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Responses of sap flux and intrinsic water use efficiency to canopy and understory nitrogen addition in a temperate broadleaved deciduous forest

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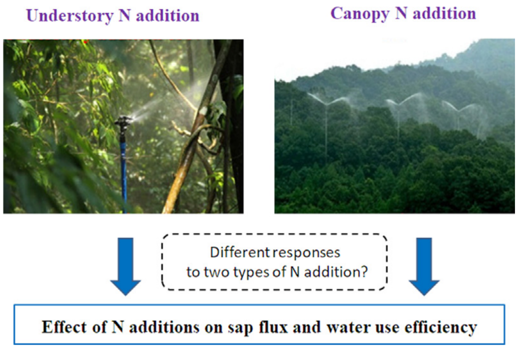
HIGHLIGHTS

- Research was conducted at a novel platform with canopy and understory N addition.
- N addition decreased J_s and its sensitivity to *PAR* and *VPD* during some periods.
- Canopy leaf N content was unaffected by external N addition.
- Canopy N addition increased WUE_i of *Quercus variabilis*.
- Understory N addition could not fully reflect effects of increased N deposition.

GRAPHICAL ABSTRACT



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ABSTRACT

Increasing atmospheric nitrogen (N) deposition could profoundly impact structure and functioning of forest ecosystems. Therefore, we conducted a two-year (2014–2015) experiment to assess the responses of tree sap flux density (J_s) and intrinsic water use efficiency (WUE_i) of dominant tree species (*Liquidambar formosana*, *Quercus acutissima* and *Quercus variabilis*) to increased N deposition at a manipulative experiment with canopy and understory N addition in a deciduous broadleaved forest. Five treatments were administered including N addition of 25 kg ha^{-1} year^{-1} and 50 kg ha^{-1} year^{-1} onto canopy (C25 and C50) and understory (U25 and U50), and control treatment (CK, without N addition). Our results showed neither canopy nor understory N addition had an impact on leaf N content and C:N ratio ($P > 0.05$). Due to the distinct influencing ways, canopy and understory N addition generated different impacts on J_s and WUE_i of the dominant tree species. Canopy N addition increased WUE_i of *Q. variabilis*, whereas understory addition treatment had a minimal impact on WUE_i. Both N additions did not exert impacts on WUE_i of *L. formosana* and *Q. acutissima*. Canopy N addition exerted negative impacts on J_s and its sensitivity to micrometeorological factors of *Q. acutissima* and *Q. variabilis* in 2014, while understory addition showed no effect. Neither canopy nor understory N addition had an influence on J_s of *L. formosana* in 2014. Probably owing to the increased soil acidification as the experiment proceeded, J_s of *L. formosana* and *Q. variabilis* was decreased by understory N addition while canopy addition had a minimal effect in 2015. Thus, the traditional

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understory addition approach could not fully reflect the effects of increased N deposition on the canopy-associated transpiration process indicated by the different responses of J_s and WUE_i to canopy and understory N addition, and exaggerated its influences induced by the variation of soil chemical properties.

1. Introduction

Atmospheric deposition of reactive nitrogen (N_r), originating mainly from fossil fuel combustion and artificial fertilizer applications, has increased dramatically over the past century (BergstrÖM and Jansson, 2006; Gruber and Galloway, 2008; Janssens et al., 2010; Liu et al., 2013). It is estimated that the global rate of nitrogen deposition has increased from approximately 32 Tg $year^{-1}$ in 1860 to 103 Tg $year^{-1}$ in 1993 and will continue to increase up to 195 Tg $year^{-1}$ by 2050 (Galloway et al., 2004; Galloway et al., 2008). Increased N_r emissions have also increased atmospheric N deposition in China from 13.2 kg ha^{-1} in 1980 to 20.6 kg ha^{-1} in 2014 based on summarization of nationwide data (Liu et al., 2013; Xu et al., 2015). Excess N deposition has aroused concerns about its negative impacts on forest ecosystem, including plant diversity (Phoenix et al., 2006; Bobbink et al., 2010; Lu et al., 2010), carbon assimilation (Nakaji et al., 2001; Fleischer et al., 2013), net primary production (Sutton et al., 2008), soil buffering capacity (Bowman et al., 2008).

Variations of canopy stomatal conductance induced by increased N deposition exert an impact on plant transpiration depending upon the tree species and nutrition status (Welander and Ottosson, 2000; Jose et al., 2003; Forrester et al., 2012), and consequently runoff and river flow would be influenced due to the changed forest hydrologic partitioning (Oishi et al., 2010; Schlesinger and Jasechko, 2014). Model analysis showed that N deposition accounts for about 5% of the variation in simulated global scale river flow (Shi et al., 2011). Improved understanding of plant transpiration response to increased N deposition would then in turn contribute to explaining the response mechanism of hydrologic process in forest ecosystem (Felzer et al., 2011). Moreover, the response of canopy conductance to increased N deposition which aims at adjusting the intrinsic interactions between photosynthesis and transpiration would also bring about influences on net assimilation and carbon sequestration capacity (Nakaji et al., 2001; Tuzet et al., 2003; Fleischer et al., 2013). Investigation on sap flux and water use efficiency responses to increased N deposition will be conducive for elucidating the reasons for the variation of forest vegetation carbon storage.

