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The influence of a five-year nitrogen fertilization treatment on hydraulic architecture of *Pinus sylvestris* var. *mongolica* in a water-limited plantation of NE China

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ABSTRACT

The increase in nitrogen (N) deposition is expected to have strong influences on forest ecosystems through its direct and indirect effects on tree performance. One way that N deposition can greatly affect tree performance is by altering plant hydraulic architecture and water relations especially in water-limited habitats; however, the magnitude and direction of response are shown to be species and habitat specific and the underlying mechanism requires further investigations. In the present study, we looked at the potential impact of N deposition on stem xylem hydraulics and leaf level water relations of *Pinus sylvestris* var. *mongolica* (Mongolian pine), using a five-year N fertilization experiment at a typical plantation site in NE China. Our results showed that N addition significantly enhanced tree growth and altered tree hydraulic architecture in the upper canopy. Hydraulic architecture responses to N addition were mainly attributable to changes in allometric relationship between leaf and stem rather than through its impact on xylem conductive efficiency as indicated by the non-significant differences in stem hydraulic conductivity and decreased leaf area to sapwood area ratio in N-fertilized trees. The N-fertilized Mongolian pine trees exhibited characteristics simulating plants from more water-limited habitats, such as lower leaf osmotic potentials at full turgor and turgor loss, which indicates a less favorable water status related to higher nitrogen availability in a water limited habitat. Moreover, a tendency of reduced leaf lifespan may make the N-fertilized trees more susceptible to carbon imbalance. Our results suggest that, despite tree growth was enhanced in the present experiment, N deposition may negatively affect Mongolian pine plantations through its negative impacts on plant water relations, which may likely deteriorate in more water-limited conditions. Management measures aimed at reducing water use, such as tree thinning, may mitigate the negative influence of N deposition on survival of Mongolian pine trees in water-limited plantations of the vast areas of Northern China.

1. Introduction

The worldwide increase in nitrogen (N) deposition is expected to have great impact on global forest ecosystems by affecting many aspects of tree performance (Magill et al., 2004; LeBauer and Treseder, 2008; Bobbink et al., 2010; Wang et al., 2016). Nitrogen deposition has been found to have significant impact on forest productivity since N is a limiting nutrient in many forest ecosystems (Lovelock et al., 2004; Gruber and Galloway, 2008; Fisher et al., 2012; Villagra et al., 2013). Tree growth rate is often enhanced by N addition through increased efficiency of photosynthetic carbon assimilation (Evans, 1989; Fleischer et al., 2013; Santiago and Goldstein, 2016). Increased N availability can also strongly affect plant allometry. For example, when N limitation was relieved, higher proportion of carbon would be allocated to leaf expansion and stem growth (Gleeson and Good, 2003; Luis et al., 2010; Gessler et al., 2017), which is in contrast with the enhanced allocation to root when N availability is low (Bae et al., 2015; Gessler et al., 2017). Consequently, hydraulic architecture and water relations of trees can be substantially altered by N fertilization due to its influences on plant xylem vascular system construction and the allometric scaling between water demand and supply organs (Lautner et al., 2007; Lim et al., 2015; Borghetti et al., 2017). Nitrogen deposition is thus expected to have great influence on water balance of trees through its impacts on tree hydraulic architecture, especially in water-limited environments; however, its impact on xylem hydraulics and water relations are far from conclusive due to mixed results found in the literature and its

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interactions with other environmental factors (Sperry and Tyree, 1990; Lovelock et al., 2004; Bucci et al., 2006; Allen et al., 2010).

Nitrogen deposition can potentially have a strong influence on tree hydraulic architecture that accompanies its significant impact on tree growth and allocation (Goldstein et al., 2013; Wang et al., 2016). Enhanced tree growth rate under higher N availability can substantially modify stem xylem anatomical properties, such as results in higher xylem conduit density, larger xylem conduits, different spatial arrangement of conduits in the xylem and modified pit membrane characteristics (Bucci et al., 2006; Sperry et al., 2008; Goldstein et al., 2013; Borghetti et al., 2017), which can significantly affect xylem water transport efficiency (Tyree and Zimmermann, 2002; Bucci et al., 2006; Goldstein et al., 2013; Plavcová et al., 2013). Moreover, N addition can affect hydraulic safety such that resistance to drought-induced embolism can be significantly altered although no consensus regarding the directions of change have been found in the literature (Harvey and van den Driessche, 1997; Goldstein et al., 2013; Plavcová et al., 2013; Villagra et al., 2013; Pivovaroff et al., 2016; Gessler et al., 2017). Higher N availability often leads to larger total leaf area, higher leaf area to sapwood area ratio and reduced root to shoot ratio in trees (Phillips et al., 2001; Bucci et al., 2006; Bae et al., 2015; Gessler et al., 2017), which can have strong impact on plant water balance.

