencies and play an important role in plant nutrient economy and ecosystem nutrient cycling (Freschet et al. 2010; Lü et al. 2012). Knowledge about the response of nutrient resorption of non-leaf organs to soil nutrient availability is of primary importance, especially in herbaceous-dominated ecosystems.

In temperate wetlands, plant growth is severely limited by soil nutrient availability, due to the low nutrient mineralization rates caused by cool temperature, water-logging conditions and poor substrate quality (Aert et al. 1999). Therefore, plant species in these ecosystems strongly depend on internal nutrient cycling and thus have great nutrient resorption efficiency

(Aert et al. 1999; Bedford et al. 1999; Yuan and Chen 2009a). During the past decades, wetlands in these regions have been experiencing increasing soil nitrogen (N) availability mainly because of agricultural fertilization applications and atmospheric N deposition (Vitousek et al. 1997). N enrichment in ecosystems has substantially stimulated plant growth and increased biomass N concentration (Xia and Wan 2008). Additionally, increased N loading may cause a shift from N-limited towards P-limited ecosystems, which may lead to lower phosphorus (P) concentration in plants due to the growth dilution effect (van Heerwaarden et al. 2003b). Since nutrient resorption is highly dependent on leaf nutrient status globally (Kobe et al. 2005; Vergutz et al. 2012), increased N input to ecosystems may produce a marked influence on plant nutrient resorption in temperate wetlands.

In the present study, we conducted a 7-year N fertilization experiment in a freshwater wetland in the Sanjiang Plain, Northeast China, and the aim was to examine the effects of multi-level N addition gradients on nutrient resorption of leaf and non-leaf (sheath and stem) organs in temperate wetlands. We hypothesized that increased N loading to temperate wetlands would decrease leaf, sheath and stem N resorption efficiency and proficiency, and increase P resorption efficiency and proficiency. Thus, N addition would lead to a greater litter N concentration and a lower litter P concentration. In addition, we also hypothesized that the magnitude of N addition effect on these nutrient resorption parameters would vary with fertilization rates.

## Materials and methods

### Study site and experiment design

This study was conducted in a long-term N fertilization experiment started in 2005 in a freshwater wetland located near the Sanjiang Mire Wetland Experimental Station (47°35'N, 133°31'E, 56 m a.s.l) in the Sanjiang Plain, Heilongjiang Province, Northeast China. The Sanjiang Plain is one of the largest freshwater wetlands in China (Zhao 1999), and wetlands cover an area of  $8.10 \times 10^5$  hm<sup>2</sup> in 2005 (Wang et al. 2011). The study site belongs to the temperate continental monsoon climate. Mean annual (1990–2010) precipitation is about 566 mm with approximately 50 % falling in July and

August. Mean annual temperature is 2.5 °C with monthly mean temperature ranging from −20.4 °C in January to 21.6 °C in July. The soil is a typical meadow marsh soil, and is classified as Inceptisols in the US soil taxonomy classification system. Vegetation is dominated by perennial grasses in the study site; the dominant plant species are *Deyeuxia angustifolia* and *Glyceria spiculosa*, accounting for more than 90 % of the total above-ground biomass. *D. angustifolia*-dominated marshes are one of the main wetland types in the Sanjiang Plain, and occupy about 31 % of the total wetland area (Zhao 1999). During the period 1954–2005, freshwater wetlands have been extensively drained and converted to agricultural lands in the Sanjiang Plain (Wang et al. 2011). Consequently, natural freshwater wetlands received increasingly N loading due to the fertilization application during agricultural activities and atmospheric N deposition (Zhang et al. 2007). Detailed information regarding the study site was described by Zhang et al. (2007).

In 2004, 12 plots of 1 m×1 m were selected on a very flat ground with a *D. angustifolia*-dominated community. These plots were separated by approximately 1 m buffer zones. During autumn 2004, plastic (PVC) frames (1 m×1 m, 0.5 m depth) were established to avoid horizontal movement and lateral loss of the added N, and permanent boardwalks were installed within the experimental area to minimize site sampling disturbances. Four N addition levels (control, 0 g N m<sup>-2</sup> year<sup>-1</sup>; low, 6 g N m<sup>-2</sup> year<sup>-1</sup>; moderate, 12 g N m<sup>-2</sup> year<sup>-1</sup>; high, 24 g N m<sup>-2</sup> year<sup>-1</sup>) were randomly assigned to the 12 plots, and each treatment had three replicate plots. Since 2005, N was added as ammonium nitrate (NH<sub>4</sub>NO<sub>3</sub>) during the growing season. In each year, N fertilizer was divided into nine equal doses, mixed with 1 L surface marsh water and applied biweekly from May to September. At the same time, the control plots received 1 L surface marsh water without N fertilizer. Low N addition level was comparable to the sum of agricultural inputs and atmospheric deposition in wetlands in this region, and moderate and high N addition levels were used to study the response of this ecosystem to N enrichment that may occur in the future (Zhang et al. 2007).

