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Does foliar nutrient resorption regulate the coupled relationship between nitrogen and phosphorus in plant leaves in response to nitrogen deposition?

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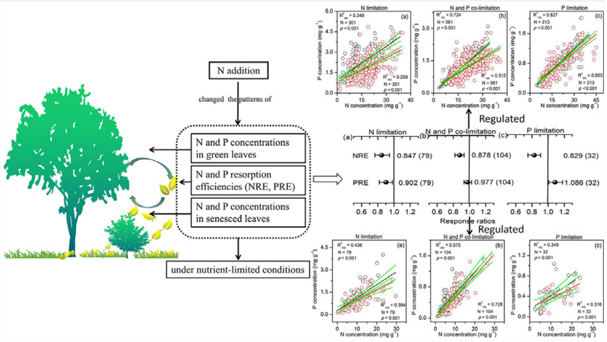
HIGHLIGHTS

- Global NRE and PRE under natural condition are run by biotic and abiotic factors.
- N addition decreased the NRE but slightly affected the PRE on a global scale.
- Nutrient-limited conditions regulated response of nutrient resorption to N addition.
- Different response of N and P relationship to N addition in green and senesced leaves
- Nutrient resorption regulated N and P relationships in leaves response to N addition.

GRAPHICAL ABSTRACT



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ABSTRACT

Nutrient resorption from senescing leaves is an important process of internal nutrient cycling in plants, but the patterns of nutrient resorption and the coupled relationship between nitrogen (N) and phosphorus (P) in plant leaves as affected by N deposition remain unclear. We analysed the effects of N addition on the nutrient resorption and coupled relationship between N and P in plant leaves under different nutrient-limited conditions based on a global meta-analysis. Globally, the mean N resorption efficiency (NRE) and P resorption efficiency (PRE) under natural conditions were 47.4% and 53.6%, respectively, which were significantly regulated by geographical and climatic factors as well as plant characteristics. Furthermore, N addition significantly decreased the NRE by 13.3% but slightly affected the PRE on a global scale, and N addition rates and latitude directly and negatively affected the effects of N addition on NRE. Specifically, N addition significantly decreased the NRE under all nutrient-limited conditions, while it had negative, positive, and neutral effects on the PRE under N-limited, P-limited, and N and P-co-limited conditions, respectively. Moreover, the relationships between N and P in green and senesced leaves were tightly coupled under different nutrient-limited conditions in natural ecosystems. However, N addition significantly weakened the relationships between N and P concentrations in green leaves but slightly affected the relationship in senesced leaves, which were mainly modulated by the effects of N addition on nutrient resorption efficiency, especially NRE. These results highlight that nutrient-limited conditions determine the response of nutrient resorption to N deposition and emphasize the effect of nutrient resorption regulation on the coupling of N and P responses to N enrichment. The findings are important for understanding

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plant nutrient use strategies and the mechanisms underlying the stoichiometric coupling of N and P in response to climate change, and can be used in global biogeochemical models.

1. Introduction

Nutrient resorption of senesced organs is an important strategy for plants to conserve and reuse nutrients, especially nitrogen (N) and phosphorus (P) (Aerts, 1996; Chen et al., 2015; Killingbeck, 1996; Kobe et al., 2005; Vergutz et al., 2012), which can improve plant nutrient use efficiency and reduce plant growth dependence on soil nutrients (Aerts and Chapin III, 1999; Wright and Cannon, 2001). Therefore, nutrient resorption plays a paramount role in guaranteeing plant growth and reproduction and maintaining productivity and nutrient cycles in global ecosystems (Yan et al., 2015; Yuan and Chen, 2009); in addition, it provides a key scientific basis for understanding how plants adapt to climate change (e.g., N deposition) (Mayor et al., 2014; Rejmánková and Snyder, 2008; Wang et al., 2014). It is well known that increasing N deposition alters the plant nutrient regime and elemental balance (Peñuelas et al., 2013; Peñuelas et al., 2015), and has far-reaching effects on the structure, function and nutrient cycling of ecosystems (An et al., 2011; Deng et al., 2017; Li et al., 2016; Niu et al., 2016). However, the pattern of the effects of N deposition effects on nutrient resorption in global ecosystems has not been well characterized.

