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RESEARCH

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Effect of shrub encroachment on leaf nutrient resorption in temperate wetlands in the Sanjiang Plain of Northeast China

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Abstract

Background: Nutrient resorption is an important plant nutrient conservation strategy in wetlands. However, how shrub encroachment alters plant nutrient resorption processes is unclear in temperate wetlands. Here, we collected green and senesced leaves of common sedge, grass, and shrub species in wetlands with high (50–65%) and low (20–35%) shrub covers in the Sanjiang Plain of Northeast China, and assessed the impact of shrub encroachment on leaf nitrogen (N) and phosphorus (P) resorption efficiency and proficiency at both plant growth form and community levels.

Results: The effects of shrub cover on leaf nutrient resorption efficiency and proficiency were identical among shrubs, grasses, and sedges. Irrespective of plant growth forms, increased shrub cover reduced leaf N resorption efficiency and proficiency, but did not alter leaf P resorption efficiency and proficiency. However, the effect of shrub cover on leaf nutrient resorption efficiency and proficiency differed between plant growth form and community levels. At the community level, leaf N and P resorption efficiency decreased with increasing shrub cover because of increased dominance of shrubs with lower leaf nutrient resorption efficiency over grasses and sedges. Accordingly, community-level senesced leaf N and P concentrations increased with elevating shrub cover, showing a decline in leaf N and P resorption proficiency. Moreover, the significant relationships between leaf nutrient resorption efficiency and proficiency indicate that shrub encroachment increased senesced leaf nutrient concentrations by decreasing nutrient resorption efficiency.

Conclusions: These observations suggest that shrub encroachment reduces community-level leaf nutrient resorption efficiency and proficiency and highlight that the effect of altered plant composition on leaf nutrient resorption should be assessed at the community level in temperate wetlands.

Keywords: Biodiversity, Freshwater marsh, Nutrient conservation strategy, Plant growth form, Species composition

Background

Plant nutrient resorption, a process that resorbs nutrients from senescing organs, is one of the most important plant nutrient conservation strategies (Aerts and Chapin 2000; Brant and Chen 2015). Plant nutrient resorption capacity is often characterized by nutrient resorption efficiency and proficiency (Killingbeck 1996; van Heerwaarden et al. 2003). Nutrient resorption efficiency is defined as the proportion of nutrients resorbed from senescing organs and can reflect the genetic adaptation of plants to substrate nutrient availability (Vergutz et al. 2012; Yuan and Chen 2015). Plants with greater nutrient resorption efficiency are less dependent on exterior nutrient availability and thus have higher plant fitness and competition ability (Eckstein et al. 1999; Brant and Chen 2015;

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Lü et al. 2019; Liang et al. 2022). Nutrient resorption proficiency represents the absolute level to which nutrients are reduced in senesced organs and is expressed as the terminal nutrient concentrations in senesced organs (Killingbeck 1996). Plants with higher nutrient resorption proficiency have slower litter decomposition rates due to the lower litter nutrient concentrations (Aerts and Chapin 2000; Xu et al. 2020). Therefore, knowledge on the dynamics of plant nutrient resorption processes is essential to understand plant-mediated carbon (C) and nutrient cycling in terrestrial ecosystems.

Temperate wetlands are nutrient-poor ecosystems due to the slow organic matter mineralization under waterlogging and cool conditions and associated low soil nutrient availability (Jonasson and Shaver 1999; Mao et al. 2012). Accordingly, plants often develop high nutrient resorption capacity to minimize the plant dependence on soil nutrient availability (Eckstein et al. 1999; Vergutz et al. 2011). In recent decades, shrub encroachment has widely occurred in temperate wetlands primarily because of drainage, climate warming, and drought events (Saintilan and Rogers 2015; Carlson et al. 2018; Zhang et al. 2021a). Shrub encroachment is often observed to accelerate microbial decomposition of soil organic matter mainly by increasing the quantity and quality of plant litter inputs and altering microclimate in northern high latitudes, leading to increased nutrient availability in soils (Buckeridge et al. 2010; DeMarco et al. 2014). Because plant nutrient resorption is highly dependent on soil nutrient availability (Aerts and Chapin 2000; Yuan and Chen 2015; You et al. 2021), shrub encroachment is believed to change plant nutrient resorption efficiency and proficiency at the species/plant growth form level. Moreover, the responses of plant nutrient resorption to shrub encroachment may be species-specific because of the interspecific differences in nutrient use strategies (Eckstein et al. 1999; Brant and Chen 2015; Zhang et al. 2021b). Therefore, further studies are needed to clarify the plant nutrient resorption responses to shrub encroachment at the species/plant growth form level in temperate wetlands.

