



Effects of long-term nitrogen and phosphorus addition on plant defence compounds in a freshwater wetland

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ABSTRACT

Prominent theories of plant defence have predicted that alleviating nutrient limitation will result in decreased production of defence compounds. Yet effects of nutrient addition on plant defence compounds have been found to vary, and research on plant resource allocation in different organs in response to long-term nutrient addition is limited. In this study, we aimed to elucidate effects of 12-yr nitrogen (N) addition and 10-yr phosphorus (P) addition on plant defence compounds (total polyphenols, condensed tannins, cellulose and lignin) in both leaves and stems of dominant specie *Glyceria spiculosa* in a freshwater wetland in the Sanjiang Plain, Northeast China. Both N addition and P addition reduced the production of defence compounds in plant leaves, but increased the production of lignin in the stems. Notably, the concentrations of plant secondary metabolites closely correlated with the plant C:N:P stoichiometric ratios. The results suggest that long-term nutrient addition can alter plant carbon allocation to C-based defence compounds, and thus potentially exert influences on nutrient cycling and ecological processes in freshwater wetlands.

1. Introduction

Excessive fertilizer application and sewage discharge from anthropogenic activities led to increasing nutrient inputs to aquatic ecosystem worldwide (Craft et al., 2007; Simboura et al., 2016). Increasing nutrient availability may alter plant carbon (C) allocation to chemical defence compounds, specifically polyphenols, which can defend against environmental stressors, such as UV radiation, microbial pathogens and herbivory (Scalbert, 1991; Close and McArthur, 2002). In addition to chemical carbon-based defences, plants also modify carbon allocation to structural defence compounds to achieve their physical defence strategies in response to nutrient enrichment. Carbon allocation to cellulose will contribute to leaf toughness and enhance leaf lifespan (Choong, 1996; Kitajima et al., 2012), and lignin can provide plants with structural supports as the main polymer of cell walls (Humphreys and Chapple, 2002). Moreover, as a broad class of secondary metabolites, plant carbon-based defence compounds are also considered as having important roles in nutrient cycling through influencing ecological processes (Kraus et al., 2003; Cornelissen and Aerts, 2004; Chomel et al., 2016). Specifically, high content of lignin can make plants less palatable to herbivores, which can decrease litter decomposability and the rates of nutrient cycling concomitantly (Hideki and Takayuki, 2011). Polyphenols in plants are also considered to regulate nutrient

cycling by reducing soil N mineralization rates through plant-soil feedbacks (Fierer et al., 2001; Kraus et al., 2004). Studying how plant defence compounds in response to nutrient addition can not only help understand the defence strategies of plant species, but also can indicate nutrient cycling under eutrophic conditions.

Prominent theories of plant defence have predicted that nitrogen (N) enrichment will result in a decrease in production of plant carbon-based secondary compounds (Bryant et al., 1983; Coley and Bryant, 1985), and phosphorus (P) availability has no significant effects on polyphenols production (Jones and Hartley, 1999). However, the responses of polyphenols production to increasing nutrient availability have been found to vary (Sundqvist et al., 2012; Zhang et al., 2012; Nybakken et al., 2016). Structural defence indicators of cellulose and lignin in plants were also shown to be significantly affected by nutrient enrichment, but the effects were inconsistent among studies (Haukioja et al., 1998; Santiago et al., 2005; Dias et al., 2013). Research on effects of long-term nutrient addition on plant defence compounds is also limited. Furthermore, the production of defence compounds was reported to be strongly correlated with plant stoichiometric ratios under nutrient enrichment (De Long et al., 2016). Specifically, the C:N ratio is usually regarded as an indicator of plant growth, so studying on the link between plant defence compounds and the ratio of C:N can indicate the trade-off between plant growth and defence (Royer et al., 2013).

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Another key issue is identifying the defence strategies in different plant organs in response to nutrient enrichment. Plant non-leaf organs also play important roles in nutrient cycling due to their high nutrient resorption efficiencies (Freschet et al., 2010; Lü et al., 2012). Research on responses of plant defence compounds in both leaf and non-leaf organs to nutrient enrichment can help understand the plant defence strategies comprehensively. Previous studies have demonstrated that responses of plant defence compounds to environmental stressors vary with plant organs, and compared with the leaves, non-leaf organs are widely considered to have less significant responses to adverse environmental factors including fertility (Kraus et al., 2004; Wallis et al., 2010; Lavin et al., 2015). Knowledge about effects of increasing nutrient availability on the plant defence indicators in different organs of plants remain uncertain, and need to be further studied.

In order to determine the effects of nutrients enrichment on defence compounds in different plant organs, we have conducted long-term multi-levels nutrient addition experiments in the Sanjiang Plain, Northeast China. The Sanjiang Plain is one of the largest freshwater marshes in China (Zhao, 1999), and most marshes in this region are dominated by emergent aquatic plants, such as *Glyceria spiculosa* and *Deyeuxia angustifolia* (Zhang et al., 2014). Over the past few decades, the Sanjiang Plain has been widely reclaimed and converted into agricultural lands (Wang et al., 2011). Consequently, excessive fertilizer application due to agricultural activities has resulted in increasing N and P inputs in the freshwater wetlands. To imitate the further nutrient enrichment in freshwater wetlands, 12-yr N addition and 10-yr P addition experiments were conducted. Leaves and stems from the dominant specie *G. spiculosa* were collected to test the following hypotheses: (1) Long-term N addition will decrease the production of defence compounds [total polyphenol (TP), condensed tannins (CT), cellulose and lignin] in both plant leaves and stems, and the decrease will be greater in higher N addition levels, because plants will reduce resources allocation to carbon-based secondary metabolites when more nutrients are provided (Bryant et al., 1983); (2) Long-term P addition will have no significant effects on plant defence compounds because P availability does not directly affect the phenylalanine pathway (Jones and Hartley, 1999); (3) The effects of nutrient addition on stems would be not as significant as that on leaves of *G. spiculosa*, because non-leaf organs are insensitive to adverse environmental conditions (Kraus et al., 2004; Wallis et al., 2010; Lavin et al., 2015). The linear relationships between plant defence compounds and nutrient ratios were studied to investigate the link between nutrient availability and plant defence compounds. Thus, studying the responses of plant defence compounds to nutrient addition in the Sanjiang Plain will allow us to better indicate plant resource allocation strategies and nutrient cycling under eutrophic conditions in freshwater wetlands.