#### Field sampling and measurement

*D. angustifolia* and *G. spiculosa*, two dominant perennial grasses in the study site, were selected to examine

the response of nutrient resorption to N enrichment. In late July 2011, twenty shoots with similar height were randomly selected for *D. angustifolia* and *G. spiculosa* in each plot, respectively. Ten of shoots were sampled for determination of biomass and nutrient concentration of leaf (only blade), sheath and stem. We collected three fully expanded leaf and corresponding sheath per shoot, and one culm per shoot. Moreover, we determined the total number of leaves produced per shoot by counting intact green leaves, dead leaves and leaf scars (representing lost leaves) (Whitman and Aarssen 2010). Another ten shoots were marked with plastic labels. Furthermore, we tagged three fully expanded leaves per shoot by tying a small tag to the leaf base. Censuses of the labeled organs were performed every 3 days from late September to early October in 2011, because of the different phenological patterns between two dominant species. The label organs were considered senesced when they thoroughly turned yellow or brown. Senesced organs were harvested following the same protocol as the mature organs.

Both mature and senesced leaf, sheath and culm samples were oven dried at 65 °C for 48 h and weighed separately, and the average masses of individual leaf, sheath and culm were calculated. Plant samples were ground and stored for determination of N and P concentrations. For each plant sample, 0.1-g subsample was digested with H<sub>2</sub>SO<sub>4</sub>-H<sub>2</sub>O<sub>2</sub>, and then N concentration (mg g<sup>-1</sup>) was determined by the indophenol blue colorimetric method, and P concentration (mg g<sup>-1</sup>) was determined by the molybdenum blue colorimetric method (Temminghoff and Houba 2004). Total N or P pool of individual organ (for both mature and senesced materials) was calculated from the individual organ mass (g) and its N or P concentration. Given the mass loss during plant organ senescence, N (NRE, %) or P (PRE, %) resorption efficiency was calculated as the ratio of the difference in N or P pool between mature and senesced organs to mature organ N or P pool (van Heerwaarden et al. 2003a; Lü et al. 2012). Nitrogen (NRP, mg g<sup>-1</sup>) or P (PRP, mg g<sup>-1</sup>) resorption proficiency was defined as the level to which N or P concentration was reduced in senesced material, that is, the senesced organ N or P concentration, with low senesced organ N or P concentration corresponding to high proficiency (Killingbeck 1996).

For each shoot, the amount of nutrient resorbed from leaf, sheath and culm was calculated from the



total mature organ mass, mature organ nutrient concentration and the organ nutrient resorption efficiency (Lü et al. 2012). Since leaf and sheath generally senesced throughout the growing season, total leaf or sheath mass per shoot included lost and dead organs and was calculated by multiplying the mean mass per leaf or sheath with the leaf number (Whitman and Aarssen 2010). Because we did not measure the seasonal pattern of mature leaf or sheath nutrient concentration and nutrient resorption efficiency, we assumed that these related nutrient resorption parameters did not change with plant growth stage during the growing season. The amount of nutrient resorbed from the whole shoot was calculated by adding up the total amount of nutrient from leaf, sheath and culm.

### Statistical analyses

All statistical analyses were performed with SPSS 13.0 for windows (SPSS Inc. 2004) and the accepted significance level was  $\alpha=0.05$ . Before statistical analysis, data of N and P concentrations, and litter mass were  $\log_{10}(x)$  transformed, and N and P resorption efficiencies were  $\arcsine(x)$  transformed, and litter allocation was  $\arcsine[\sqrt{x}]$  transformed. Data were tested for normality with Levene's test, and all transformed data followed a normal distribution. Three-way analysis of variances (ANOVAs) was used to examine the effects of N addition levels, species, plant organs and their interactions on nutrient resorption parameters. Fisher's least significant difference method was used to determine significant difference in nutrient resorption parameters of each plant organ among all treatments.