At the community level, plant nutrient resorption is co-regulated by the intrinsic plant nutrient resorption ability and species dominance (Richardson et al. 2005; Mao et al. 2015). In temperate wetlands, the increased abundance of deciduous shrubs such as *Betula* and *Salix* species is observed to reduce the dominance of sedges and grasses (Zhang et al. 2021a). Previous studies have found that plant composition structure may exert a stronger influence on community-level plant nutrient resorption than intraspecies variations of plant nutrient resorption because of the substantial differences in plant nutrient resorption among species/plant growth forms (Lü et al. 2020; Zhang et al. 2021b). Moreover, the responses of plant nutrient resorption to shrub encroachment-induced changes in soil nutrient availability may be different among shrubs, grasses, and sedges (Vergutz et al. 2012; Brant and Chen 2015). Therefore, knowledge on the dynamics of plant nutrient resorption at the species or plant growth form level could not clearly reflect the effect of shrub encroachment on plant nutrient resorption at the community level. Understanding community-level response is essential for accurately assessing and predicting the consequence of shrub encroachment on plant nutrient resorption processes in temperate wetlands.

The Sanjiang Plain, an alluvial flood plain in the Heilongjiang Province, covers one of the largest freshwater wetlands in China. Recently, the freshwater wetlands have experienced increased dominance of shrubs at the expense of grasses and sedges in this region (Zhang et al. 2021a). In this study, we compared the differences in leaf nutrient resorption efficiency and proficiency at both plant growth form and community levels in freshwater wetlands with different shrub covers (low versus high) in the Sanjiang Plain, and used this space-for-time approach to assess the effects of shrub encroachment on plant nutrient resorption processes in temperate wetlands. We hypothesized that: (1) the effect of shrub cover on leaf nutrient resorption would differ among shrubs, grasses, and sedges; and (2) leaf nutrient resorption efficiency and proficiency at the community level would decline with increasing shrub cover.

Materials and methods

Site description and sampling

This study was conducted in freshwater wetlands in the Sanjiang Mire Wetland Experimental Station, Chinese Academy of Sciences (47°35′N, 133°31′E), which is located in the center of the Sanjiang Plain, Northeast China. The study site has a sub-humid continental monsoon climate with an average annual temperature of 2.5 °C and annual precipitation of 566 mm (Zhang et al. 2021b). Soils are developed from alluvial lacustrine sediments and belong to Histosols in the Soil Classification System developed by the United States Department of Agriculture. In the intact wetlands, the dominant species are sedges (e.g., *Carex meyeriana*, *Carex pseudocuraica*, and *Carex lasiocarpa*) and grasses (e.g., *Glyceria spiculose* and *Deyeuxia angustifolia*). In recent decades, the abundance of deciduous shrubs such as *Spiraea salicifolia*, *Salix myrtilloides*, *Salix rosmarinifolia*, *Salix floderusii*, and *Betula fruticosa* has increased in these wetlands primarily due to climate warming, artificial drainage, and drought events.

In late July 2015, we chose three spatially isolated wetlands and established one pair of plots (20 m × 20 m in size) with low (20–35%) and high (50–65%) shrub covers in each wetland. In early August, four 5 m × 5 m subplots per plot were randomly established, and the cover of species was estimated with the ground-based line-intercept method (Moffet et al. 2009). The relative cover of a certain species was obtained as the proportion of total cover in each plot. According to the results of the vegetation survey, we selected eight species (i.e., *C. lasiocarpa*, *C. meyeriana*, *C. pseudocuraica*, *G. spiculose*, *D. angustifolia*, *S. salicifolia*, *S. myrtilloides*, and *S. rosmarinifolia*) in the plots with low shrub cover, and 10 species (i.e., *C. lasiocarpa*, *C. meyeriana*, *C. humda*, *G. spiculose*, *D. angustifolia*, *S. salicifolia*, *S. myrtilloides*, *S. rosmarinifolia*, *S. floderusii*, and *B. fruticosa*) in the plots with high shrub cover.

