Science of the Total Environment 624 (2018) 611–620

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Simulated nitrogen deposition affects stoichiometry of multiple elements in resource-acquiring plant organs in a seasonally dry subtropical forest

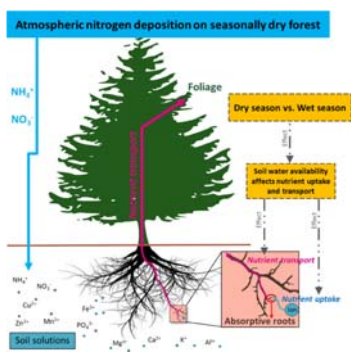
Liang Kou [a,1], Weiwei Chen [a,b,1], Lei Jiang [a,b], Xiaoqin Dai [a], Xiaoli Fu [a], Huimin Wang [a,b,c], Shenggong Li [a,b,*]

[a] Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China
[b] College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China
[c] Jiangxi Provincial Key Laboratory of Ecosystem Processes and Information, Taihe 343725, China

HIGHLIGHTS

- Stoichiometric responses of foliage and absorptive roots depend on rate of N added.
- Seasonal drought mediates N effects on stoichiometry depending on element and organ.
- Effect of N addition on P limitation is intensified in dry season.
- Base cations respond more strongly in absorptive roots than in foliage in wet season.
- N addition increases Mn concentration and decreases Fe:Mn ratio in both organs.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 15 September 2017
Received in revised form 5 December 2017
Accepted 7 December 2017
Available online xxxx

Editor: Elena PAOLETTI

Keywords:
Biogeochemical cycles
Elemental stoichiometry
Foliage
Absorptive roots
Global change
Nitrogen addition

ABSTRACT

Increase of anthropogenic atmospheric nitrogen (N) deposition markedly influences biogeochemical cycles of elements in a wide range of ecosystems. However, our knowledge of how N deposition affects stoichiometry of plants in forests experiencing regular seasonal droughts remains limited. Using a 3-year (2013–2015) N-manipulative experiment, we examined the stoichiometric responses of ten mineral elements, including the most limiting elements (N and P) to plant growth, base cations (K, Ca, and Mg), and trace metal cations (Mn, Zn, Cu, Al, and Fe) in resource-acquiring organs (foliage vs. absorptive roots) of *Pinus elliottii* to N additions in both wet and dry seasons in a seasonally dry subtropical forest. Stoichiometric responses of both organs depended on rate of N addition (generally stronger under high rate) and season. N additions increased foliar [N] and decreased foliar [P] only in dry season and the relative changes in foliar N:P ratio were twice higher in dry than wet seasons, suggesting an aggravated P limitation in dry season. The stoichiometry of absorptive roots was more responsive to N additions than that of foliage, especially for the base cations. N additions increased [Mn] and decreased Fe:Mn ratio in both organs, indicating increased risk of Mn^{2+} toxicity to this tree species. Our results have implications for understanding the N-induced changes in nutrient limitation of forests influenced by seasonal drought, and highlight the contrasting stoichiometric responses of above- and below-ground resource-acquiring plant organs to N loading.

* Corresponding author at: Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China.
E-mail address: lisg@igsnrr.ac.cn (S. Li).

[1] These authors contributed equally to this work.

https://doi.org/10.1016/j.scitotenv.2017.12.080
0048-9697/© 2017 Published by Elsevier B.V.

1. Introduction

Anthropogenic nitrogen (N) deposition has a profound effect on biogeochemical cycles of elements in terrestrial ecosystems globally. The elemental stoichiometry is often used to characterize nutrient economy of plants (Elser et al., 2000) and shifts in magnitude and direction of nutrient limitation in ecosystems (Güsewell, 2004). To maintain stoichiometric homeostasis, plants generally exhibit stoichiometric plasticity in response to N deposition or experimental nutrient additions (Mayor et al., 2014; Mao et al., 2015, 2016; Kou et al., 2017a). Seasonally dry ecosystems exist in many regions of the world (Mirabello et al., 2013; Arndt et al., 2015), which may also experience increased N deposition. A decrease in soil water content can influence the release and mobility of elements and also a wide range of physiological processes (Gonzalez-Dugo et al., 2012; Sardans et al., 2012). One may thus expect that stoichiometry of plants in these ecosystems may respond to N deposition in a potentially different manner, particularly in dry season. However, our understanding of effects of N deposition on stoichiometry of plants in seasonally dry ecosystems remains limited.

N deposition can influence stoichiometry of plants via a suite of mechanisms (Matson et al., 1999). Firstly, increased N deposition can directly increase soil N availability and/or alter microbe-mediated N transformations in soil (mineralization, nitrification, and denitrification), both of which can affect plant N uptake. Secondly, increased N availability can increase soil acidity and decrease soil phosphorus (P) availability by binding PO_4^{3-} to metal ions, e.g. Al^{3+} and Fe^{3+} (Bünemann et al., 2011). The relative changes in these two nutrients may thus result in increased foliar N:P ratio and aggravated P limitation (Chen et al., 2015; Li et al., 2016). Additionally, elevated concentrations of NH_4^+ may directly exchange for positively charged ions in soils (Cusack et al., 2016), which can influence the concentrations of cation ions in plant tissues (Sardans et al., 2008). Despite the potential influences of N deposition, the stoichiometric responses may be affected by the limited water availability in dry season. Water-deficit can restrict the mobility of elements from dehydrated soil, uptake by roots, and vertical translocation towards foliage (Gonzalez-Dugo et al., 2012), which can generate asymmetrical changes in element concentrations among different plant tissues (Sardans and Peñuelas, 2007; Sardans et al., 2008). Moreover, drought-induced decreases in soil organic matter decomposition or clay formation can reduce the cation exchange capacity, and thus decrease cation availability to plants (Sardans et al., 2008).

