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Difference in response of water use to evaporative demand for codominant diffuse-porous versus ring-porous tree species under N addition in a temperate forest

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Abstract

In this study, we explored the impacts of nitrogen (N) addition on water transpiration of codominant trees with different wood anatomy and their response of water use to varying vapor pressure deficit (VPD). Three tree species, diffuse-porous *Liquidambar formosana* Hance (maple), ring-porous *Quercus variabilis* Blume (cork oak), and *Quercus acutissima* Carruth (sawtooth oak), were selected for this research. These temperate forest trees grow in a climatic transitional zone located in Henan Province of Central China, and have been under N addition treatments of different levels since April 2013. The N treatments include control, low N (25 kg N ha^{-1} year^{-1}), and high N levels (50 kg N ha^{-1} year^{-1}). The measured data of stem sap flow from April to October 2015 showed that maple trees used more water than oak trees and N addition generally decreased the water transport of maple and sawtooth oak but induced no significant change of water transpiration for cork oak. Water use in maple increased with VPD, whereas relatively flat response for both oaks was observed, suggesting a much stricter stomatal control. Under N addition, water transport in all tree species showed a significant decline in the wet period (August), during which there were more precipitation and cloudy days than in dry May when VPD is >1.80 kPa. However, changes of vessel size, hydraulic conductivity, and root biomass that are associated with N addition for both ring- and diffuse-porous species remain unknown and require further investigation.

KEYWORDS

N addition, vapor pressure deficit, water use, wood anatomy

1 | INTRODUCTION

Plants' survival and growth depend on the effective regulatory mechanisms that allow plants to modulate water transport in response to dramatic changes in the environment (Martinez-Vilalta, Poyatos, Aguade, Retana, & Mencuccini, 2014). These mechanisms are closely linked to morphological and physiological traits and thus vary with plant size, species, and function type (Köcher, Horna, & Leuschner, 2013). As the main component of hydraulic system, the xylem provides a low resistance pathway for water movement from roots to the evaporation sites in leaves. Therefore, the xylem characteristics, such as density of intact vascular bundle, vessel size, and fiber dimensions, can influence water transport efficiency and resistance to drought-induced cavitation (Lachenbrunch & McCulloh, 2014; Santini et al., 2016).

Among angiosperm tree species, xylem anatomy is generally divided into two types: ring-porous vessel versus diffuse-porous vessel. The diffuse-porous trees have narrow vessels evenly dispersed across a growth ring, whereas ring-porous stem produces a band of wide vessels in the early wood followed by much narrower and more dispersed vessels in the latewood (Wheeler & Baas, 1993; Zimmermann, 1983). A previous study suggested that plants possessing wide diameter xylem vessels and low density of intact vascular bundle might be able to continuously access water, with concomitant high rates of transpiration, carbon gain and growth (King, Davies, Tan, & Noor, 2006). Owing to greater maximum conductivity, ring-porous stems, even after 90% loss in conductivity, can still have a similar conductivity as that of nonembolized diffuse-porous stems (Hacke, Sperry, Wheeler, & Castro, 2006). Nevertheless, recent work suggested that ring-porous xylem is much more vulnerable than diffuse-porous xylem

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to cavitation resulted from the effect of water stress (Li, Sperry, Taneda, Bush, & Hacke, 2008; Schuldt, Leuschner, Brock, & Horna, 2013). In theory, the ring-porous strategy should work if the trees were isohydric and maintained similar water status through the seasons, whereas the isohydry would be less essential to diffuse-porous function (Hacke et al., 2006). Consistent with this expectation, ring-porous trees appear to show stricter stomatal regulation of transpiration in response to extremes in vapor pressure deficit (VPD) than diffuse-porous trees (Bush et al., 2008). Differing from the aforementioned research, several previous studies, however, have reported that ring-porous species have lower leaf water potential thresholds for stomatal closure, exhibiting more anisohydric regulation of leaf water potential (Cavender-Bares & Bazzaz, 2000; Ewers, Mackay, & Samanta, 2007). These traits may contribute to the overall lower responsiveness of transpiration to soil drying in ring-porous trees than in diffuse-porous species (Ford, Hubbard, & Vose, 2011; Stoy et al., 2006). Other studies suggested that sensitivity of stomatal conductance to VPD is lower in ring-porous species than in diffuse-porous species (Ford et al., 2011; Hölscher, Koch, Korn, & Leuschner, 2005; Oren et al., 1999). However, one research conducted on irrigated urban trees concluded that stomatal sensitivity to VPD was greater in ring-porous than in diffuse-porous species (Bush et al., 2008), whereas another found no difference in sensitivity between the species (Litvak, McCarthy, & Pataki, 2012). Therefore, although differences in anatomy and leaf traits are evident between ring- and diffuse-porous species, results from previous studies are mixed with regard to how these differences affect water use and stomatal regulation of different tree species with distinct xylem structure.