## Results

### Effects of species and plant organs on nutrient resorption parameters

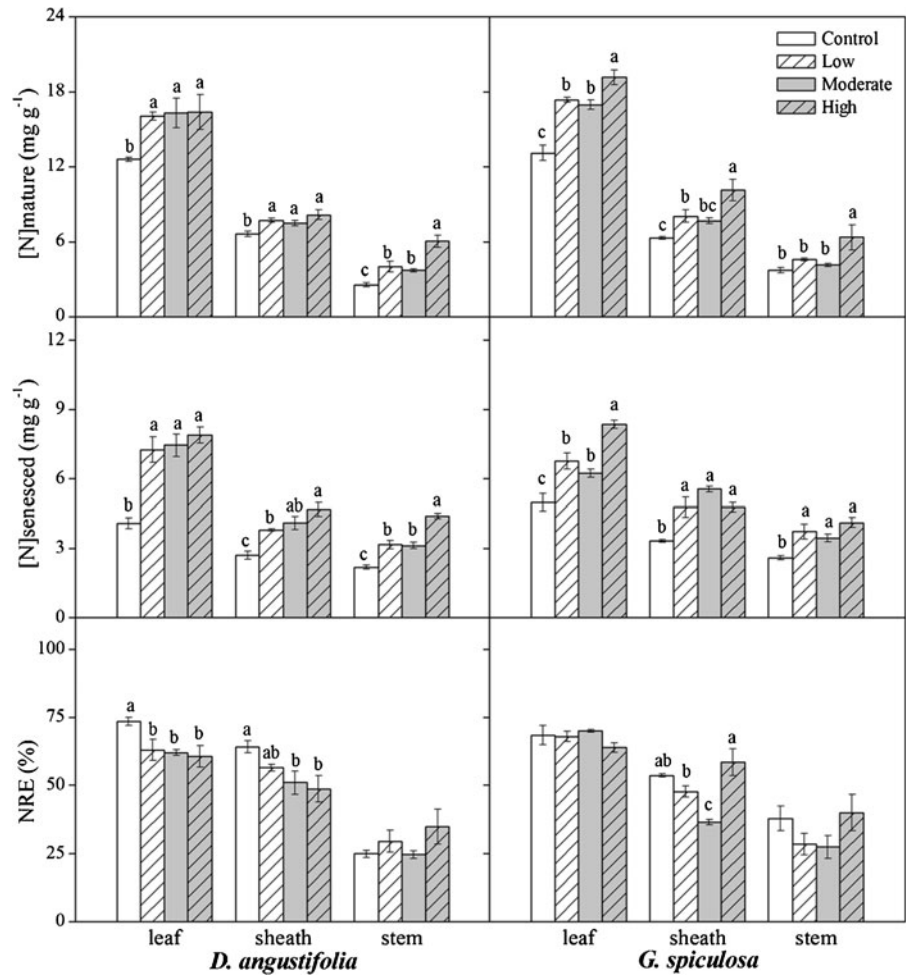
Mature and senesced organ N concentration, mature organ P concentration varied with plant species and organ types, whereas senesced organ P concentration only changed with plant organ types (Table 1). In the unfertilized treatment, among the three mature or senesced plant organs, leaf had the greatest N and P concentrations, and stem had the lowest, while sheath had the intermediate values (Figs. 1 and 2). Additionally, mature leaf ( $2.11 \text{ mg g}^{-1}$ ), sheath ( $1.94 \text{ mg g}^{-1}$ ) and stem ( $1.32 \text{ mg g}^{-1}$ ) of *G. spiculosa* in the controls had higher P concentration than the corresponding organs ( $1.88$ ,  $1.42$  and  $1.13 \text{ mg g}^{-1}$ , respectively) of *D. angustifolia* (Fig. 2).