Studies have given higher priority to the functionally and quantitatively most important elements to plants (e.g., N and P) (Elser et al., 2007; Vitousek et al., 2010), while lower to other mineral elements which are also physiologically essential in maintaining plant fitness and function (Ågren and Weih, 2012). Among base cations (potassium, K; calcium, Ca; magnesium, Mg), K is important in controlling water conductance and transpiration, and maintaining osmotic pressure (Sardans and Peñuelas, 2015). Ca is a major component of the cell wall (Hepler and Wayne, 1985) and plays an important role in buffering toxicity of some metal cations (e.g., Al^{3+}). Likewise, Mg is essential for chlorophyll synthesis, and thus indispensable for leaf photosynthesis (Laing et al., 2000). Trace metal cations (manganese, Mn; zinc, Zn; copper, Cu; aluminum, Al; iron, Fe) are essential to plant growth as micronutrients when below a critical value (Lambers et al., 2008), but are detrimental as phytotoxic ions when above the value (Krämer, 2010). For instance, elevated rates of nitrification and NO_3^- leaching can decrease soil base cation: Al ratios and increase Al accumulation in roots, leading to Al stress and thus decreased root longevity (Smithwick et al., 2013). Considering the coupling relationship of elements in biogeochemical cycles, it is imperative to seek a holistic understanding of the responses of multiple elements in plant tissues.

Although both foliage and absorptive roots (i.e., the distal nonwoody rootlets within the fine root system) (Pregitzer et al., 2002; Xia et al., 2010; McCormack et al., 2015) are resource-acquiring plant organs, stoichiometric studies have traditionally focused on foliage. Different plant tissues generally present contrasting stoichiometric responses to environmental changes (Schreeg et al., 2014; Mo et al., 2015; Sardans et al., 2017). For instance, evidence has shown that mineral nutrients in roots are more responsive to altered soil nutrient availability than foliage (Huang et al., 2015). As the "starting point" of nutrient and water flux into plants, absorptive roots can sense changes in soil resource availability rapidly, while foliage representing the "terminal point" towards which nutrient and water transport may respond weakly or with a time lag (Walter and Schurr, 2005; Schachtman and Goodger, 2008). Moreover, absorptive roots are also indicative of environmental stress and are efficient at stabilizing and removing potentially toxic metals (e.g. Cu and Zn) via rapid turnover (Guo et al., 2013). Given the important role and potentially differential responses of absorptive roots, combining foliage with absorptive roots to explore stoichiometric response patterns will facilitate a better understanding of the links between above- and below-ground parts of plants in the context of environmental changes (Sardans et al., 2017).

In recent years, N deposition has dramatically increased in southeast China (Jia et al., 2014) where ecosystems typically suffer seasonal drought (Wen et al., 2010). Using a 3-year (2013–2015) N-manipulative experiment, we examined the stoichiometric responses of ten mineral elements (N, P, K, Ca, Mg, Mn, Zn, Cu, Al, and Fe) in both foliage and absorptive roots of slash pine (*Pinus elliottii*) to varying rates of N additions in subtropical China. To explore the potential differences in effects of N addition on stoichiometry in contrasting seasons, we employed the method as described by other studies in seasonally dry ecosystems (Mirabello et al., 2013; Arndt et al., 2015), i.e., spanning the sampling events across both wet and dry seasons over the entire experimental period. We hypothesized that: (i) stoichiometry of absorptive roots would be more responsive to N additions than foliage in terms of the number of elements, because absorptive roots are spatially close to soil and thus respond more rapidly while foliage would respond with a time lag due to the long-distance transport; (ii) N effects on stoichiometry of both organs would be stronger in dry than wet seasons, especially for the most limiting macroelements (i.e., N and P), due to restricted uptake and translocation of nutrients under water-deficit conditions; and (iii) the stoichiometric responses of both organs to N additions depend on N rates, with stronger responses under high N rate.

2. Materials and methods

2.1. Site description and experimental setup

The experimental site is situated at the Qianyanzhou (QYZ) Experimental Station of Red Soil and Hilly Land, Chinese Academy of Sciences, Jiangxi province, southern China (26°44′29.1″ N, 115°03′29.2″ E, 102 m a.s.l.). This region is characterized by a subtropical monsoon climate with the annual mean air temperature and precipitation 17.1 °C and 1377 mm, respectively (Yang et al., 2015). The scarce rainfall and high temperature in the late summer frequently cause seasonal droughts at the QYZ site (Wen et al., 2010), and the dry season is from July to October (Fig. 1) and the wet season is from November to June (Yang et al., 2015). Referring to US soil taxonomy, the soil weathered from red sandstone and mud stone is classified as Typic Dystrudepts Udepts Inceptisols (Wang et al., 2012). The background wet N deposition is approximately 33 kg N ha^{-1} $year^{-1}$ (Zhu et al., 2015). The original vegetation was evergreen broad-leaved forests, which was heavily destroyed prior to the 1980s. The vegetation was restored around 1985 by planting slash pine (*Pinus elliottii* Englem), Masson pine (*Pinus massoniana* Lamb), and Chinese fir (*Cunninghamia lanceolata* Hook).

To reduce the potential influence of soil heterogeneity, the chronic N-fertilization experiment was designed as a randomized complete block design and established in a 28-year-old slash pine plantation forests in November 2011. Stand density at the study site was ca.