Previous studies have demonstrated that, on a global scale, nutrient resorption is modulated by biotic factors such as plant growth type (Yuan and Chen, 2015a), species specificity (Mayor et al., 2014; Wang et al., 2014) and leaf characteristics (Chen et al., 2015; Heerwaarden et al., 2003; Huang et al., 2007; Kobe et al., 2005) and abiotic factors including climatic factors (Yuan and Chen, 2009), geography factors (Yuan and Chen, 2009) and soil nutrient content (Aerts and Chapin III, 1999; Vergutz et al., 2012). Recently, many experimental studies have focused on the effects of N addition on nutrient resorption (Lü and Han, 2010; Lü et al., 2016; Mayor et al., 2014; Wang et al., 2014; Yan et al., 2015) and have found that N addition significantly decreases N resorption efficiency (NRE) (Chen et al., 2015; Mayor et al., 2014; Wang et al., 2014). In contrast, the responses of P resorption efficiency (PRE) to N addition have varied greatly among studies, showing positive (Wang et al., 2014), negative (Lü et al., 2016) and neutral (Lü et al., 2013) effects. These uncertainties may be attributed to different patterns of nutrient limitation (such as N-limited, N and P-co-limited and P-limited conditions). For instance, N addition can increase soil N availability and alleviate the limitation of plant growth by N (Li et al., 2016; You et al., 2017), whereas excessive N addition can stimulate phosphate enzyme activities and promote soil P availability (Deng et al., 2016; Fujita and Wassen, 2010; Marklein and Houlton, 2012), with these effects ultimately altering the patterns of nutrient resorption in plants. However, little information has been available on how different nutrient-limited conditions regulate the responses of NRE and PRE to N addition on a global scale.

N and P are two essential nutritional elements that couple from molecular to global scales to control biological growth, respiration, and decomposition as well as the biochemical cycles in ecosystems (Finzi et al., 2011; Peñuelas et al., 2015). Many comprehensive analyses have discussed the relationship between N and P in different organs, populations, plant functional groups and ecosystems (He et al., 2008; Reich and Oleksyn, 2004; Yuan et al., 2011). However, few studies have assessed the relationship between N and P in green and senesced leaves under different nutrient-limited conditions. Meanwhile, N addition can significantly affect the N and P concentrations in green and senesced leaves as well as the pattern of nutrient resorption (Lü et al., 2016; Mayor et al., 2014; Yan et al., 2015; Yuan and Chen, 2015a). In addition, previous studies have shown that increasing N deposition has aggravated P limitation of plant growth (Li et al., 2016) and altered the limitation of nutrient patterns in ecosystems (Elser et al., 2007; Harpole et al., 2011; Vitousek et al., 2010). However, as an important process of element transfer between green leaves and senesced leaves, the role of nutrient resorption during leaf senescence in regulating the relationship between N and P in response to N addition under different nutrient-limited conditions remains unclear.

Here, we performed a global meta-analysis of studies across multiple ecosystems to specifically understand how nutrient resorption controls the response of the relationship between N and P in green and senesced leaves to N addition under different nutrient-limited conditions. Following previous analyses of the effects of N addition on nutrient resorption, and the N and P concentrations in green and senesced leaves (Kozovits et al., 2007; Mayor et al., 2014; Wang et al., 2014; Yuan and Chen, 2015a), we predicted that nutrient-limited conditions determine the response of nutrient resorption to N addition, and that the NRE and PRE correspondingly regulate the relationship of N and P to N enrichment. To test this hypothesis, this study addressed the following questions: (1) What is the average NRE and PRE under N addition on a global scale, and do different nutrient-limited conditions produce significantly different NRE and PRE values? (2) Is there a significant relationship between N and P in green and senesced leaves under different nutrient-limited conditions? (3) How does N addition affect the N and P relationship in green and senesced leaves, and do the NRE and PRE regulate this relationship in response to N enrichment?

2. Materials and methods

2.1. Data compilation

We used Web of Science, Google Scholar and China National Knowledge to collect data from primary studies published before September 2017. The fundamental purpose of the data collection was to compile a database that included the responses of NRE, PRE and N and P concentrations in green and senesced leaves to N enrichment. Thus, the search terms were "N addition", "N deposition", "N fertilization", "nutrient resorption efficiency", "foliar N and P concentrations", "senesced leaves N and P concentrations" and "foliar stoichiometry", and the following criteria were used to minimize the bias of the publications and select appropriate case studies. (1) The data had to be derived from experimental studies that explored the influence of N deposition on the target variables, and the effects of fertilization management on plant nutrients were excluded. (2) At least one of the target indicators was measured, and the N and P concentrations in green leaves were included or calculated. (3) The data had to be derived from mature leaves or fresh litter leaves of dominant plants and only included the data at the individual level, while community-level data were excluded. (4) For multifactorial studies, only control and N addition treatments were included, and other treatments and interacting effects were not selected. (5) The data from control and N addition treatments were derived under the same conditions, and the duration of N addition was not less than one year. Finally, (6) if target variables from the same field observation experiment were published in different journal articles, we only used the average values for the analysis. In addition, to better understand and analyse the data, we also collected the N addition rates, geographic factors (including altitude (m), latitude (°) and longitude (°)) (Fig. S1 in the Supporting Information) and climatic factors (i.e., mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm)) (Table S3 in the Supporting Information). We used the Get Data Graph