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Canopy and understory nitrogen addition increase the xylem tracheid size of dominant broadleaf species in a subtropical forest of China

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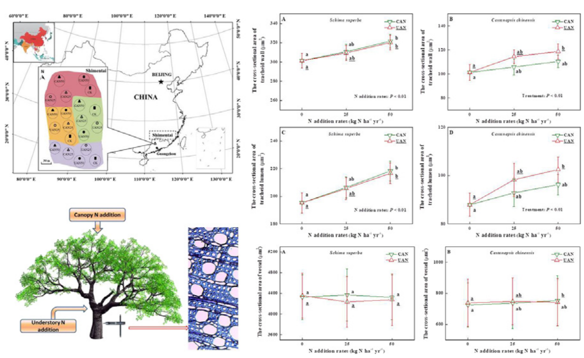
HIGHLIGHTS

- N addition increased xylem tracheid size of dominant broadleaf species in Southern China.
- Effect of N addition on the xylem anatomy was dependent on N addition approaches.
- Understory N addition did not fully simulate canopy N deposition.
- Tree growth of broadleaf species was not affected by canopy or understory N addition.

GRAPHICAL ABSTRACT



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ABSTRACT

Tree xylem anatomy is associated with carbon accumulation and wood quality. Increasing nitrogen (N) deposition can cause a significant effect on xylem anatomy, but related information is limited for subtropical broadleaf tree species. A 3-year field N addition experiment, with different N addition approaches (canopy and understory) and addition rates (0, 25, and 50 kg N ha^{-1} yr^{-1}), was performed beginning in 2013 in a subtropical forest of China. N addition effects on xylem tracheid (wall and lumen) size, vessel, and growth of dominant broadleaf species (*Schima superba Gardn. et Champ.* and *Castanopsis chinensis* (*Sprengel*) *Hance*) were investigated. The results showed that The effect of N addition on tracheid size was dependent on the tree species and addition approaches. Canopy N addition did not affect the tracheid size of *C. chinensis*, while both addition approaches increased the tracheid size of *S. superba*. The vessel size of both species was not affected by N addition. There was no difference in radial growth or other growth-related variables between the control and N-treated trees. These findings indicated that short-term N addition could significantly affect xylem anatomy, but might not influence tree growth. Meanwhile, understory N addition may pose challenges for mechanistic understanding and forest dynamics projection.

1. Introduction

Atmospheric CO_2 can be captured and converted to structural carbohydrates as newly formed xylem components (tracheid and vessel) in trees (Rossi et al., 2016). Xylem formation is one of the strongest C

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sinks in trees, making xylem formation a vital process of C accumulation in forest ecosystems (Huang et al., 2014). On the other hand, xylem contributes to the transport system and provides structural support; therefore, the xylem characteristics (e.g. tracheid size, vessel size and fiber dimensions) can affect water transport efficiency, wood quality, and tree resistance to drought (Lachenbruch and McCulloh, 2014; Santini et al., 2016). Concurrently increasing atmospheric N deposition (resulting from fossil-fuel combustion and agricultural fertilization) is likely to affect the xylem anatomy and productivity of forest trees (Thomas et al., 2010; Ibanez et al., 2016). However, most previous studies about the N effects on xylem anatomy and productivity were conducted in boreal or temperate forests (N-limited ecosystems), and largely focused on coniferous tree species (Makinen et al., 2002; Zhao and Liu, 2009; Rossi et al., 2016). Information about the effect of N deposition on the xylem anatomy of the broadleaf tree species in subtropical or tropical forests is limited. Current N deposition rates in the subtropical region of China range from 15 to 73 kg N hm^{-2} yr^{-1} (Lu et al., 2014; Lu et al., 2015) and are projected to continuously increase in the coming decades (Galloway and Cowling, 2002). Therefore, it is necessary to investigate the effect of N deposition on the xylem anatomy of broadleaf species in subtropical forests.

Tree wood is formed through a series of processes, including cell division, expansion, cell wall lignification, and cell maturation (Samuels et al., 2006). The mechanical properties of tree wood are closely associated with the physical structure of xylem (Pratt et al., 2007; Onoda et al., 2010), which further determines the suitability of tree wood in the wood-processing industry. The xylogenesis process and the anatomical properties of wood (i.e., cell size, wall-thickness) are strongly influenced by many environmental factors, such as nutrients (Hacke et al., 2010) and water (Arend and Fromm, 2007). Hacke et al. (2010) reported that N addition could increase the vessel size and water conductivity of a hybrid poplar. Previous studies have reported positive (Hutchison and Henry, 2010) or insignificant (Dao et al., 2015) effects of increased N availability on xylogenesis, xylem anatomy, and tree growth. In boreal forests, low nutrient availability (mainly N) has been identified as a key limiting factor for tree growth (Lukac et al., 2010). For boreal trees, elevated N availability can increase xylem tracheid size due to increased photosynthetic rates, higher transpiration requirements, and prolonged mitotic activity (Hawkins et al., 1995; Beets et al., 2001; Makinen et al., 2002). In contrast to temperate or boreal forests, subtropical and tropical forests are not N-limited ecosystems with higher soil N availability and faster N cycling rates (Wright et al., 2011; Brookshire et al., 2012). Subtropical and tropical forests contribute greatly to the regional or biome C cycle (Findlay, 2005; Townsend et al., 2011). The potential changes in xylem anatomy of subtropical broadleaf tree species following increasing N deposition may substantially influence forest productivity.