N resorption efficiency and litter allocation only differed with plant organ types, and P resorption efficiency varied with plant species (Table 2). In addition, plant species and organ types affected litter mass (Table 2). In the control treatment, leaf, sheath and stem N resorption efficiencies, respectively, were 73.5 %, 64.1 % and 24.8 % for *D. angustifolia*, and 68.4 %, 53.6 % and 37.8 % for *G. spiculosa* (Fig. 1). Moreover, *D. angustifolia* leaf (65.3 %), sheath (52.9 %) and stem (48.7 %) in the unfertilized plots generally had lower P resorption efficiency than *G. spiculosa* (66.7 %, 71.3 % and 61.1 %, respectively) (Fig. 2, Table 2). In the control plots, leaf, sheath and stem litter masses were respectively 245, 124 and 398 mg per plant for *D. angustifolia*, and 307, 237 and 133 mg per plant for *G. spiculosa* (Fig. 3).

**Table 1** Results of three-way ANOVAs on the effects of N addition (N), species (S), plant organs (O) and their interactions on nutrient concentrations in mature and senesced organs

	Mature organ N concentration			Mature organ P concentration			Senesced organ N concentration			Senesced organ P concentration		
	d.f.	F	P	d.f.	F	P	d.f.	F	P	d.f.	F	P
N	3	54.4	<0.001	3	7.4	<0.001	3	111	<0.001	3	1.8	0.161
S	1	16.9	<0.001	1	110	<0.001	1	18.0	<0.001	1	0.6	0.429
O	2	944	<0.001	2	288	<0.001	2	330	<0.001	2	121	<0.001
N × S	3	0.5	0.704	3	0.4	0.742	3	3.1	0.035	3	1.2	0.310
N × O	6	5.1	<0.001	6	2.8	0.022	6	2.5	0.033	6	5.3	<0.001
S × O	2	2.0	0.150	2	7.8	0.001	2	5.9	0.005	2	4.8	0.013
N × S × O	6	2.3	0.047	6	0.4	0.876	6	3.0	0.015	6	1.4	0.234

**Fig. 1** Effect of N addition on N resorption parameters in a freshwater wetland of Northeast China. Control, 0 g N m<sup>-2</sup> year<sup>-1</sup>; Low, 6 g N m<sup>-2</sup> year<sup>-1</sup>; Moderate, 12 g N m<sup>-2</sup> year<sup>-1</sup>; High, 24 g N m<sup>-2</sup> year<sup>-1</sup>; [N]<sub>mature</sub>, mature organ N concentration; [N]<sub>senesced</sub>, senesced organ N concentration; NRE, N resorption efficiency. Error bars are SE (n=3). Different letters indicate significant differences (P<0.05) among treatments for each plant organ



N addition effect on nutrient concentration in mature and senesced plant organs

Mature organ N and P concentrations varied with N addition levels (Table 1). For *D. angustifolia* and *G. spiculosa*, N addition increased leaf, sheath and stem N concentrations (Fig. 1). Compared with low and moderate N addition rates, high N addition rate caused a greater N concentration for *G. spiculosa* leaf, sheath and stem, and only for *D. angustifolia* stems (Fig. 1). However, *D. angustifolia* leaf, sheath and stem P concentrations generally did not change following N fertilization, whereas low and moderate N addition level caused a general decline in P concentration for *G. spiculosa* sheath and stem (Fig. 2).