2. Materials and methods

2.1. Study site and experimental design

This study was conducted in a freshwater marsh at the Sanjiang Mire Wetland Experimental Station, which is located in the Sanjiang Plain, Northeast China (47°35'N, 133°31'E, 56 m above sea level). The study site is characteristic of a temperate humid and sub-humid continental monsoon climate. The annual (1990–2010) precipitation ranges from 500 to 600 mm, with substantial seasonal variation, and the monthly mean temperature of the study site ranges from -20.4°C in January to 21.6°C in July, with a mean annual temperature of 2.5°C (Mao et al., 2013).

To mimic future nutrient enrichment in the freshwater wetlands, four N addition levels (control, $0\text{ g N m}^{-2}\text{ year}^{-1}$; N1, $6\text{ g N m}^{-2}\text{ year}^{-1}$; N2, $12\text{ g N m}^{-2}\text{ year}^{-1}$; N3, $24\text{ g N m}^{-2}\text{ year}^{-1}$) and four P addition levels (control, $0\text{ g P m}^{-2}\text{ year}^{-1}$; P1, $1.2\text{ g P m}^{-2}\text{ year}^{-1}$; P2, $4.8\text{ g P m}^{-2}\text{ year}^{-1}$; P3, $9.6\text{ g P m}^{-2}\text{ year}^{-1}$) were designed, and each treatment had three replicates. Moreover, N addition

and P addition had the same control treatment. In total, 21 plots ($1\text{ m} \times 1\text{ m}$) were established at the experimental station. The N addition plots and P addition plots were established in 2004 and 2006, respectively. Stainless steel frames were established ($1\text{ m} \times 1\text{ m}$, 0.5 m in depth) to avoid the loss of added N and P. These plots were separated by 1 m-width buffer zones, and boardwalks across the plots were installed to prevent disturbance during sampling. During the plant growing seasons from May to September, N fertilizer was added as NH_4NO_3 biweekly since 2005, while P was added as NaH_2PO_4 since 2007.

2.2. Field sampling and measurement

In mid-August 2016, when the plants reached their maximal biomass, 30 shoots of the dominant specie *G. spiculosa* were randomly collected from each plot. Both leaves and stems were sampled from *G. spiculosa* to determine the effects of N addition and P addition on plant defence compounds. All the samples were dried at 40°C to a constant weight and then ground ($< 0.25\text{ mm}$) for chemical analysis. For each sample, concentrations of total N and P were determined using a continuous-flow auto-analyzer (AA3, Seal Analytical Germany) following digestion of a 0.1-g subsample with concentrated H_2SO_4 . The multi N/C 2100 analyzer (Analytik Jena, Germany) was used to measure the plant C concentration by the dry combustion method. Additional subsamples of leaves and stems from *G. spiculosa* were extracted in analysis-grade methanol and then shaken for 1 h. The extracts of these subsamples were measured for total polyphenols and condensed tannins using Folin-Ciocalteu technique with Gallic acid standard (Stern et al., 1996) and acid butanol method with procyanidin standard (Porter et al., 1985), respectively. Concentrations of cellulose and lignin were determined using acid detergent fiber methods (Chemists, 1990; Prudhomme et al., 2012).

2.3. Statistical analysis

All statistical analyses were performed with SPSS 16.0 for Windows, and the accepted significance level was $P = 0.05$. Data were tested for normality by Kolmogorov-Smirnov test before the statistical analysis, and all data followed a normal distribution. One-way analysis of variance (ANOVA) was used to examine the effects of N and P addition on plant stoichiometric ratios and defence compounds at the species level. Two-way ANOVA was used to examine the effects of N and P addition levels, plant organs, and their interaction on plant defence compounds. Tukey's honestly significant difference test was further used to assess the significant difference in the measured properties among treatments. Simple linear regression was used to investigate the relationships between plant defence compounds and stoichiometric ratios.

3. Results

3.1. Effects of N addition on plant defence compounds

The N addition level had significant effects on the concentrations of total phenols, condensed tannins, cellulose and lignin in *G. spiculosa*, and the effects varied with plant organs except on the concentration of total phenols (Table 1). For *G. spiculosa* leaves, the N addition exerted significant effects on the concentrations of chemical and structural defence compounds (Fig. 1). Relative to the control treatment, the concentrations of total phenols significantly decreased in the N3 treatment, whereas the concentrations of condensed tannins were lower in the N1 and N2 treatment. Moreover, N addition generally resulted in the decrease of cellulose and lignin concentrations. Regarding *G. spiculosa* stems, however, the concentrations of total phenols, condensed tannins and cellulose did not significantly change with N addition, and only the lower N addition levels, i.e. N1 and N2, lead to a significant increase of the lignin concentration (Fig. 1).

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