Most past and ongoing experiments about N deposition effects on tree growth were conducted using understory N addition or with high amounts of added N (May et al., 2005; Hogberg et al., 2006; Talhelm et al., 2013; Zhang et al., 2015), which could not simulate natural N deposition (deposited above the canopy layer). Naturally deposited N passes through the canopy layer first before it reaches the forest floor, and the composition of inorganic N will be changed during this process (Houle et al., 2015). Meanwhile, chemical retention in the bark, immobilization in dead organic matters, and volatilization as a gaseous state can lead to less availability of deposited N to plants (Hanson and Lindberg, 1991; Dail et al., 2009; Matson et al., 2014). Therefore, it is necessary to compare the potential impacts of different N addition approaches (canopy and understory N addition) on xylem anatomy and tree growth.

This study aims to test the effects of different N addition approaches (canopy and understory N addition) and different N addition rates on the xylem anatomy of the broadleaf tree species in subtropical forests. We aim to investigate 1) how N addition affects xylem anatomy of broadleaf species and 2) how xylem anatomy and tree growth respond to different approaches of N addition. To fill these knowledge gaps, a 3-year field N addition manipulative experiment has been performed in a subtropical forest of southern China beginning in 2013.

2. Materials and methods

2.1. Field experimental design

In our study, a field N manipulative experiment was conducted in the Shimentai National Nature Reserve (24°22′-24°31′ N, 113°05′-113°31′ E) of Guangdong Province, in southern China. The study site is dominated by a subtropical monsoon climate with alternate dry and moist seasons. In this region, annual rainfall and temperature are 2364 mm and 20.8 °C, respectively. The forest type belongs to evergreen broadleaf forest, and the tree species in the study site include *S. superba*, *C. chinensis*, *Cryptocarya concinna Hance*, *Machilus chinensis* (*Champ. ex Benth.*) *Hemsl.*, and *Engelhardia roxburghiana Wall.* In southern China, *S. superba* and *C. chinensis* are two dominant broadleaf tree species widely distributed in subtropical forests. In general, *S. superba* grows in relatively nutrient-poor soils, whereas *C. chinensis* grows in relatively nutrient-rich soils (Kong et al., 1997; Mo et al., 2008). The forest age is 50 (thinned in 1965) with a stand density of 818 tree ha^{-1}. Trees with a diameter at breast height (DBH) ≥ 10 cm were investigated on July 2012. Mean tree DBH and tree height are 18.6 cm and 13.8 m, respectively. Soil type in this region is latosolic red soil with a pH from 5.0 to 5.5. Subtropical forests are not N-limited ecosystems compared with P availability, with high soil N availability, rapid rates of N cycling, and the lack of N limitation to NPP (Hedin et al., 2009; Wright et al., 2011; Brookshire et al., 2012). Forests in this region are not N-limited compared with most temperate and boreal ecosystems (Mo et al., 2008; Lu et al., 2010; Lu et al., 2013). Indeed, soils in these ecosystems are highly weathered, with low base cation concentrations and high Al concentrations (Lu et al., 2014). In recent measurements, the N deposition rate of this region was 34.1 kg N ha^{-1} yr^{-1} (Zhang et al., 2015), comparable to the highest levels of N deposition occurring in Europe (MacDonald et al., 2002). Therefore, 25 kg N ha^{-1} yr^{-1} was chosen as the medium level of the N addition rate in our study, which was close to the N deposition rate of this region.

The field N addition experiment includes two N addition approaches, canopy N addition (CAN) and understory N addition (UAN). This experiment is designed with five different N treatments, which include: 1) CAN of 25 kg N ha^{-1} yr^{-1} (CAN25), 2) CAN of 50 kg N ha^{-1} yr^{-1} (CAN50), 3) UAN of 25 kg N ha^{-1} yr^{-1} (UAN25), 4) UAN of 50 kg N ha^{-1} yr^{-1} (UAN50), and 5) control (CK, without N addition). Within the study site, four blocks were established, and five treated plots (represented as five different N treatments) were randomly assigned within each block. The area of each circular plot is 907 m^2 with a radius of 17 m. Treated plots were separated by a 20 m buffer zone to minimize contamination of the N solution between plots. The location of Shimentai National Nature Reserve and the experimental design of field N addition were listed in Fig. 1.

The N addition experiment was initiated in April 2013. For CAN, a supporting tower was installed in the center of each CAN-treated plot. The supporting tower is 35 m high and a canopy spraying system, which was used to deliver the N solution, was installed on the top of the tower (above the forest canopy). The canopy spraying system includes 4 sprinklers (with different spraying ranges), which can turn 360° and spray the solution as far as 17 m. N addition events were performed monthly from April to October (the growing season of this forest) each year (Zhang et al., 2015). The application of solution was at a rate of 3 mm precipitation, equivalent for each addition event, and the total additional solutions account for <1% of the total annual precipitation of our study site. All the technical parameters and operations were controlled by a central computer. NH_4NO_3 was used as N source and mixed with surface water drained from a nearby lake. Lake water was sampled and analyzed before each N addition event to ensure the