In each plot, 50 mature and fully unfolded leaves per species were collected in early August. From early October to early November, we also sampled 50 freshly senesced leaves per species in each plot. Leaf samples were oven-dried, weighed, and milled (< 0.15 mm) for chemical analyses. In addition, five soil cores (5 cm in diameter) per plot were randomly collected in August and mixed to obtain a homogenous soil. After removing plant roots, soil samples were oven-dried at 45 °C, milled (< 0.15 mm), and stored for chemical analyses.

Chemical measurement and calculation

Leaf N and P concentrations were measured colorimetrically on a continuous-flow AutoAnalyzer (AA3, Seal, Germany) after acid digestion. Leaf mass loss correction factor (MLCF) was calculated from the difference between the dry mass of mature and senesced leaves. Soil organic C concentration was measured with the dry combustion method on a Multi N/C 2100 Analyzer (Analytik Jena, Germany), and total N and P concentrations were also measured colorimetrically on a continuous-flow AutoAnalyzer after acid digestion. In this study, we used the C:N and C:P ratios to indicate soil nutrient availability (Ordoňez et al. 2009).

At the species level, leaf nutrient resorption efficiency was quantified with the following formula (Vergutz et al. 2012):

$$\text{Nutrient resorption efficiency} = \left(1 - \frac{\text{Nmature}}{\text{Nsenesced}} \times \text{MLCF}\right) \times 100\%, \tag{1}$$

where Nmature and Nsenesced represent the nutrient concentrations in mature and senesced leaves, respectively. Leaf nutrient resorption proficiency was assessed with the nutrient concentration in senesced leaves, and the higher senesced leaf nutrient concentration indicates the lower leaf nutrient resorption proficiency. At both plant growth form and community levels, leaf nutrient resorption efficiency and proficiency were calculated from the relative cover and corresponding leaf nutrient resorption parameters of species. Detailed information on the leaf nutrient resorption parameters of the selected species is shown in Additional file 1: Table S1.

Statistical analyses

All data were assessed for normality with the Shapiro–Wilk test, and data that did not follow a normal distribution were natural log-transformed before statistical analyses. A two-way analysis of variance (ANOVA) was used to test the effects of plant growth form and shrub cover on leaf nutrient resorption parameters. A one-way ANOVA with Tukey's HSD test was conducted to compare the differences in leaf nutrient resorption parameters among plant growth forms in the same wetland. Meanwhile, the paired *t*-test was conducted to compare differences in soil properties and community-level nutrient resorption parameters between wetlands with low and high shrub covers. In addition, the simple linear regression analysis was used to assess the relationship between senesced leaf nutrient concentration and leaf nutrient resorption efficiency at the plant growth form level. All statistical analyses were performed using the SPSS 19.0 Windows package, and $P < 0.05$ was considered statistically significant.

Results

The relative covers of sedges and grasses were higher in the wetlands with low shrub cover relative to that with high shrub cover (Table 1). Wetlands with high shrub cover had lower soil organic C, total N, and total P concentrations than that with low shrub cover (Table 1). Moreover, wetlands with low shrub cover had 24.9% and 61.5% higher soil C:N and C:P ratios than those with high shrub cover, respectively (Table 1).

Leaf N and P concentrations in both mature and senesced leaves were significantly affected by plant growth form, while only senesced leaf N concentration significantly increased with elevating shrub cover (Table 2). Irrespective of shrub cover, shrubs had the greatest N concentration in mature and senesced leaves, whereas sedges had the lowest values among the three growth forms (Fig. 1). In addition, shrubs had higher mature leaf P concentration than sedges only in the wetlands with low shrub cover, although there was no significant difference in the wetlands with high shrub cover (Fig. 1). In contrast, shrubs had greater senesced leaf P concentration than sedges and grasses in all wetlands (Fig. 1).