Due to the great potential influence of N addition on tree hydraulic architecture, it can have a strong impact on plant water relations and plant overall performance especially in water-limited environments (Bucci et al., 2006; Pivovaroff et al., 2016). Nitrogen addition can cause increases in tree water demand and greater drought sensitivity due to larger canopy size and a lower root to shoot ratio (Aber et al., 1989; Phillips et al., 2001; Kozlowski and Pallardy, 2002; Bucci et al., 2006). For example, Dziedek et al. (2016) showed that N fertilization resulted in increased drought sensitivity in European beech that was primarily due to decreased root biomass. In most cases, N fertilization results in decreased leaf-specific hydraulic conductance and consequently more negative leaf water potential even when stronger stomatal control to water loss occurs (Bucci et al., 2006; Samuelson et al., 2008). Water potential decrease under N fertilization can result in a smaller hydraulic safety margin (Tyree and Sperry, 1988), which makes trees more susceptible to drought-induced hydraulic failure. Climate change models predict that drought will occur with greater frequency and intensity across many regions of the globe (Breshears et al., 2005; IPCC, 2014; Allen et al., 2015), which would have cascading effects on forest functions and may induce regional tree mortality especially in water-limited environments (Aber et al., 1989; Allen et al., 2010). Under these circumstances, studies on the influence of N addition on plant water relations and drought tolerance would have both scientific merit and realistic meaning for forest management.

China is among the regions where the severity N deposition is alarming, which mainly occurs due to intensive human activities, including the heavy use of fertilizers in agriculture and burning of fossil fuels (Aber et al., 1989; Galloway and Cowling, 2002; Galloway et al., 2008; Liu et al., 2013). Forest ecosystems of Northern China are in general N limited compared to ecosystems in the southern part of this country that are mostly phosphorous limited (Han et al., 2005; Liu et al., 2011; Huang et al., 2013; Li et al., 2015), which suggests a strong potential influence of N fertilization on forests of Northern China. Moreover, vast areas of Northern China are water limited, which makes it especially relevant and important to study the influence of N deposition on tree hydraulic architecture and water relations in this region. *Pinus sylvestris* var. *mongolica* (Mongolian pine), a geographical variation of Scots pine distributed in Northeast Asia, is one of the most important tree species widely used for afforestation in arid and semi-arid regions of Northern China. It is strongly tolerant to drought and low temperature stresses (Zeng et al., 1996) and is especially suitable to be planted in habitats with deep sandy soil where both nutrients and water are usually limited (Zheng et al., 2012).

Since the 1950s, large areas of Mongolian pine plantations have been created in the Three-North (northwest, north and northeast) regions of China, which provided significant ecological and social benefits (Zheng et al., 2012). However, severe decline in Mongolian pine plantations started to occur since early 1990s (Jiao, 2001; Zhu et al., 2008). Among the many potential reasons causing the decline, water limitation is considered to be a key determinant (Zhu et al., 2008; Song et al., 2016). In the present study, we aimed to look at the impact of simulated N deposition on hydraulic architecture and water relations of Mongolian pine trees under a water-limited plantation growth conditions. Specifically, we tested the following hypotheses: (1) by relieving or partially relieving N limitation, the N fertilization treatment would result in higher leaf photosynthetic rate and greater growth rate in Mongolian pine trees; (2) higher growth rate in N-fertilized trees would be associated with increased stem hydraulic conductivity but this will result in reduced resistance to drought-induced xylem embolism due to a trade-off between hydraulic efficiency and safety; (3) changes in hydraulic architecture and allocation (e.g. the tendency to produce more leaves under higher N availability) would be accompanied by changes in water-relations, such as lower water potential and turgor loss points in the water limited growth conditions.

2. Materials and methods

2.1. Growth conditions and experimental design

This experiment was carried out at the Daqinggou Ecological Research Station of the Institute of Applied Ecology, Chinese Academy of Sciences (42°54′N, 122°24′E; 260 m altitude), which is located in the southeast part of the Horqin Sandy Land in Inner Mongolia, NE China. This area is located in a transitional zone from the typical temperate sub-humid to semi-arid continental climate. It has a cold and dry winter and a relatively hot and moist summer with a mean annual temperature of 5.7 °C (ranging from −23.2 °C in January to 32.4 °C in July) and a frost-free period of 150 days. The mean annual precipitation is about 450 mm and more than 60% of the rainfall occurs between June and August and the annual potential evaporation is 1780 mm (Hu et al., 2013). The soil is an aeolian sandy soil that is characterized by coarse texture and loose structure and poor in nutrients and organic matters. The average organic carbon and total N contents are 4.52 and 0.28 m g^{-1}, respectively (Lin et al., 2013).

In 2011, we chose a Mongolian pine plantation with a tree age of 11 years and started the N fertilization experiment. The plantation had a spacing of 5 m × 2 m (1000 stems ha^{-1}). The selected area of plantation was divided into eight plots (25 m × 14 m for each) with a buffer zone of 4 m between neighbouring plots. We used a completely randomized design consisting of four replications, i.e. four randomly selected plots (N+) were fertilized while the other four were used as control plots (CK). From May to September, urea particles were sprayed in the four N+ plots monthly for five times with an intensity of 20 kg N ha^{-1} each time (100 kg N ha^{-1} yr^{-1}). In total, there are 112 individual trees in the four fertilized plots and 112 trees in the control plots. The diameter at breast height (DBH) censored in 2011 showed no significant difference between plots and treatments. Tree growth analyses did not show significant difference among the four plots within a treatment due to the homogeneity nature of the plantation. Considering the lack of variation between plots within a treatment and the time-consuming nature of the measurements in hydraulic related physiological traits, we randomly sampled trees from the 112 trees within each of the two treatments for the current investigation.

2.2. Stem hydraulic conductivity

Ten four-year old fully sun-exposed branches, each from a different tree were randomly selected from the 112 trees of a treatment, were sampled early in the morning. The cutting ends of the branches were re-cut immediately under water to remove embolized tracheids and the