Nitrogen (N) is one of the main plant nutrients that is essential for and affects plant growth (Hacke et al., 2010). Plants would allocate more carbon to roots compared with leaves to enhance nutrient uptake when nutrient is limited (Domec et al., 2009; Palmroth et al., 2006). On the other hand, when nutrient limitation is relieved by fertilization, the pattern of biomass allocation may change, favoring the expansion of the leaf surface area to enhance carbon dioxide capture (McCarthy, Oren, Finzi, & Johnsen, 2006). Therefore, increasing N deposition would alleviate the limitation of N for the forest development. Trees would thus regulate the physiological characteristics and hydraulic structure to maximize acquisition of N resource and adapt to the harsh environmental conditions (Wallace, Lovett, Hart, & Machona, 2007). A more conductive xylem would be more able to support faster shoot growth and greater leaf areas that are typically associated with N addition. For example, Hacke et al. (2010) investigated the influence of N on hydraulic traits of hybrid poplar saplings and found increased leaf area, wider vessels, and higher specific conductivities in high N plants. Another study reported that N addition significantly increased specific conductivity of terminal stems and average daily sap flow whereas decreased leaf-specific conductivity and wood density (Bucci et al., 2006). The impact on hydraulic architecture following N addition would consequently affect the stomatal behavior, as well as the leaf water relations (Domec et al., 2009). It has been noted that N limitation would tend to lower stomatal conductance and transpiration (Felzer et al., 2011). Ward et al. (2012) reported that N addition tended to alleviate the decreased stomatal conductance (g_s) induced by elevated atmospheric carbon dioxide, suggesting a

transient direct effect of N on g_s. In short, an improved understanding of stomatal regulation driven by the adjustment of hydraulic structure following N addition is essential to understand the mechanism of how the changes in N resource affect tree water use.

Compared with other regions of the world, the atmospheric N deposition in Asia has been increasing fast for the past two decades. By the early 1990s, it was higher than 10 kg N ha^{-1} year^{-1} in most areas of Asia and is expected to be higher than 50 kg N ha^{-1} year^{-1} in 2050 in Central and Eastern China and in India (Galloway et al., 2004; Yao, Wang, Liu, & Song, 2011). To illustrate the effect of N deposition on tree water use, we conducted an experiment of simulated N deposition in a temperate forest in Jigongshan (JGS), Henan Province, Central China. According to the report of Zhang et al. (2015), the N deposition in precipitation is about 19.6 kg N ha^{-1} year^{-1} in JGS, which has greatly exceeded the critical load of temperate region (10 kgN ha^{-1} year^{-1}; Ochoa-Hueso et al., 2011). Anthropogenic activities have already increased and will continue to aggrandize the pressure of N deposition on forest ecosystems. The hydraulic structure change induced response of tree with different anatomy to N deposition would change their water use in both intensity and pattern, which inevitably impacts regional eco-hydraulic cycle. The main objectives of this study are (a) to investigate the inherent differences in water use of the dominant tree species in a temperate forest, particularly those differences in linkage with divergent stem anatomy (ring-porous vs. diffuse-porous) and (b) to evaluate the effect of N addition on water use strategy of the studied tree species and the response to climatic condition. On the basis of the studies cited and the analyses above, we hypothesized that the whole tree transpiration and stomatal adjustment in ring-porous plants might be more sensitive to evaporative demand (VPD) compared to those in diffuse-porous plants under N addition.