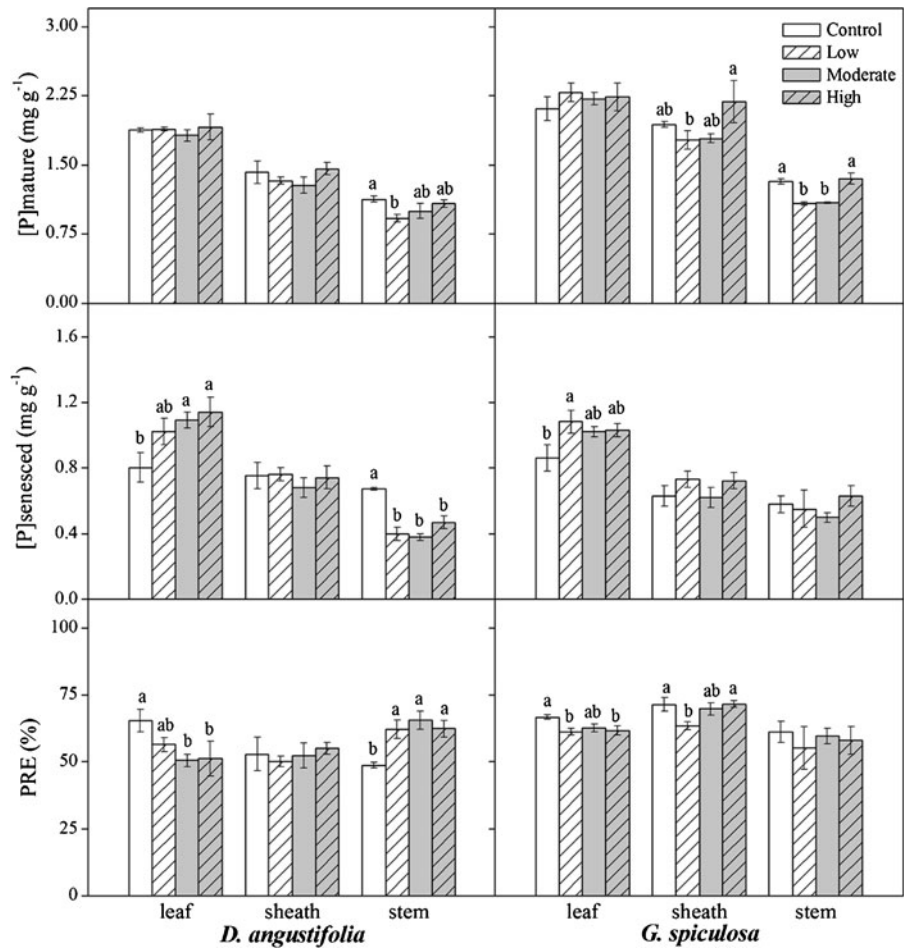
N addition affected senesced organ N concentration, but did not influence senesced organ P

concentration (Table 1). N fertilization led to an increase in N concentration in litters (low N resorption proficiency), and the effect magnitude varied with species and plant organs (Fig. 1, Table 1). Compared with low and moderate N addition levels, high N addition level generally caused a greater N concentration in senesced sheath and stem of *D. angustifolia*, and only in leaf of *G. spiculosa* (Fig. 1). In addition, N addition generally increased P concentration in senesced leaf of *D. angustifolia* and *G. spiculosa*, and decreased in senesced stem of *D. angustifolia* (Fig. 2).

N addition effect on nutrient resorption efficiencies

N addition interacted with species and plant organs to affect N resorption efficiency (Table 2). N fertilization

**Fig. 2** Effect of N addition on P resorption parameters in a freshwater wetland of Northeast China. Control, 0 g N m<sup>-2</sup> year<sup>-1</sup>; Low, 6 g N m<sup>-2</sup> year<sup>-1</sup>; Moderate, 12 g N m<sup>-2</sup> year<sup>-1</sup>; High, 24 g N m<sup>-2</sup> year<sup>-1</sup>; [P]mature, mature organ P concentration; [P]senesced, senesced organ P concentration; PRE, P resorption efficiency. Error bars are SE (n=3). Different letters indicate significant differences (P<0.05) among treatments for each plant organ



generally decreased *D. angustifolia* leaf and sheath N resorption efficiency, while only low and moderate N addition levels caused a decline in sheath N resorption efficiency for *G. spiculosa* (Fig. 1). However, N addition and plant organs produced an

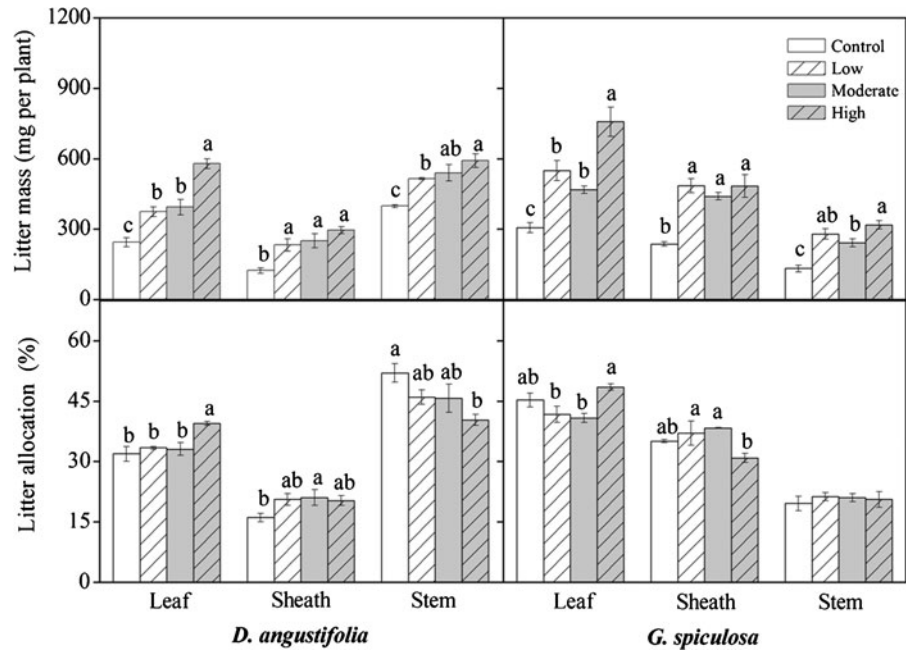
interactive effect on P resorption efficiency (Table 2). Specifically, N addition generally decreased leaf P resorption efficiency for *D. angustifolia* and *G. spiculosa*, and increased for *D. angustifolia* stem (Fig. 2).

