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Effects of Nitrogen Addition on Plant Functional Traits in Freshwater Wetland of Sanjiang Plain, Northeast China

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Abstract: To clarify the responses of plant functional traits to nitrogen (N) enrichment, we investigated the whole-plant traits (plant height and aboveground biomass), leaf morphological (specific leaf area (SLA) and leaf dry mass content (LDMC)) and chemical traits (leaf N concentration (LNC) and leaf phosphorus (P) concentration (LPC)) of *Deyeuxia angustifolia* and *Glyceria spiculosa* following seven consecutive years of N addition at four rates (0 g N/(m^2·yr), 6 g N/(m^2·yr), 12 g N/(m^2·yr) and 24 g N/(m^2·yr)) in a freshwater marsh in the Sanjiang Plain, Northeast China. The results showed that, for both *D. angustifolia* and *G. spiculosa*, N addition generally increased plant height, leaf, stem and total aboveground biomass, but did not cause changes in SLA and LDMC. Moreover, increased N availability caused an increase in LNC, and did not affect LPC. Thus, N addition decreased leaf C∶N ratio, but caused an increase in leaf N∶P ratio, and did not affect leaf C∶P ratio. Our results suggest that, in the mid-term, elevated N loading does not alter leaf morphological traits, but causes substantial changes in whole-plant traits and leaf chemical traits in temperate freshwater wetlands. These may help to better understand the effects of N enrichment on plant functional traits and thus ecosystem structure and functioning in freshwater wetlands.

Keywords: nitrogen addition; *Deyeuxia angustifolia*; *Glyceria spiculosa*; leaf chemical traits; leaf morphological traits; whole-plant traits; Sanjiang Plain

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1 Introduction

Plant functional traits reflect the adaptation of plants to environmental changes and trade-offs among different functions within a plant, and strongly control ecosystem structure and functioning (Díaz *et al*., 1998; Wright *et al*., 2004; Westoby and Wright, 2006). In recent years, some easily-measured ('soft') traits, such as plant height, specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen (N) concentration (LNC) and leaf phosphorus (P) concentration (LPC) (Hodgson *et al*., 1999), have been widely used to predict the responses of plants to environmental changes (Lavorel and Garnier, 2002; Shipley, 2006). Generally, these 'soft' traits correlate tightly with the 'hard' traits, such as photosynthetic capacity, species diversity, plant primary productivity, and ecosystem carbon (C) and nutrient cycles (Craine *et al*., 2002; Shipley, 2006; De Deyn *et al*., 2008; Moles *et al*., 2009; Jin *et al*., 2011).

In recent decades, human activities have approximately doubled the rate of reactive N input to the Earth's land surface, largely via agricultural fertilization and

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combustion of fossil fuel (Vitousek *et al.*, 1997). Moreover, climate warming would accelerate net N mineralization and increase soil N availability, especially in the northern mid- and high- latitudes (Rustad *et al.*, 2001). Increased N loading may exert strong influences on plant functional traits, because of the N limitation of plant growth globally (Lebauer and Treseder, 2008). It has been well-documented that increased N availability stimulates plant growth, and thus increases plant height and net primary productivity (Xia and Wan, 2008). However, previous N-addition experiments have yielded ambiguous results regarding most ′soft′ plant functional traits (Chiang *et al.*, 2000; Knops and Reinhart, 2000; Feller *et al.*, 2007; Chen *et al.*, 2010; Bubier *et al.*, 2011; Ren *et al.*, 2011). Moreover, most N-addition experiments have lasted for less than five years, and only have examined the short-term effects of N enrichment on plant functional traits. Indeed, N addition effects on plant functional traits may vary with experimental duration (Güsewell *et al.*, 2002). Given the important roles of plant functional traits in ecosystem structure and functioning, additional studies are needed to identify mid-term or long-term patterns in plant functional trait responses to N enrichment.