2 | MATERIALS AND METHODS

2.1 | Site description

The experiment was conducted in a temperate natural forest located in the Jigongshan National Nature Reserve (31°46′–31°52′N, 114°01′–114°06′E), Henan Province, Central China. The area is within the transitional zone from subtropical to warm temperate climate region. The average annual rainfall is about 1101.7 mm and seasonally unevenly distributed (80% of the precipitation falls in the time period of April and October). The mean annual temperature and relative humidity are approximately 15.3 °C and 79%, respectively. Zonal vegetation at this site was a temperate deciduous broadleaf forest, and the dominant canopy tree species were *Liquidambar formosana*, *Quercus variabilis* and *Quercus acutissima*, accompanying with some occasionally scattered tree species (such as *Acer buergerianum* and *Celtis sinensis*) (Figure S1). The forest contains a yellow-brown sandy-loam soil with pH value of about 5~6.

Experimental plot was established in the forest on a steep southwest-facing slope for long-term ecological research. We adopted random block design for the experiment of elevated N application, and the different N addition treatments were achieved by uniform spraying of ammonium nitrate of different concentrations using the back type

electric sprayer. Three treatments are designed as follows: (a) control (CK, without N addition, same amount of water with the elevated N application treatments instead); (b) understory addition of low N (25 kg N ha^{-1} year^{-1}, UN25); and (c) understory addition of high N (50 kg N ha^{-1} year^{-1}, UN50). We chose these N addition levels mainly by referring to the background value of N deposition and simulation research in local stated in the introduction section. Three blocks for the repetitions of the above treatments were established within the studied forest, and the treated plots were randomly assigned within each block. The N addition treatment was started in April 2013 and maintained throughout the experimental period. The treatments were performed once a month during the growing season (from April to October). More detailed information of plot design and N addition was listed in Table 1. Lateral contamination of N solution between plots was minimal as the plots were separated by at least 20 m buffer zone, and polyvinylchloride boards were inserted between two adjacent plots when necessary. On the basis of the preliminary community survey, we calculated the frequency of occurrence in the experimental plot using the measured basal area and the number of every tree species. By dividing the above values by the sum of the frequencies of all species, the sum of basal area of all individuals, and the total number of all plants, we obtained the relative abundance, relative frequency, and relative dominance for each tree species, respectively. The values of important value index were calculated by summing the relative abundance, relative frequency, and relative dominance, and the results were shown in Figure S1. Three tree species that have the highest importance value index, *L. formosana* (maple; diffuse porous), *Q. variabilis* (cork oak), and *Q. acutissima* (sawtooth oak; both ring porous), were selected as sample trees for sap flow measurement. Their important value indexes were 0.61, 0.43, 0.42, respectively (Figure S1). Summary of biometric parameters of the studied tree species, including tree height, sapwood length, sapwood area, and diameter breast height, was showed in Table 2.

2.2 | Micrometeorology

Photosynthetically active radiation (PAR) was quantified with a SQ-110 quantum sensor (USA). Temperature (T) and air relative humidity

(RH) were recorded by a thermo-hygrometer (HygroClip 2, Rotronic AG, Switzerland), and VPD was calculated from T and RH using the equation described in Campbell and Norman (1998). All the sensors were deployed on a supporting frame at an open site roughly 50 m away from the experimental plots. The documented data represented the micrometeorological factors above the canopy. Precipitation was recorded in a nearby meteorological station. All measurements were synchronized with sap flux density and lasted for the whole growth period (from April to October).

2.3 | Sap flux

Sap flux density (J_s) was measured by self-made thermal dissipation probes following Granier's design (Granier, 1987). The sensor comprises two probes and each probe has a length of 20 mm and a diameter of 2.0 mm. The upper probe of the sensor contains a copper-constantan thermocouple and a heating element of constantan, which is continuously heated with a constant power of 0.2 W, and the unheated lower probe serves as a temperature reference. The two probes were typically inserted radially into the stem at 10–15 cm apart and 1.3 m above the ground on the northern side of tree stem. The probes were covered with plastic locket and insulated with aluminum film to avoid mechanical disturbance and direct solar heating. Temperature difference between the two probes was used to calculate the sap flux density (J_s, g H$_2$O m^{-2} s^{-1}) following the empirical relationship of Granier (1987):

$$J_s = 119 \left(\frac{\Delta T_m - \Delta T}{\Delta T} \right)^{1.231}, \tag{1}$$

where ΔT_m is the maximum temperature difference under zero-flux conditions and ΔT is the temperature difference between the heated and the unheated probes. To scale the sap flux measurements to whole tree level, it is necessary to take into account of the radial variation of J_s with the sapwood depth. Here, we used the consistent relationship for angiosperm trees summarized by Pataki, McCarthy, Litvak, and Pincetl (2011):