**Table 2** Results of three-way ANOVAs on the effects of N addition (N), species (S), plant organs (O) and their interactions on nutrient resorption efficiency, litter mass and allocation

	N resorption efficiency			P resorption efficiency			Litter mass			Litter allocation		
	d.f.	F	P	d.f.	F	P	d.f.	F	P	d.f.	F	P
N	3	6.7	0.001	3	0.8	0.490	3	94.8	<0.001	3	0.1	0.989
S	1	0.1	0.728	1	26.7	<0.001	1	1.4	0.247	1	0.1	0.875
O	2	212	<0.001	2	0.7	0.520	2	52.9	<0.001	2	104	<0.001
N × S	3	1.8	0.165	3	1.0	0.410	3	3.5	0.022	3	0.2	0.996
N × O	6	3.2	0.010	6	2.7	0.023	6	7.5	<0.001	6	6.5	<0.001
S × O	2	5.5	0.007	2	12.7	<0.001	2	160	<0.001	2	360	<0.001
N × S × O	6	3.1	0.011	6	1.7	0.148	6	0.8	0.546	6	4.1	0.002



**Fig. 3** Effect of N addition on litter mass and allocation in a freshwater wetland of Northeast China. Control, 0 g N m<sup>-2</sup> year<sup>-1</sup>; Low, 6 g N m<sup>-2</sup> year<sup>-1</sup>; Moderate, 12 g N m<sup>-2</sup> year<sup>-1</sup>; High, 24 g N m<sup>-2</sup> year<sup>-1</sup>. Error bars are SE ( $n=3$ ). Different letters indicate significant differences ( $P<0.05$ ) among treatments for each plant organ



#### N addition effect on litter mass and allocation

N addition interacted with plant organs or species to affect litter mass (Table 2). N fertilization increased leaf, sheath and stem litter mass for *D. angustifolia* and *G. spiculosa* (Fig. 3). Compared with low and moderate N addition rates, high N addition rate generally had greater litter mass for leaves and stems (Fig. 3). In addition, N addition, species and plant organs produced an interaction on litter allocation (Table 2). Compared with the controls, low, moderate and high N fertilization rates generally caused lower litter allocation to stems for *D. angustifolia*, and greater to sheaths (Fig. 3). Moreover, *D. angustifolia* under high N addition level had higher leaf litters than those under other three treatments (Fig. 3). For *G. spiculosa*, low and moderate N fertilization rates decreased the proportion of leaf litters, and increased the proportion of sheath litters, while high N fertilization rate caused a reverse pattern in litter allocation between leaves and sheaths (Fig. 3).

#### Discussion

##### Responses of nutrient resorption efficiency and proficiency to N addition

Our data partly supported the hypothesis that N addition caused a decline in N resorption efficiency.

Increased N availability only decreased N resorption efficiency for *D. angustifolia* leaf and sheath and *G. spiculosa* sheath, albeit there was an increase in N concentration of mature organs. Globally, nutrient resorption efficiency decreased with increasing green leaf nutrients (Kobe et al. 2005; Vergutz et al. 2012). However, in the previous fertilization experiments, the effect of increased N availability on leaf N resorption efficiency was species-specific (e.g. van Heerwaarden et al. 2003b; Lü and Han 2009; Norris and Reich 2009). In this study, we also observed that N resorption efficiency of the two dominant species responded differentially to N enrichment regarding certain plant organ (Fig. 1). More notably, leaf, sheath and stem responses to N addition were idiosyncratic for the same plant species. Our findings suggest that N enrichment effect on N resorption efficiency varies with species and plant organs in temperate freshwater wetlands, and also highlight that, similar to leaves, there is no nutritional control on N resorption efficiency for non-leaf organs.