Table 1 Effect of shrub encroachment on vegetation composition and soil organic C, total N, and total P concentrations in freshwater wetlands of Northeast China

Wetland type	**Relative cover (%)**			**Organic C**	**Total N**	**Total P**	**C:N ratio**	**C:P ratio**
	Sedge	**Grass**	**Shrub**	**mg g^{-1}**	**mg g^{-1}**	**mg g^{-1}**		
Low shrub cover	25.0 (1.1)*	48.6 (2.6)*	26.4 (3.0)	189 (2)**	8.38 (0.44)**	1.22 (0.03)*	22.6 (1.3)*	155 (5)**
High shrub cover	14.6 (1.9)	24.2 (2.3)	61.2 (3.4)*	88 (9)	4.86 (0.37)	0.91 (0.04)	18.1 (1.4)	96 (7)

Data in the parentheses are the standard error of the mean values ($n = 3$). In the same column, * and ** indicate the significant level at $P < 0.05$ and $P < 0.01$, respectively

Table 2 Effects of plant growth form and shrub cover on leaf nutrient resorption parameters in freshwater wetlands of Northeast China

Sources of variation	**Mature leaf N concentration**	**Mature leaf P concentration**	**Senesced leaf N concentration**	**Senesced leaf P concentration**	**N resorption efficiency**	**P resorption efficiency**	**N:P resorption ratio**
Plant growth form	30.1***	9.7**	40.2***	43.7***	9.2**	13.0**	8.9**
Shrub cover	0.5	0.1	28.7***	1.5	64.7***	3.3	1.7
Plant growth form × Shrub cover	0.2	1.5	0.9	1.1	0.1	0.1	0.1

*, **, and *** indicate the significant levels at $P < 0.05$, $P < 0.05$, and $P < 0.001$, respectively