TABLE 1 Information of plot design and N treatment

Treatment	Shape of plot	Area (m^2)	N additive	N concentration (kg N ha^{-1} year^{-1})	Annual N addition (g)	Single N addition (g)	Single water addition (L)
CK	Square	400	H$_2$O	—	—	—	40
UN25	Square	400	NH$_4$NO$_3$	25	2,857.1	408.2	40
UN50	Square	400	NH$_4$NO$_3$	50	5,714.3	816.3	40

TABLE 2 Summary of biometric parameters of the studied tree species

Species	*Liquidambar formosana*			*Quercus variabilis*			*Quercus acutissima*		
Code	Maple			Cork oak			Sawtooth oak		
Treatment	CK	UN25	UN50	CK	UN25	UN50	CK	UN25	UN50
n	6	19	4	7	6	15	11	4	7
Height (m)	22.3 ± 14.6	18.3 ± 6.5	28.9 ± 28.1	35.3 ± 27.7	22.8 ± 6.3	18.4 ± 3.1	25.2 ± 7.1	25.4 ± 8.0	27.4 ± 15.3
Sapwood depth (cm)	7.64 ± 2.3	9.61 ± 3.5	11.76 ± 9.4	6.26 ± 0.8	6.43 ± 1.1	5.98 ± 0.8	5.62 ± 1.0	5.06 ± 1.0	6.14 ± 1.0
Sapwood area (m^2)	0.0303	0.0592	0.1579	0.0666	0.0749	0.0585	0.0616	0.0470	0.0766
Diameter at breast height (cm)	18.8 ± 10.1	26.6 ± 12.0	29.1 ± 24.4	40.8 ± 7.6	42.1 ± 9.7	37.9 ± 8.1	40.3 ± 9.0	35.2 ± 9.3	44.9 ± 7.8

$$J_i/J_o = 1.033 \times \exp\left[-0.5\left(\frac{x-0.09963}{0.4263}\right)^2\right], \quad (2)$$

where J_i/J_o is the ratio of sap flux at the actual to the outermost (2 cm in our study) sapwood depth and x is the relative sapwood depth. We standardized the sap flux density and sapwood depth on the basis of J_s and stem radius, then integrated the obtained standardized function to get the standardized mean sap flux density ($\bar{J}_{stan}$) and finally obtained the actual mean sap flux density $\bar{J}_s = \bar{J}_{stan} \times J_s/1$.

For the sap flow monitoring, three to five sample trees of each tree species from every treatment were selected. The numbers (n) of the selected trees for every treatment were listed in Table 2. Sapwood area of the sampled trees was estimated from allometric equation (Matheny et al., 2015; von Allmen, Sperry, & Bush, 2015). The estimation was based on several felled trees of each species with different diameter at breast height (DBH) outside and close to the experimental plot. The sapwood depth was directly obtained from the sawed stem disk by the distinction of large color difference between sapwood and heartwood. Finally, the allometric equation for the sapwood area of the three sampled tree species using the DBH was respectively determined as below

$$As = 0.0068 \times e^{0.0677DBH} \left(R^2 = 0.96, n = 10, \text{maple}\right), \quad (3)$$

$$As = 0.0071 \times e^{0.0512DBH} \left(R^2 = 0.98, n = 9, \text{sawtooth oak}\right), \quad (4)$$

$$As = 0.0083 \times e^{0.0495DBH} \left(R^2 = 0.95, n = 10, \text{cork oak}\right). \quad (5)$$

The whole-tree sap flux ($Q = \bar{J}_s \times A_s$, $g\,s^{-1}$) was estimated by multiplying the mean sap flux density with the sapwood area, and the daily water use per tree was calculated as the integral of the daily courses of the whole tree sap flux.