The Sanjiang Plain, located in the eastern Heilongjiang Province of Northeast China, includes one of the largest freshwater marshes in China (Zhao, 1999), with the marsh area of 8.10×10^5 ha in 2005 (Wang *et al.*, 2011). In the recent decades, more than half of the freshwater marshes have been drained and converted into agricultural lands in this region (Wang *et al.*, 2011). Therefore, N loading of natural wetlands has been increasing as a result of fertilizer application in the adjacent agricultural lands. Previous studies have found that plant net primary production was limited by N availability in the freshwater marshes in this region (Xu *et al.*, 2006; Zhang *et al.*, 2007). Will increased N inputs to freshwater wetlands alter plant functional traits? To answer the question, we established an N-addition experiment in 2005 in a freshwater marsh in the Sanjiang Plain of Northeast China, and investigated the changes in plant height, leaf, stem and aboveground biomass, SLA, LDMC, LNC, LPC and leaf C∶N∶P stoichiometry of *Deyeuxia angustifolia* and *Glyceria spiculosa* following seven years of N addition. We hypothesized that 1) N addition would increase plant height and aboveground plant biomass due to the N limitation of plant growth in this ecosystem; 2) increased N availability would increase SLA, and decline LDMC; and 3) N addition would enhance LNC and decrease LPC, and thus cause a decline in leaf C∶N ratio, and increases in leaf C∶P and N∶P ratios.

2 Materials and Methods

2.1 Study site and experiment design

This study was conducted in a *D. angustifolia*-dominated seasonally inundated freshwater marsh 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. *D. angustifolia*-dominated freshwater marsh accounts for about 31% of the wetland area in the Sanjiang Plain (Zhao, 1999). The study site is characteristic of a temperate continental monsoon climate. Mean annual precipitation (1990–2010) is 566 mm (approximately 50% falling in July and August), and mean annual temperature (monthly value ranging from –20.4℃ in January to 21.6℃ in July) is 2.5℃. In the experimental site, *D. angustifolia* is the dominant species, and *G. spiculosa* is the main companion species.

In the study site, annual N input to freshwater marshes was about 6 g N/m^2 mainly through atmospheric N deposition, surface runoff and leaching from adjacent agricultural lands (Zhang *et al.*, 2007; Mao *et al.*, 2013). Therefore, we chose one N addition level at 6 g N/(m^2·yr) (6N) to represent current N inputs, and additional two N addition levels at 12 g N/(m^2·yr) (12N) and 24 g N/(m^2·yr) (24N) to represent future N enrichment in this wetland ecosystem. Therefore, there were four treatments (control, 6N, 12N and 24N) in the present study. In 2004, we selected 12 plots of 1 m × 1 m in a *D. angustifolia*-dominated freshwater marsh; for each plot, polyvinyl chloride frame (1 m × 1 m, 0.5 m depth) was established to avoid horizontal and lateral loss of the added N. These plots were separated from each other by a 1 m buffer zone, and boardwalks were installed to minimize site disturbance during sampling. The experiment was established in 2005, and three replicate plots were randomly assigned to each treatment. In each year, N fertilizer (NH_4NO_3) was divided into nine equal doses, dissolved in 1 L surface marsh water and applied biweekly from May to September. Simultaneously, control plots were only treated with the same volume of surface marsh water.

2.2 Field sampling and measurement

In late July 2011, we randomly selected 10 plants for *D. angustifolia* and *G. spiculosa* at each plot, respectively, and determined the height of each plant by measuring the distance from the basal stem to the natural crown. After the measurement of plant height, the whole shoot of each plant was collected and transported to the laboratory for determination of other functional traits. For each sampled plant, the total leaf number produced was measured by counting intact green leaves, dead leaves and leaf scars (representing lost leaves) (Whitman and Aarssen, 2010). Meanwhile, three fully expanded leaves per shoot were collected and used for determination of SLA and LDMC (Cornelissen *et al.*, 2003). These leaves were rehydrated for 12 h, weighed, and scanned digitally. Leaf area was measured using Adobe Photoshop 7.0 (Adobe Systems, Inc., San Jose, CA). Subsequently, these leaves were oven-dried at 60℃ to a constant mass and weighed. Stem was also oven-dried for determination of biomass. Leaf biomass produced per plant (mg/plant) was adjusted to take account of lost leaves and determined by multiplying the mean leaf dry mass with the leaf number (Whitman and Aarssen, 2010). Specific leaf area ($cm^2/(g·leaf)$) was calculated by dividing leaf area to its dry mass, and LDMC (mg/g) was assessed by dividing the leaf dry mass by its water-saturated fresh mass.