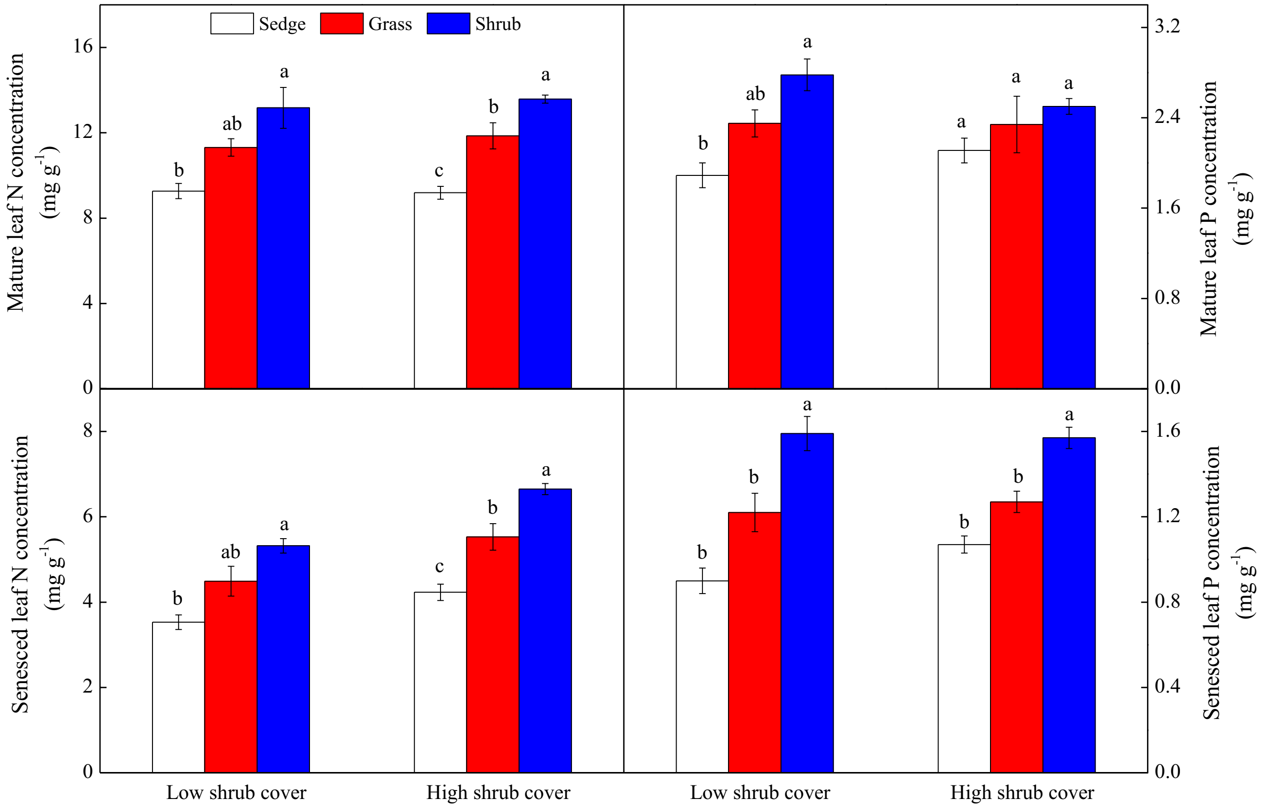

Fig. 1 Effect of shrub encroachment on leaf nutrient concentrations at the plant growth form level in freshwater wetlands of Northeast China. Error bars are the standard errors of the mean ($n = 3$). Different lowercase letters indicate the significant difference ($P < 0.05$) among plant growth forms within each wetland type

Leaf N and P resorption efficiencies were significantly affected by plant growth form, and only leaf N resorption efficiency was significantly affected by shrub cover (Table 2). Leaf N resorption efficiency showed no significant difference among shrubs, grasses, and sedges in the wetlands with low shrub cover, but was lower for shrubs than for sedges and grasses in the wetlands with high shrub cover (Fig. 2). Regardless of shrub cover, shrubs had lower leaf P resorption efficiency than sedges and grasses (Fig. 2). In addition, shrubs had higher leaf N:P resorption ratio than sedges only in the wetlands with high shrub cover (Fig. 2). At the plant growth form level, senesced leaf N and P concentrations were negatively correlated with the corresponding leaf nutrient resorption efficiency, respectively (Fig. 3).

At the community level, mature leaf N and P concentrations did not significantly vary with shrub cover in these wetlands (Table 3). However, community-level senesced leaf N and P concentrations were higher in the wetlands with high shrub cover than in the wetlands with low shrub cover (Table 3), showing that leaf nutrient resorption proficiency declined with elevating shrub cover. In addition, wetlands with low shrub cover had greater leaf N and P resorption efficiencies than that with high shrub cover (Table 3).

Discussion

For the selected three plant growth forms, shrub encroachment reduced leaf N resorption efficiency and proficiency but did not affect leaf P resorption efficiency