Many studies that addressed the influence of N deposition on forest evapotranspiration have been conducted. Some of these studies investigated the impacts of N addition on leaf-level transpiration based on leaf gas exchange measurements (Maurer et al., 1999; Jose et al., 2003), while some studies discussed the response mechanism of forest evapotranspiration (including both transpiration and evaporation) through applying the eddy covariance technique (Jassal et al., 2010; Dou et al., 2014). However, relatively few investigations have been conducted on the response of plant transpiration to increased N deposition at the tree level, and these existing studies were mainly confined to plantations and seedlings (Welander and Ottosson, 2000; Forrester et al., 2012). How tree transpiration will respond to increased N deposition in the natural forest has not yet been fully understood. Moreover, the sensitivity of transpiration to meteorological factors can reflect the stomatal regulation of leaf water potential, and this is related to changes in whole-plant hydraulics (Franks and Farquhar, 1999; Oren et al., 2001; Addington et al., 2004). Plants which have a higher sensitivity to vapor pressure deficit (*VPD*) usually can increase transpiration under low *VPD* and therefore maintain/increase their growth rate (Litvak et al., 2012; Gao et al., 2017), and exhibit more strict regulation of leaf water potential as *VPD* increases (Oren et al., 1999). Investigating the sensitivity response to increased N deposition would contribute to understanding the factors affecting the tree transpiration and carbon gain.

WUE is a key characteristic of ecosystem function that is central to the global cycles of water, energy and carbon (Beer et al., 2009; Keenan et al., 2013). Intrinsic water use efficiency (WUE_i), defined as the ratio of leaf photosynthesis or net assimilation to stomatal conductance to water vapor, represents the balance between C gain and water loss (Policy et al., 1993; Betson et al., 2007). Thus, how the WUE_i responds to increased N deposition has received extensive attention. Depending upon the experimental conditions, tree species and plasticity in plant physiological processes, the response of WUE_i to N addition was diverse (Ripullone et al., 2004; Jennings et al., 2016). Several studies have shown that N addition would improve WUE_i of *Quercus velutina* and *Populus* × *euroamericana* (Ripullone et al., 2004; Jennings et al., 2016). In contrast, some studies have demonstrated that N addition has no effect on WUE_i of *Fagus sylvatica* L. and *Pinus sylvestris* L. (Elhani et al., 2005; Betson et al., 2007), and estimations of WUE_i from foliar $\delta^{13}C$ determination in phosphorus-limited subtropical forests suggest negative effects of increased N deposition on WUE_i (Huang et al., 2016). Therefore, how changes in N deposition would affect the coupling between transpiration and CO_2 assimilation warrants further research.

Previous studies have demonstrated that leaf photosynthetic capacity is usually correlated with foliar N content (Dejong and Doyle, 1985; Mitchell and Hinckley, 1993; Kattge et al., 2009), thus the foliar N content variation induced by N addition may consequently exert impacts on photosynthetic capacity and carbon storage. It is generally accepted that the external N inputs in the high concentration range to forests would result in higher foliar N concentrations (Magill et al., 2000; Pitcairn et al., 2001; Talhelm et al., 2011), while the situation was different for the low to medium range of N deposition (Aber et al., 2003; Bauer et al., 2004). Some studies showed that leaf N concentration is relatively insensitive to relatively moderate increased N deposition for some tree species (Aber et al., 2003; Bauer et al., 2004). Thus, whether the foliar N content for a specific species would be affected by increased N deposition depends on the quantity of external N input.

Previous experiments mimicking N deposition have been conducted by adding nitrogen solution or fertilizer directly onto the understory plants or forest floors (Mo et al., 2008; Lu et al., 2010; Ward et al., 2012; Lu et al., 2014). Moreover, N retention by the forest canopy is an important process of the biogeochemical cycle of forests, and its quantification is a key issue in determining the impacts of atmospheric N deposition on forest ecosystems (Sparks, 2009; Guerrieri et al., 2010; Guerrieri et al., 2011; Fenn et al., 2013). Traditional N manipulative experiments with the understory N addition approach neglected the effects of atmospheric N deposition on the canopy-associated processes, thus these experiments may not realistically simulate N deposition on forest ecosystems (Zhang et al., 2015). To better simulate the natural N deposition processes in forest canopies, there are some experiments using aircrafts to spray N solution onto the canopy (Adams et al., 2007; Gaige et al., 2007; Dail et al., 2009). However, these experiments were expensive and had the disadvantage that the N solution may not be uniformly dispersed onto the canopy (Zhang et al., 2015).

A novel manipulative experimental platform with both canopy and understory N addition has been established to examine forest ecosystem responses to increased atmospheric N deposition in a deciduous broadleaved forest located in Central China. Our experiment was conducted based on this designed experimental platform, where the main objectives were: (1) to examine whether leaf nitrogen content and intrinsic water use efficiency (WUE_i) of dominant tree species would be affected by canopy and/or understory N addition; (2) to assess the