For each species, we also sampled 30 green leaves (including leaf blade and sheath) for measuring C, N and P concentrations (Cornelissen *et al.*, 2003). Leaf samples were oven-dried, ground and stored for measurement of C, N and P concentrations. Leaf C concentration was assessed by dry combustion using a multi N/C 2100 analyzer (Analytik Jena, Germany). Leaf N and P concentrations were determined by colorimeter analysis following digestion with H_2SO_4-H_2O_2 (Temminghoff and Houba, 2004). Leaf C, N and P concentrations were expressed on a mass basis.

2.3 Statistical analyses

All data were tested for normality using Levene′s test before statistical analysis, and non-normal data were log-transformed. When data did not follow a normal distribution after transformation, data were analyzed using non-parametric test. Two-way analysis of variance was used to assess the effects of N addition, species and their interaction on plant functional traits. Fisher′s least significant difference method was used for multiple comparisons of plant functional traits among treatments. Statistical analyses were performed using SPSS 13.0 for Windows and the accepted significance level was α = 0.05.

3 Results

3.1 Effect of N addition on whole-plant traits

Nitrogen addition and species independently had significant influences on plant height, leaf biomass and stem biomass, and only N addition significantly affected individual aboveground biomass (Table 1). For both *D. angustifolia* and *G. spiculosa*, N addition increased plant height, leaf biomass, stem biomass and total aboveground biomass (Fig. 1). Compared with the treatments 6N and 12N, 24N generally had higher leaf biomass, stem biomass and total aboveground biomass for the two marsh species. However, N addition only increased leaf/stem ratio for *D. angustifolia*, but had no effect for *G. spiculosa*. Moreover, *D. angustifolia* in the treatment 24N generally had higher leaf/stem ratio than those in the treatments 6N and 12N.

3.2 Effect of N addition on leaf morphological traits

Leaf area, leaf dry mass, LDMC, leaf number and SLA significantly varied with species, and N addition only had significant effects on leaf area, leaf dry mass and leaf number (Table 1). N addition significantly increased

Table 1 Results (*p*-values) of two-way ANOVAs on effects of N addition (N), species (S) and their interaction on plant functional traits

	Plant height	Leaf biomass	Stem biomass	Aboveground biomass	Leaf/stem ratio	Leaf area	Leaf number	Leaf dry mass	SLA	LDMC
N	< 0.001	< 0.001	< 0.001	< 0.001	0.641	< 0.001	< 0.001	< 0.001	0.372	0.922
S	0.001	< 0.001	< 0.001	0.320	< 0.001	0.008	< 0.001	< 0.001	< 0.001	< 0.001
N×S	0.439	0.178	0.647	0.163	0.404	0.176	0.221	< 0.001	0.212	0.023