To remove the effect of tree size on water use, we adopted a relationship between daily maximum sap flow (Q_{max}) and DBH established by von Allmen et al. (2015). Briefly, the Q_{max} for each tree was the average of top five 10 min Q values for each selected day (under well-watered, full sun, and high VPD conditions), averaged again over all selected days from late June to early September. The confounding effect of tree size in subsequent comparisons can be removed by dividing sap flow by $(DBH)^q$:

$$Q_s = Q/\left((DBH)^q\right), \quad (6)$$

where Q_s refers to the size standardized water flow rate, q is the regression exponent. To assess the response of water use to VPD, we plotted average daily whole-tree water flux for diffuse-porous and ring-porous species against average daytime VPD in May and in August, which represented dry and wet time period, respectively.

The sap flow monitoring facilities were set up in April 2014 and had run from then on to the end of 2015, except for the winter time when air temperature was below 5 °C, during which the trees defoliated and the sap flow was almost zero. The data we used for the analyses in this paper were collected from April to October, 2015.

2.4 | Statistical analyses

The linear fitting of Q_s and VPD and the correlation between whole tree water use and the DBH were analyzed by performing a linear regression in Origin 8.0. To determine the significant differences of N addition in maple and oak regressions, we performed homogeneity of regression slopes and an analysis of covariance in SPSS software package (SPSS Inc., 2003). Differences between the treatments were considered to be statistically significant at $p < .05$.

3 | RESULTS

3.1 | Micrometeorological conditions

The monitored air temperature (T), relative humidity (RH), PAR, recorded precipitation (P) and calculated VPD are presented in Figure 1. Monthly mean values (using the data of daytime hours) of T and RH showed similar trends from April to October in 2015, with maximum values (28.61 °C and 81.21%) occurring in July and August. Rainfall primarily occurred between July and August, the wet season, which accounted for approximately 74% of the total precipitation during the tree growth period. Monthly mean PAR values (also using the data of daytime hours) ranged from 300 to 600 µmol m^{-2} s^{-1} in the same period, and the minimum PAR value occurred in October. The trend of monthly mean VPD (also using the data of daytime hours) was similar with that of the PAR, reaching the highest value (1.31 kPa) in July and the lowest (0.76 kPa) in October.

3.2 | Sap flow and tree water use

The established relationship between Q_{max} and DBH was shown in Figure 2, with a regression exponent q of 1.91, 1.78, and 1.80 for maple, sawtooth oak, and cork oak, respectively. The size function relationship with a scaling exponent less than 2 might indicate that larger trees used less water per basal area than smaller ones (von Allmen et al., 2015; Zhao, Rao, Ma, Cai, & Zeng, 2006). The similarity between oaks and maple scaling exponents allowed us to remove the confounding effect of tree size in cross-species comparison by dividing Q by DBH^q.