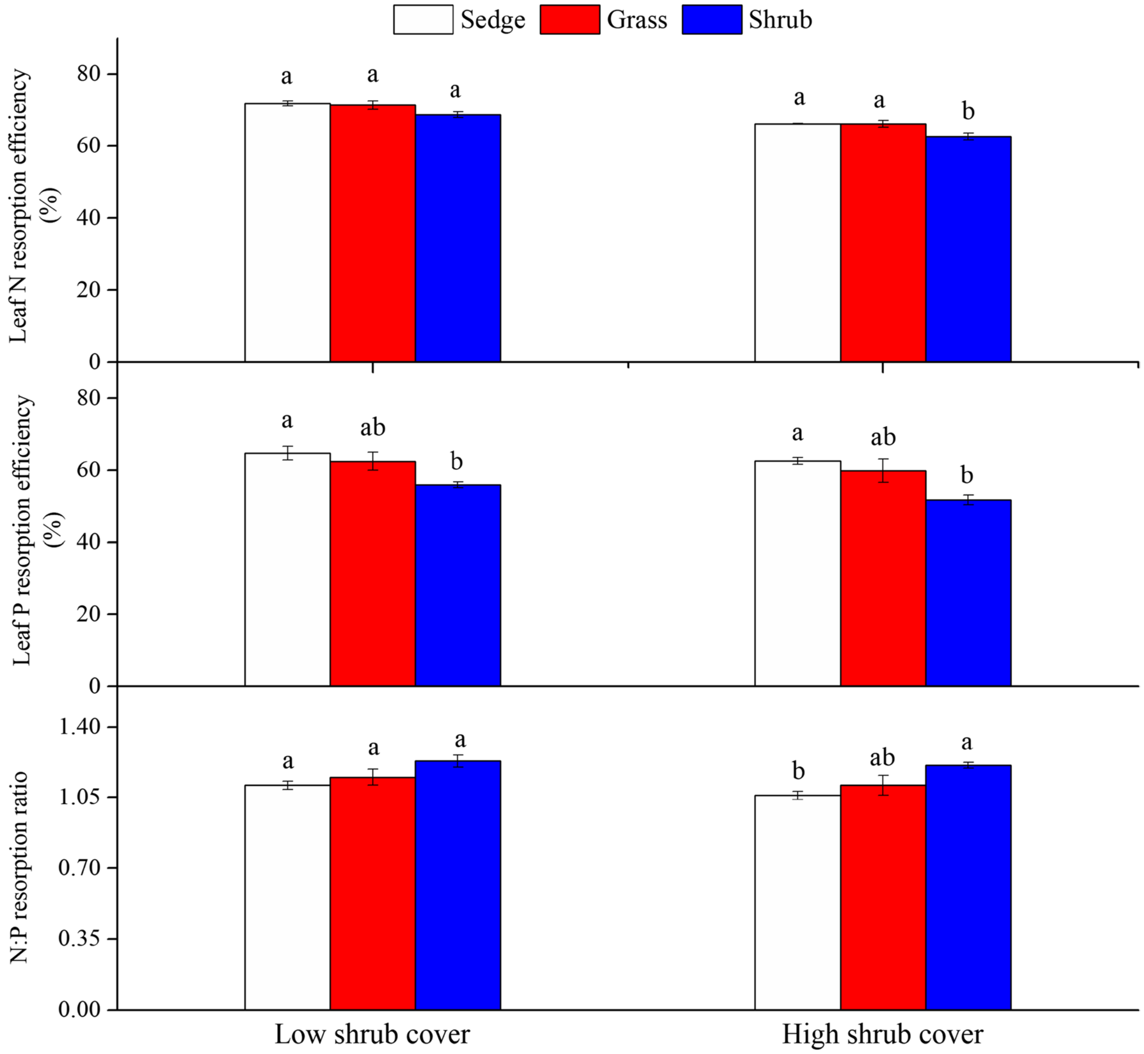

Fig. 2 Effect of shrub encroachment on leaf nutrient resorption efficiency at the plant growth form level in freshwater wetlands of Northeast China. Error bars are the standard errors of the mean ($n = 3$). Different lowercase letters indicate the significant difference ($P < 0.05$) among plant growth forms within each wetland type