Notes: SLA, specific leaf area; LDMC, leaf dry mass matter

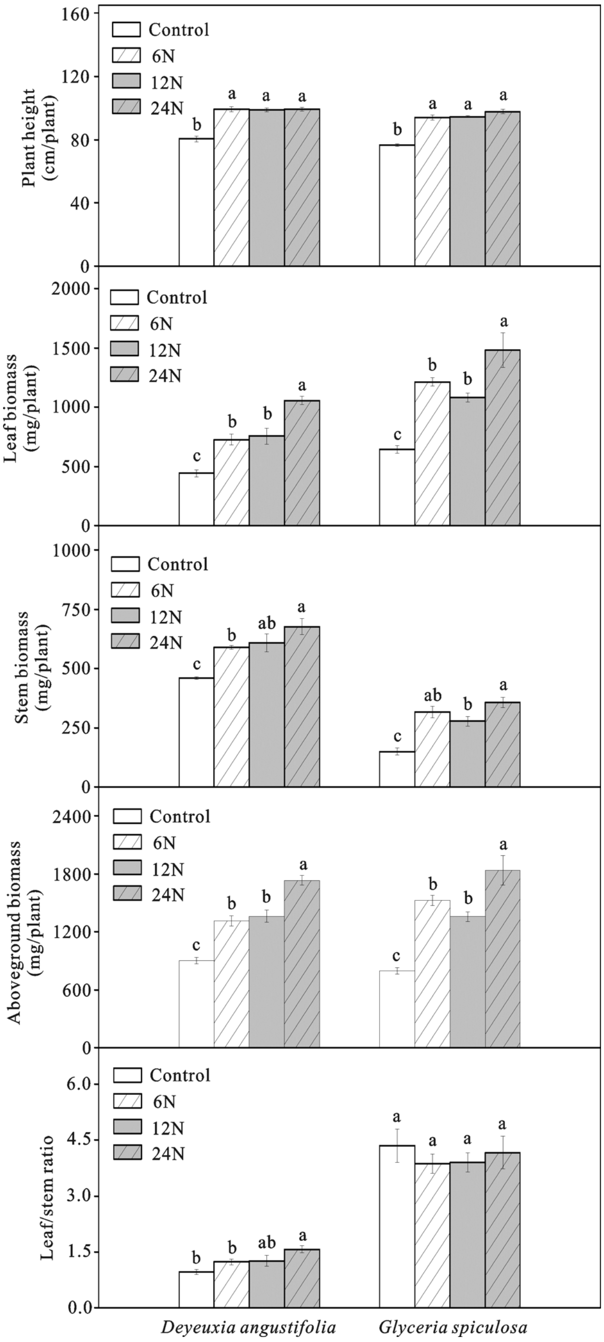

Fig. 1 Effect of N addition on whole-plant traits in a freshwater wetland of Northeast China. Control, 0 g N/(m^2·yr); 6N, 6 g N/(m^2·yr); 12N, 12 g N/(m^2·yr); 24N, 24 g N/(m^2·yr). Error bars are SE (n = 3). Different letters indicate significant differences ($p < 0.05$) in plant traits among treatments for each species

leaf area and leaf dry mass for both *D. angustifolia* and *G. spiculosa*, and did not cause a significant change in SLA (Fig. 2). Increased N inputs did not significantly affect LDMC for *D. angustifolia*, but for *G. spiculosa*, treatment 24N had lower LDMC than the control (Fig. 2). In addition, N addition increased leaf number for *G. spiculosa*, and treatment 24N had higher leaf number than the treatments 6N and 12N (Fig. 2). However, only treatment 24N caused an increase in leaf number for *D. angustifolia* (Fig. 2).