The average midday Q_s per species in Figure 3 showed that maple (diffuse porous) transported more water than oaks (ring porous) during most time of the monitoring period. Water transport of the three species was initially low in April to May but increased during June to August that are typically hot and wet. In the period from September to October, during which few precipitation events occurred and temperatures were lower, all three tree species showed the least water transport. Though the complete sap flow data are not available for all the months of the experimental period due to thunder, power failure, tree's dying, available data still show that N addition reduced average midday Q_s for maple and sawtooth oak (Figure 3). No significant difference was observed between the N addition treatment and the control for cork oak during the growing seasons.
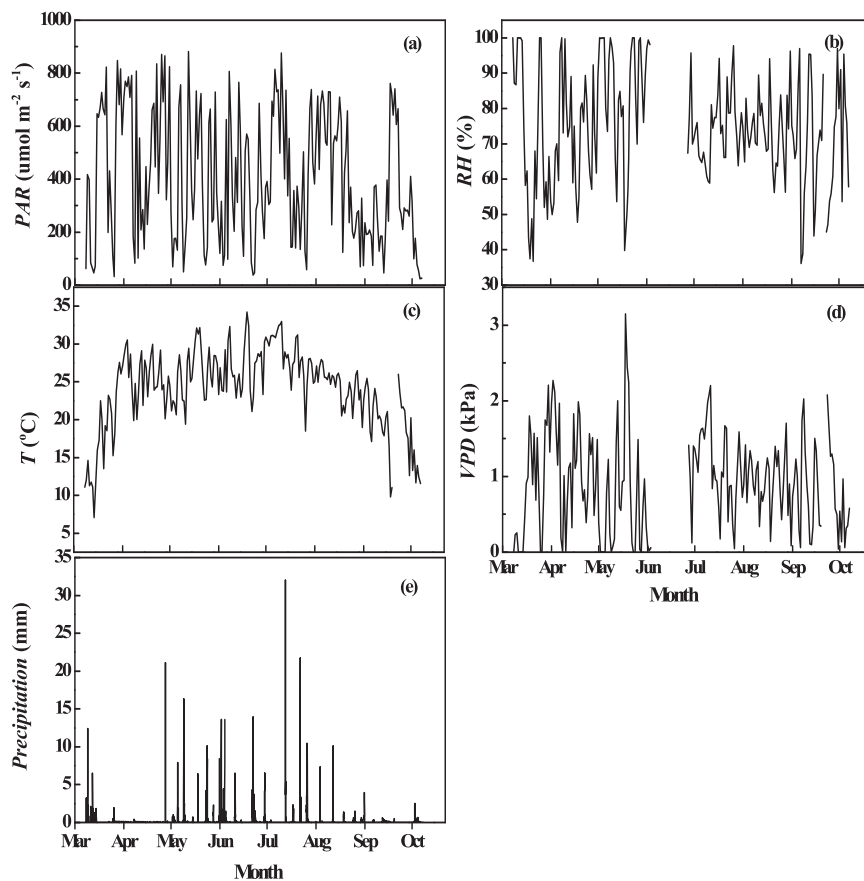
FIGURE 1 Daily means of (a) photosynthetically active radiation (PAR), (b) relative humidity (*RH*), (c) temperature (*T*), (d) vapor pressure deficit (VPD) when PAR > 0, and (e) precipitation (*P*). Missing data were due to instrument failure or power-off
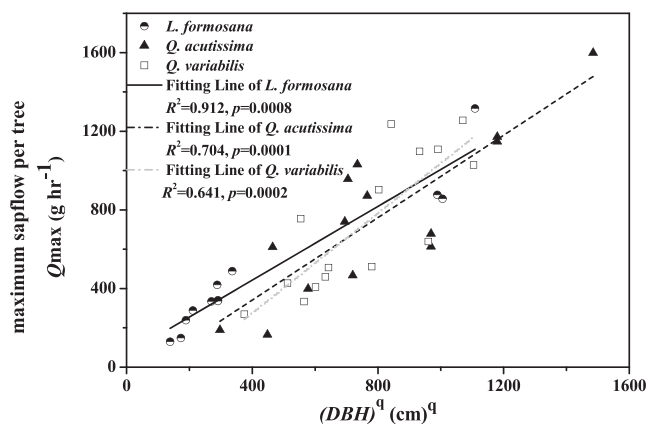

FIGURE 2 Maximum sap flow per tree (Q_{max}) for *Liquidambar formosana* (*L. formosana*; maple), *Quercus variabilis* (*Q. variabilis*; cork oak), and *Quercus acutissima* (*Q. acutissima*; sawtooth oak) shown as a function of tree diameter (diameter at breast height [DBH])

3.3 | Tree water use in response to VPD

Response of average daily Q_s to average daytime VPD for the three species in May and August was presented in Figures 4, which clearly demonstrated two distinct patterns. Under a dry condition (May) and the control treatment, the diffuse-porous species showed a clear linear relationship between Q_s and VPD, but ring-porous species showed a saturating response to the increasing VPD, and Q_s reached maximum when VPD values were around 2 kPa. N addition significantly changed the response of water transpiration to VPD for the maple trees ($p < .05$). As shown in Figure 4, the response of Q_s to increased VPD

under N addition was significantly different from that of control treatment ($p < .05$). Obviously in the wet August (Figure 4, lower row in the figure), a much weaker increase of Q_s was observed with the increasing VPD for the control treatments, and it was noticeable that an obvious decline in Q_s under N addition (for both low and high N treatments) for all tree species was observed when VPD is >1.80 kPa.