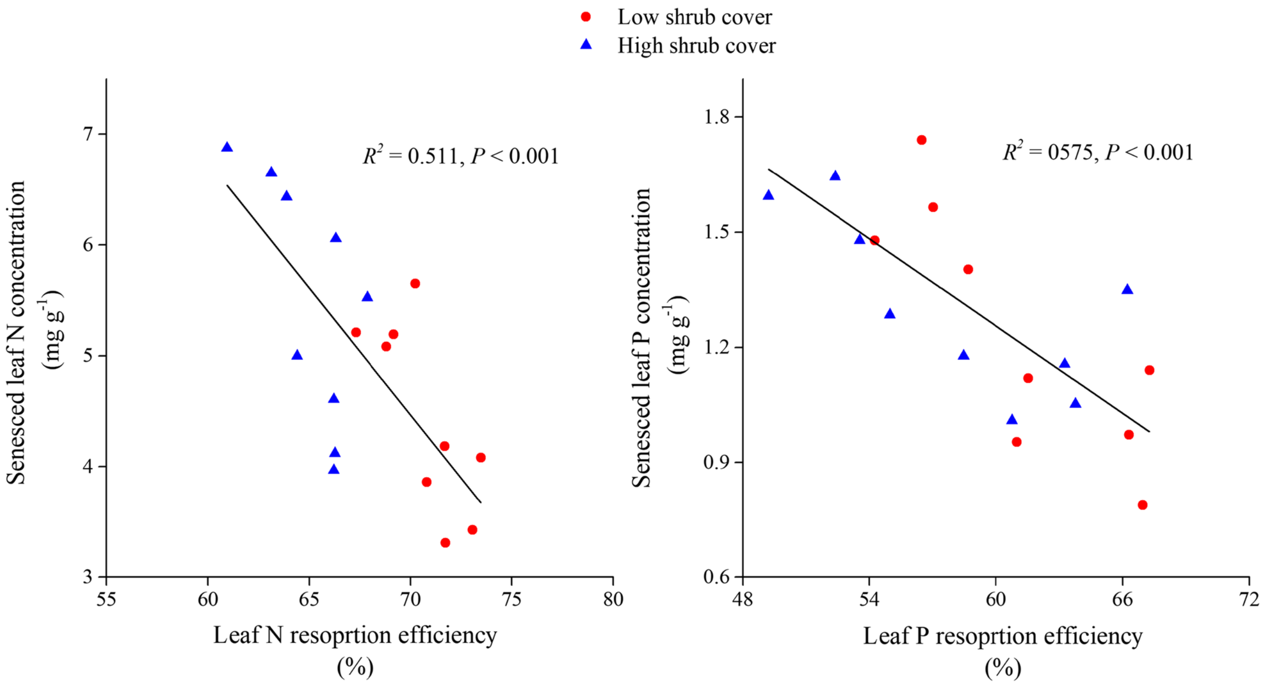

Fig. 3 The relationships between senesced leaf nutrient concentrations and leaf nutrient resorption efficiency at the plant growth form level in freshwater wetlands of Northeast China

Table 3 Effect of shrub encroachment on the community-level plant nutrient resorption parameters in freshwater wetlands of Northeast China

	Mature leaf N concentration mg g^{-1}	Mature leaf P concentration mg g^{-1}	Senesced leaf N concentration mg g^{-1}	Senesced leaf P concentration mg g^{-1}	Leaf N resorption efficiency %	Leaf P resorption efficiency %	N:P resorption ratio
Low shrub cover	11.3(0.4)	2.34(0.10)	4.48(0.17)	1.24(0.06)	70.8(0.9)*	61.2(1.4)*	1.16(0.03)
High shrub cover	12.5(0.2)	2.40(0.05)	6.00(0.09)**	1.42(0.03)*	64.1(0.7)	55.4(1.1)	1.16(0.02)

Data in the parentheses are the standard error of the mean values ($n = 3$). In the same column, * and ** indicate the significant level at $P < 0.05$ and $P < 0.01$, respectively

and proficiency in these wetlands (Figs. 1, 2). Thus, our findings did not support the hypothesis about the divergent responses of leaf nutrient resorption to shrub encroachment among shrubs, grasses, and sedges. In this study, the leaf N:P resorption ratio was above 1.0 (Fig. 2), indicating that N limits plant growth in these wetlands (Reed et al. 2012). Moreover, declined soil C:N ratio with increasing shrub cover (Table 1) showed that shrub encroachment improved soil N availability (Ordoňez et al. 2009) by enhancing soil organic matter decomposition due to the increased amount of high-quality plant litter inputs (Buckeridge et al., 2010; DeMarco et al. 2014; Zhang et al. 2021a). In general, leaf N resorption efficiency and proficiency decline with increasing soil N availability in N-limited ecosystems (Mao et al. 2012; Lü et al. 2013; Yuan and Chen 2015; You et al. 2021). Accordingly, shrub encroachment-induced declines in leaf N resorption efficiency and proficiency would be caused by the increased soil available N, despite the large variation of leaf N resorption capacity among shrubs, grasses, and sedges in these wetlands. In contrast, shrub encroachment did not alter leaf P resorption efficiency and proficiency at the plant growth form level because P is not a limiting nutrient for plant growth in these wetlands (Zhang et al. 2021b). These results suggest that leaf nutrient resorption responses to shrub encroachment are consistent among plant growth forms in temperate wetlands.

Compared with grasses and sedges, shrubs had lower leaf nutrient resorption efficiency and proficiency in these wetlands (Figs. 1, 2). Xu et al. (2021) also found that leaf N and P resorption efficiencies were lower for deciduous shrubs than for grasses and sedges in a boreal peatland of Northeast China. These interspecific patterns may be explained by the differences in nutrient use strategies and non-leaf organ biomass among shrubs, grasses, and sedges. Compared with shrubs, grasses and sedges often form a conservative nutrient use strategy to cope with low nutrient availability in temperate wetlands (Eckstein et al. 1999; Thormann 2006; Xu et al. 2021). Moreover, leaf nutrient resorption process is controlled by the amount of nutrient transfer from senesced leaves to non-leaf organs, which are mainly dependent on the biomass of non-leaf organs (Vergutz et al. 2012; Brant and Chen 2015). Compared to grasses and sedges, shrubs often have greater biomass of perennial woody organs such as roots and stems (Vergutz et al. 2012; Zhang et al., 2021a). Therefore, the relatively lower leaf nutrient resorption capacity of shrubs relative to grasses and sedges would be caused by the higher mature leaf nutrient concentrations and greater biomass of non-leaves in temperate wetlands.