According to our hypothesis, increased N availability decreased N resorption proficiency in all plant organs for both *D. angustifolia* and *G. spiculosa*, which was consistent with previous studies based on fertilization experiments (van Heerwaarden et al. 2003b; Lü and Han 2009) and natural nutrient gradients (Eckstein et al. 1999; Norris and Reich 2009). These results could be explained by the increased N

concentration of mature organs and reduced or unchanged N resorption efficiency following N fertilization (Soudzilovskaia et al. 2007). Our results confirm the presumption that N resorption proficiency is more responsive than N resorption efficiency to increased N availability (van Heerwaarden et al. 2003b; Rejmánková 2005), and indicate that N resorption proficiency of leaf and non-leaf organs responds consistently to N fertilization.

In contrary to our hypothesis, increased N availability only increased P resorption efficiency and proficiency for *D. angustifolia* stem, and even caused declines for *D. angustifolia* and *G. spiculosa* leaves. In the previous studies, the relationships between N availability and leaf P resorption efficiency or proficiency were still uncertain, and P resorption efficiency and proficiency increased (Lü and Han 2009) or decreased (van Heerwaarden et al. 2003b) following N fertilization, or remained unchanged (Kozovits et al. 2007; Soudzilovskaia et al. 2007). Interestingly, regarding P resorption efficiency and proficiency, leaf, sheath and stem responded differentially to N addition in our study. These data imply that leaf and non-leaf organs should be considered to fully understand the effect of N enrichment on plant P resorption in freshwater wetland ecosystems.

Compared with low and moderate N addition treatments, high N addition level generally lowered N resorption proficiency for *D. angustifolia* sheaths and stems, and *G. spiculosa* leaves. Moreover, N addition effect on N and P resorption efficiency, and P resorption proficiency generally did not vary with fertilization rates. Therefore, our hypothesis regarding the magnitude of N addition effect on nutrient resorption parameters was partly confirmed. Huang et al. (2008) also found that senesced leaf N concentration increased with increasing N addition levels, and N resorption efficiency showed no responses in temperate grasslands. These results clarify that, except for N resorption proficiency, elevated N loading to freshwater wetlands would produce a consistent influence on N and P resorption efficiencies, and P resorption proficiency.

Nutrient resorption efficiency and proficiency in a temperate freshwater wetland

Leaf N resorption efficiency (68.4 %–73.5 %) in the control plots was higher than the global value of

62.1 % (Vergutz et al. 2012), but was comparable to the other studies conducted in temperate fen meadows (50 %–83 %, Güsewell 2005) and subarctic peatlands (40 %–80 %, van Heerwaarden et al. 2003b). However, leaf P resorption efficiency (65.3 %–66.7 %) was very similar to the global value (64.9 %) (Vergutz et al. 2012) and the other study performed in subarctic peatlands (30 %–90 %, van Heerwaarden et al. 2003b), but was lower than the values reported in Swiss fen meadows (74 %–94 %, Güsewell 2005). Moreover, sheaths had higher N (averagely 59 %) and P (averagely 62 %) resorption efficiency than the previous studies on perennial grass performed in heathlands (on average 14 % for N and 42 % for P, Aerts 1989; 24 % for N and 44 % for P, Aerts and Berendse 1989), whereas stems (averagely 31 % for N and 55 % for P) generally had lower values than the earlier studies conducted in boreal and subarctic regions (66 % for N and 69 % for P, Aerts 1989; 68 % for N and 72 % for P, Aerts and Berendse 1989; 48 % for N and 56 % for P, Freschet et al. 2010). Notably, sheath and stem respectively contributed 16–20 % and 5–8 % to the total N pool resorbed from the shoot during senescence, and 15–34 % and 11–33 % to the P pool (data not shown). Lü et al. (2012) also found that culms (including sheath and stem) of four dominant grasses of Northern Chinese steppes accounted for 17–36 % of the N pool resorbed from aboveground senescing parts. Our results suggest that plants in temperate wetlands have great nutrient resorption efficiency, and also highlight that non-leaf organs is substantially important for plant nutrient resorption and whole-plant nutrient budget in this ecosystem, especially for P.