4 | DISCUSSION

4.1 | Effect of wood anatomy on tree water use

The codominant *L. formosana* (maple), *Q. variabilis* (cork oak), and *Q. acutissima* (sawtooth oak) showed a clear difference in water consumption. For a given tree size, diffuse-porous maple consumed more water than the two ring-porous oaks under no N addition, which was similar to the results reported by other researchers (Bush et al., 2008; von Allmen et al., 2015). The contrasting water use might be associated with the interspecific difference in stem anatomies. Previous studies reported that the ring-porous oak stems that have large diameter vessels in the early wood tend not to compensate for the greatly reduced number of vessels in the single-functioning growth ring (Poorter et al., 2010; Preston, Cornwell, & DeNoyer, 2006). They also suggested that the number of conducting vessels in the ring-porous oak stems would be further reduced by cavitation and high native embolism. Although maple (diffuse porous) has narrower vessel diameters, its higher vessel density and greater total area of sapwood
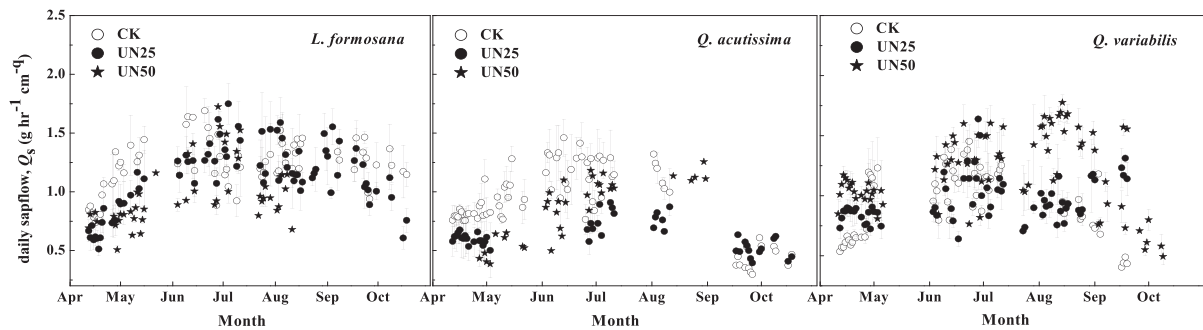
FIGURE 3 Daily sap flow (Q_s, standardized based on tree size) under different N treatments for the examined tree species. *L. formosana* = *Liquidambar formosana*; *Q. acutissima* = *Quercus acutissima*; *Q. variabilis* = *Quercus variabilis*
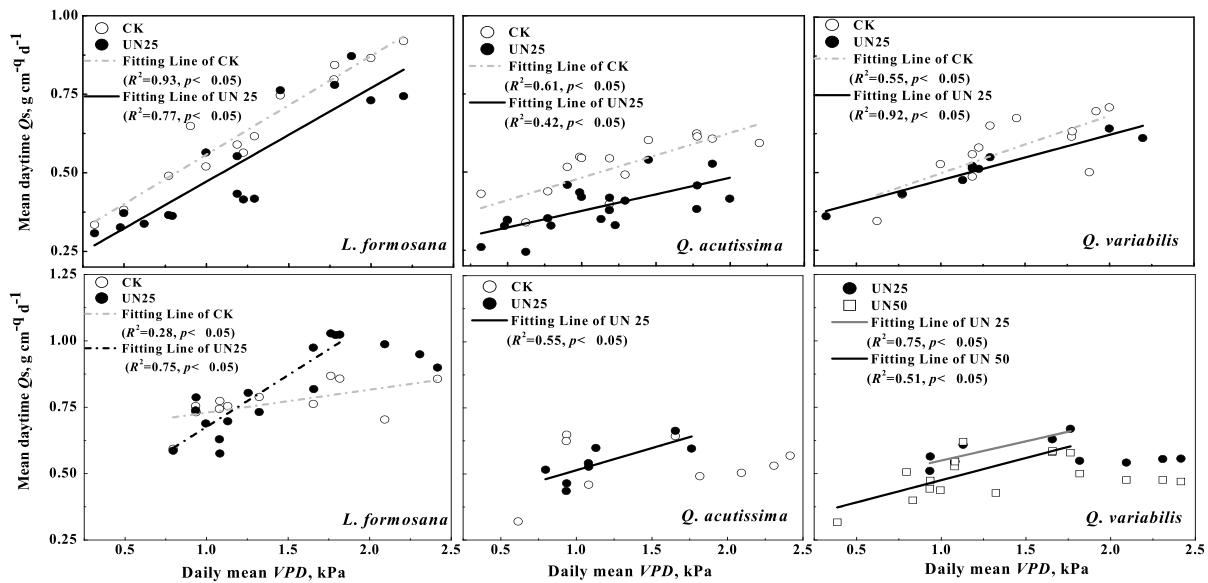