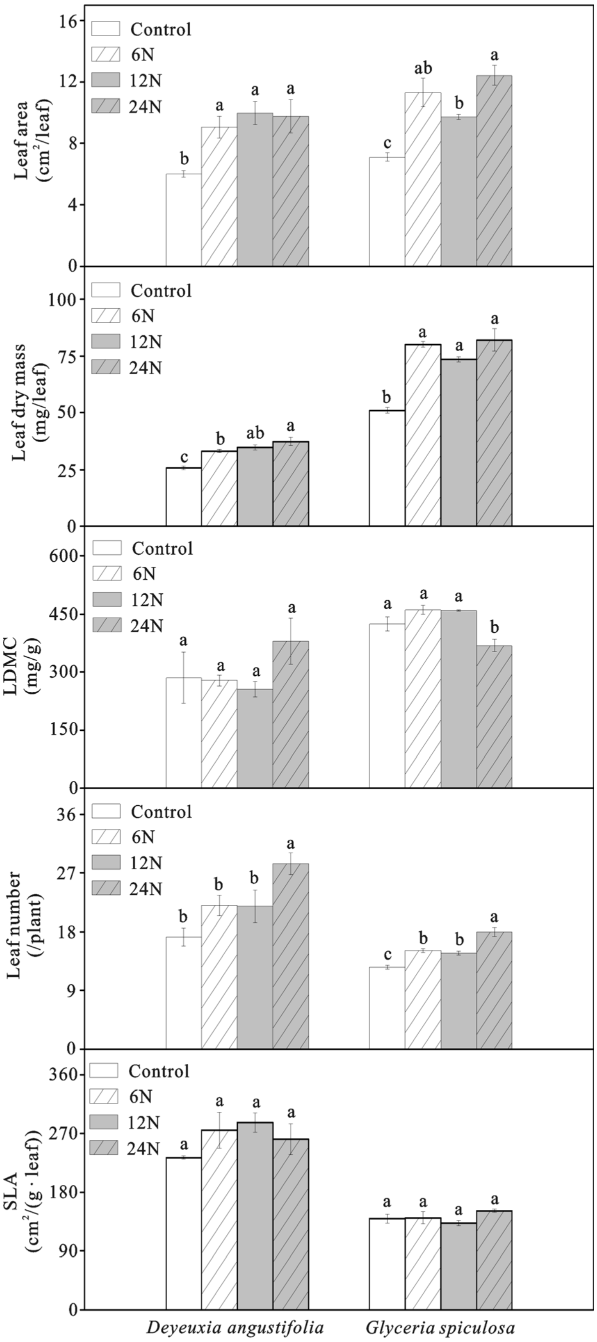

Fig. 2 Effect of N addition on leaf morphological traits in a freshwater wetland of Northeast China. Control, 0 g N/(m^2·yr); 6N, 6 g N/(m^2·yr); 12N, 12 g N/(m^2·yr); 24N, 24 g N/(m^2·yr); LDMC, leaf dry matter content; SLA, specific leaf area. Error bars are SE (n = 3). Different letters indicate significant differences ($p < 0.05$) in plant traits among treatments for each species

3.3 Effect of N addition on leaf chemical traits

Leaf N concentration did not change with species, whereas LPC varied with species (Table 2). For both *D. angustifolia* and *G. spiculosa*, N addition increased LNC, but did not produce a significant impact on LPC (Table 2; Fig. 3). Compared with the control treatment, leaves of the two marsh species in the treatments 6N, 12N and 24N had lower C ∶ N ratio, and higher N ∶ P ratio (Fig. 4). *G. spiculosa* under the treatment 24N had greater LNC and lower leaf C ∶ N ratio than those under 6N and 12N (Figs. 3 and 4). In addition, among all treatments, there was no significant difference in leaf C ∶ P ratio for the two species (Fig. 4).

Table 2 Results (*p*-values) of two-way ANOVAs on effects of N addition (N), species (S) and their interaction on leaf C ∶ N ∶ P stoichiometry

	LNC	LPC	C ∶ N ratio	C ∶ P ratio	N ∶ P ratio
N	< 0.001	0.325	< 0.001	0.287	< 0.001
S	0.480	< 0.001	0.461	< 0.001	< 0.001
N×S	0.192	0.903	0.322	0.868	0.374

Notes: LNC, leaf N concentration; LPC, leaf P concentration

4 Discussion

As hypothesized, N addition caused increases in plant height, leaf biomass, stem biomass and total individual aboveground biomass for the two marsh species (*D. angustifolia* and *G. spiculosa*). Our results were consistent with many previous N addition studies conducted in wetlands; they reported that increased N availability enhanced plant net primary production (Güsewell *et al.*, 2002; Xu *et al.*, 2006; Macek and Rejmánková, 2007; Iversen *et al.*, 2010). In contrary, some studies observed that N addition did not stimulate plant growth and increase plant biomass in wetland ecosystems (Chiang *et al.*, 2000; Feller *et al.*, 2007). These inconsistent results may be explained by the differences in species, N addition rates, experimental duration and the type of nutrient limitation. Increased plant aboveground biomass following N addition indicated that plant growth was limited by N availability in this wetland (Lebauer and Treseder, 2008). Moreover, leaf, stem and total aboveground biomass increased with elevating N addition levels. Our results suggest that increased N loading caused by agricultural activities would exert a positive effect on plant aboveground biomass in temperate freshwater wetlands.