In the control treatments, mean leaf litter N concentration ( $4.53 \text{ mg g}^{-1}$ ) was lower than the global mean value ( $10.0 \text{ mg g}^{-1}$ ), and P concentration ( $0.83 \text{ mg g}^{-1}$ ) was greater than the global value ( $0.70 \text{ mg g}^{-1}$ ) (Yuan and Chen 2009b). According to the criteria about complete and incomplete resorption proficiency for the leaves of deciduous species (Killingbeck 1996), we found that plants in this ecosystem had a complete N resorption proficiency and an incomplete P resorption proficiency. This pattern confirmed the earlier findings that plant growth in this ecosystem was N-limited rather than P-limited (Zhang et al. 2007; Song et al. 2011a).

In this study, *D. angustifolia* had greater N resorption proficiency than *G. spiculosa*, and thus lower litter N concentration (Fig. 1), whereas *D. angustifolia* had lower sheath and stem P resorption proficiency than

*G. spiculosa*, and thus lower greater P concentration (Fig. 2). Moreover, litter mass and allocation among leaf, sheath and stem varied with species (Fig. 3). Compared with *G. spiculosa*, *D. angustifolia* produced more stem litters with low nutrient concentration, and less leaf and sheath litters with high nutrient concentration. Since litter quality (e.g. N, P and lignin concentrations) and quantity is the key factor controlling nutrient return to soils via litter decomposition (Freschet et al. 2012; Mao and Zeng 2012), changes in community structure and composition would exert a strong influence on ecosystem decomposition and nutrient cycling in temperate freshwater wetlands.

#### Implications for C and nutrient cycles in the ecosystem

This study has examined the responses of nutrient resorption parameters to N addition and provides insights into the changes in ecosystem C and nutrient cycles in the context of increased N availability. On the one hand, decreased N resorption proficiency induced by N addition increased litter N concentration and hence substrate quality. Indeed, increased N availability stimulated litter decomposition and nutrient release in freshwater marshes of Northeast China (Song et al. 2011b). Moreover, N addition increased litter mass and altered litter allocation among leaf, sheath and stem. Considering that species interactions during litter mixture decomposition vary with litter mixing proportion (Mao and Zeng 2012) and interspecific variation in N concentration among component litters (Rosemond et al. 2010), N enrichment would alter litter-mixing interaction, and thus litter decomposition and concomitant nutrient release. Nevertheless, enhanced litter N concentration coupled with increased litter mass would cause an increase in the amount of N returned to the soils, and produce a positive feedback to soil N availability. On the other hand, increased N availability may make ecosystem become P-limited. Consequently, *G. spiculosa* may gain an advantage over *D. angustifolia* in P-limited wetland ecosystems, because of the high P resorption efficiency (Güsewell 2005). In this study, we did not quantitatively assess the changes in species composition, but cover estimates suggested that *G. spiculosa* increased following 7 years of N addition, and *D. angustifolia* decreased (data not shown). Compared with *D. angustifolia*, *G. spiculosa* can produce more leaf and sheath litters with greater nutrient concentration, and

less stem litters with lower nutrient concentration. Increased dominance of *G. spiculosa* following N fertilization may stimulate litter decomposition and nutrient release in wetlands. Our results emphasize that increased N availability would alter nutrient resorption and thus produce a substantial influence on plant-mediated C and nutrient cycles in temperate freshwater wetland ecosystems.

#### Conclusions

This study is the first, to our knowledge, to simultaneously examine the responses of leaf and non-leaf (sheath and stem) organ nutrient resorption to increased N availability. Our results showed that N addition had inconsistent influences on N and P resorption efficiencies and P resorption proficiency, and the effects varied with species and plant organs. However, for both leaf and non-leaf organs, 7 years of N fertilization decreased N resorption proficiency and increased litter mass. Given the potential increase in N availability in temperate wetlands as a result of enhanced agricultural fertilization application and atmospheric N deposition, our study provides critical insights into possible future changes in plant internal nutrient resorption, litter quality and quantity and thus ecosystem C and nutrient cycles.

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