In accordance with the second hypothesis, community-level leaf nutrient resorption efficiency and proficiency declined with increasing shrub cover (Table 3), although leaf P resorption efficiency and proficiency remained unchanged at the plant growth form level (Figs. 1, 2). In general, community-level nutrient resorption is controlled by the nutrient resorption of each species and species dominance (Lü et al. 2021; Zhang et al. 2021b). In these wetlands, shrubs had lower leaf N and P resorption capacity than grasses and sedges (Figs. 1, 2). However, shrub encroachment only reduced leaf N resorption efficiency and proficiency of the selected three growth forms (Figs. 1, 2). Therefore, the underlying mechanisms causing the changes in community-level leaf N and P resorption processes would be different in these wetlands. In the present study, the declined community-level leaf N resorption efficiency and proficiency after shrub encroachment may be caused by the reduction in leaf N resorption capacity of each growth form as well as the increased shrub dominance in these wetlands. In contrast, the declined dominance of grasses and sedges after shrub encroachment would account for the decreased leaf P resorption efficiency and proficiency at the community level, given the unchanged leaf P resorption at the plant growth form level (Figs. 1, 2). These results highlight the importance of shifted plant composition after shrub encroachment in driving the change in community-level leaf nutrient resorption in temperate wetlands.

Plant nutrient resorption is a key determinant of species composition, litter decomposition, and soil organic matter accumulation (Aerts and Chapin 2000; Vergutz et al. 2012; Lü et al. 2019). Accordingly, our observations will improve our understanding of plant-mediated C and nutrient cycling in temperate wetlands. First, the inconsistent P resorption responses between plant growth form and community levels imply that the effect of shrub encroachment on leaf nutrient resorption is scale-dependent. Thus, the effect of shrub encroachment on nutrient resorption should be assessed at the community level in these wetlands. Second, shrub encroachment-induced declines in leaf N and P resorption would increase nutrient concentrations in senesced leaves, and thus enhance leaf litter decomposition and nutrient release in temperate wetlands (Aerts and Chapin 2000; Xu et al. 2021). Accordingly, this increased leaf litter decomposability after shrub encroachment will reduce accumulation of soil organic matter, especially particulate organic matter, which would weaken the soil C sink in temperate wetland ecosystems. In addition, the increased quantity of high-quality leaf litter inputs after shrub encroachment would increase soil available nutrients for plants and cause nutrient uplift from subsoils to surface soils (Buckeridge et al., 2010; DeMarco et al. 2014). This shrub–litter feedback will favor the growth of shrubs and further drive shrub encroachment in temperate wetlands.

Conclusions

In this study, the effect of shrub encroachment on leaf nutrient resorption was divergent at both plant growth form and community levels in temperate wetlands in the Sanjiang Plain, Northeast China. At the plant growth form level, shrub encroachment reduced leaf N resorption efficiency and proficiency but did not alter leaf P resorption efficiency and proficiency. However, leaf N and P resorption processes at the community level were decreased by shrub encroachment primarily due to the increased dominance of shrubs over sedges and grasses. These findings highlight that altered plant composition plays a critical role in modulating the consequence of shrub encroachment on plant nutrient resorption processes. Moreover, reduced leaf nutrient resorption after shrub encroachment will increase leaf litter decomposability, which will lead to rapid soil C and nutrient turnover in temperate wetlands.

Abbreviations

C: Carbon; N: Nitrogen; P: Phosphorus; MLCF: Mass loss correction factor.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-022-00413-w.

Additional file 1: Table S1. Effect of shrub encroachment on the relative cover and nutrient resorption parameters in freshwater wetlands of Northeast China.

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Author contributions
LY analyzed the data and wrote the original draft. XZ and FS collected and analyzed the data. RM conducted the experiment, analyzed the data, and edited the manuscript. All authors read and approved the final manuscript.

Availability of data and materials
The data generated and analyzed during the present study are available from the corresponding author.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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