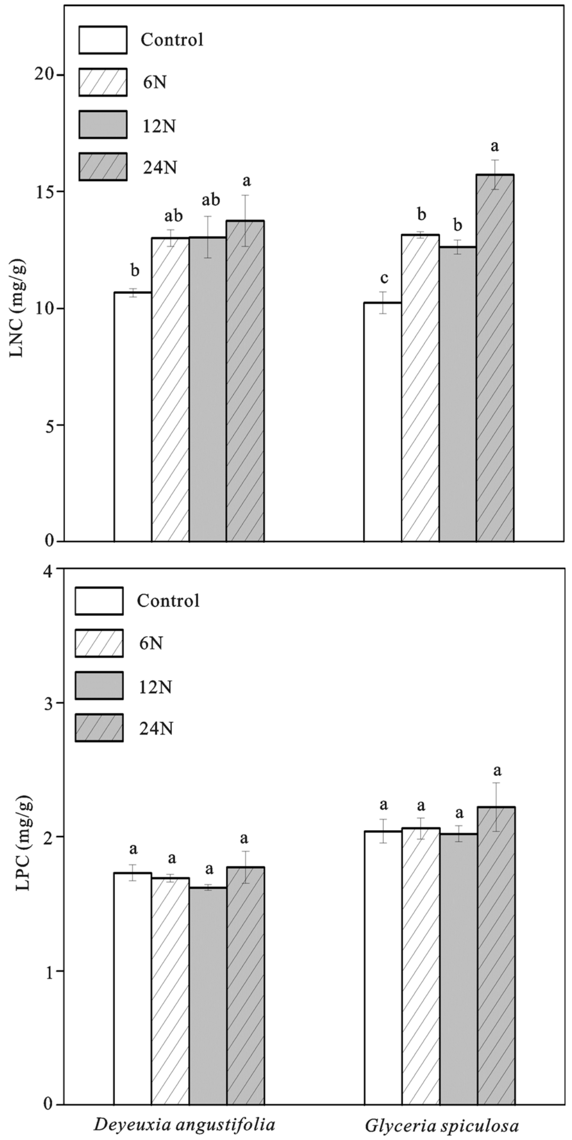

Fig. 3 Effect of N addition on leaf N (LNC) and P (LPC) concentrations in a freshwater wetland of Northeast China. Control, 0 g N/(m^2·yr); 6N, 6 g N/(m^2·yr); 12N, 12 g N/(m^2·yr); 24N, 24 g N/(m^2·yr). Error bars are SE (n = 3). Different letters indicate significant differences ($p < 0.05$) in plant traits among treatments for each species

Surprisingly, unchanged SLA and LDMC following N addition did not support the hypothesis regarding leaf morphological traits. In general, SLA is positively correlated, and LDMC is negatively correlated with light use efficiency and plant growth rate (Güsewell, 2005). Thus, competition for light induced by N addition can increase SLA (Knops and Reinhart, 2000; Bubier *et al.*, 2011), and decrease LDMC (Ren *et al.*, 2011). In the present study, we found that seven years of N addition generally did not cause significant changes in SLA and

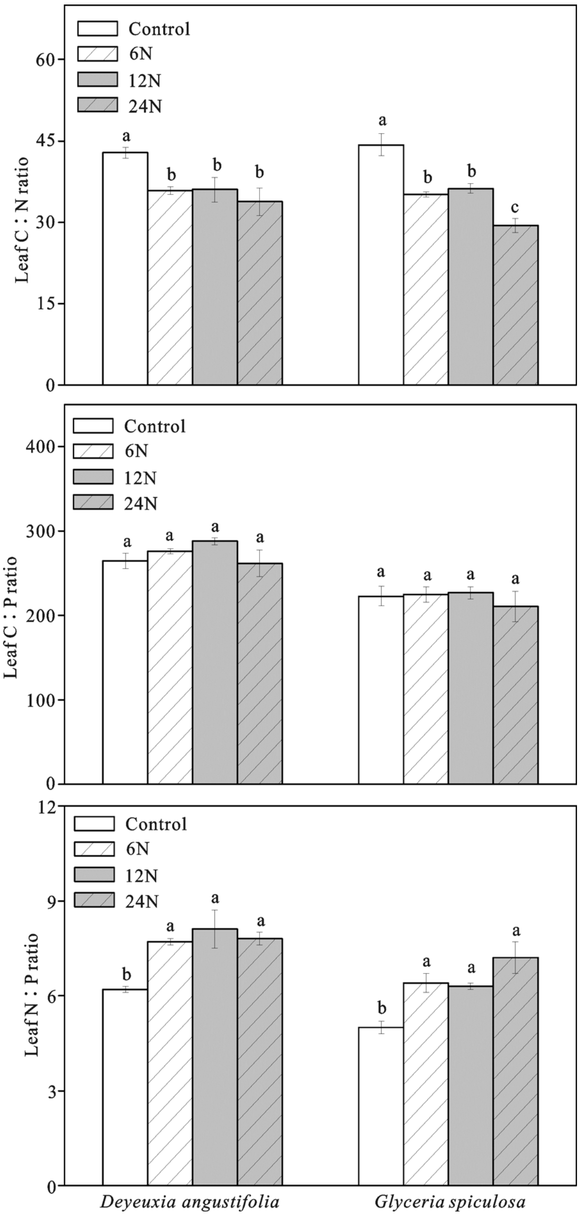

Fig. 4 Effect of N addition on leaf C ∶ N ∶ P stoichiometry in a freshwater wetland of Northeast China. Control, 0 g N/(m^{2}·yr); 6N, 6 g N/(m^{2}·yr); 12N, 12 g N/(m^{2}·yr); 24N, 24 g N/(m^{2}·yr). Error bars are SE (n = 3). Different letters indicate significant differences (p < 0.05) in plant traits among treatments for each species

LDMC for the two wetland plants (Fig. 2), which was consistent with a 9-year N addition study conducted in a peatland, Ontario, Canada (Bubier *et al.*, 2011). These results suggest that plant leaves do not exhibit morphological adjustments to mid-term N addition in wetlands.

Consistent with our third hypothesis, N enrichment increased LNC for *D. angustifolia* and *G. spiculosa* (Fig. 3), and decreased leaf C ∶ N ratio (Fig. 4). It has been well documented that N addition increased LNC and decreased leaf C ∶ N ratio (Güsewell and Koerselman, 2002; Xia and Wan, 2008; Esmeijer-Liu *et al.*, 2009). Given that LNC correlates well with leaf photosynthetic rates and leaf litter decomposition rate (Wright *et al.*, 2004; De Deyn *et al.*, 2008), increased N loading to freshwater wetlands would exert strong influences on plant-driven C and nutrient cycles.

In contrary to our hypothesis, LPC did not change following seven year of N addition (Fig. 3). Generally, it is expected that increased N availability would lower LPC due to the growth dilution effect (Güsewell and Koerselman, 2002; van Heerwaarden *et al.*, 2003). However, previous N-addition experiments did not show a consistent decrease of P concentration in leaves, and the N addition effect on LPC may vary with species (van Heerwaarden *et al.*, 2003; Kozovits *et al.*, 2007), N addition levels (Bubier *et al.*, 2011), soil fertility (Vitousek, 1998) and water availability (Lyu *et al.*, 2012). In this wetland ecosystem, the unchanged LPC may be caused by the increased plant P uptake following N addition (Fujita *et al.*, 2010), albeit there was an increase in plant biomass. Given the unchanged LPC in response to N addition, increased N availability did not affect leaf C ∶ P ratio, and increased leaf N ∶ P ratio (Fig. 4).

In our study, the average LNC (10.5 mg/g) and leaf N ∶ P ratio (5.6) in the control plots were much lower than the corresponding values (18.6 mg/g and 14.4 mg/g, respectively) reported by Han *et al.* (2005) for 753 terrestrial plants in China, whereas the average LPC (1.89 mg/g) was much higher than the value (1.21 mg/g) reported by Han *et al.* (2005). Han *et al.* (2005) pointed that soil P content in most terrestrial ecosystems in China was below the global average value, causing a low LPC for terrestrial plant species. Remarkably, we found that LPC of two wetland plants was even higher than the values reported by Reich and Oleksyn (2004) for 1251 world plant terrestrial species (1.42 mg/g) and by Güsewell and Koerselman (2002) for European wetland plants (1.02 mg/g). Given the tight correlation between leaf nutrient concentration and nutrient availability (Aerts and Chapin, 2000), these data suggested that the freshwater wetland ecosystems may be P-enriched and N-limited.

5 Conclusions

In conclusion, we examined the effects of seven years of

N addition on plant functional traits in a freshwater wetland in the Sanjiang Plain, Northeast China. Notably, plant functional traits of the two marsh species generally responded similarly to increased N availability. In the mid-term, N enrichment increased plant height, aboveground biomass and leaf N concentration, but had negligible effects on specific leaf area, leaf dry matter content and leaf P concentration. These findings would provide insights into the responses of plant-mediated C and nutrient cycling to mid-term N enrichment in temperate freshwater wetland ecosystems.

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