FIGURE 4 Response of average daily sap flux density to average daytime vapor pressure deficit (VPD) under different nitrogen treatments for the examined tree species in May (the upper row in the figure, data of UN50 were not available here) and August (the lower row in the figure, data of UN 50 for *Liquidambar formosana* [*L. formosana*] and *Quercus acutissima* [*Q. acutissima*], CK for *Quercus variabilis* [*Q. variabilis*] were not available here). Significant difference ($p < .05$) was found between CK and UN25 for the three species. Fitting lines of N treatments for *L. formosana* and *Q. variabilis* only included the data when VPD is <1.80 kPa in August

(data shown in Table 2) could more easily engender a higher water transpiration (Figure 3).

On the basis of the different responses to fluctuating environmental conditions, plants are generally classified as isohydry and anisohydry. Isohydric plants have strong stomatal control that results in a relatively constant midday leaf water potential (Ψ_{leaf}). On the contrary, anisohydric plants often have weak stomatal sensitivity to VPD and soil water content, leading to large fluctuations in the midday Ψ_{leaf} (Franks, Drake, & Froend, 2007; Martinez-Vilalta et al., 2014) and therefore induced high leaf gas exchange rates and water consumption (Franks et al., 2007). In our study, relationship between water transpiration of the three studied tree species and VPD under the wet and dry periods (Figure 4) might also reflect the different regulation mechanisms for the plants of different xylem types. Though leaf water potential was not measured in this study, the larger increase of mean daytime Q_s with the increased VPD for diffuse-porous maple might suggest a weak stomatal control and indicate a possible anisohydric regulation during the growing seasons.

For oak species, however, less water consumption and relatively flat change of transpiration with VPD would imply a deeper root system and an isohydric response (Bush et al., 2008), which was similar with other reports (Bucci, Scholz, Goldstein, Meinzer, & Arce, 2009; Meinzer et al., 2013). The different response of water transpiration to VPD between maple and oaks could be ascribed to following reasons. Firstly, as a result of large rooting depth and the ability to tap deeper sources of soil water, oaks species may have partly decoupled their leaf water potential and water uptake from changes in the availability of water at the soil depth of 50 cm (Lowenstein & Pallardy, 1998). In addition, oaks may have stabilized their sap flux through the maintenance of a constant driving force for soil-to-leaf water transport (Meinzer et al., 2013). The greater response of water use to VPD in the diffuse-porous maple than in the ring-porous oaks was consistent with previous observations of other researchers (Ford et al., 2011; Hölscher et al., 2005; Litvak et al., 2012; Oren & Pataki, 2001). In August, with much more precipitation and higher temperature, a decreased slope of the regression equation ($p < .05$) between

Q_s and VPD was observed for diffuse-porous species, similar to the results reported by Bush et al. (2008), who proposed that the progressive cavitation induced by the lack of stomatal regulation best explained the change in the relationship between J_s and VPD in growing season. However, in the case of oaks, we attribute the relatively flat (but high level) Q_s change with VPD more to the sufficient rainfall and high temperature in August that could promote the water transpiration even when VPD was less than 1 kPa.

4.2 | Impact of N addition on tree water use

Effects of N addition, as well as N availability, on tree hydraulic traits and plant water use have been investigated but results were mixed (Bucci et al., 2006; Felzer et al., 2011; Hacke et al., 2010; Ward et al., 2015; Watanabe et al., 2008). Because N supply has the potential to induce wider early wood and larger vessels, to increase leaf surface area and xylem hydraulic conductance, tree's water transpiration could increase following N addition (Bucci et al., 2006; Hacke et al., 2010; Hubbard, Ryan, Giardina, & Barnard, 2004; McCarthy et al., 2006; Watanabe et al., 2008). However, in the present study, water transpiration was generally decreased in dry condition under the N addition for maple and sawtooth oak, but N addition induced no significant change in water use for cork oak. We attributed the decrease or no significant change of water use to the relatively lower N application rate (25 and 50 kg ha^{-1} year^{-1}) compared to other studies (about 100 kg ha^{-1} year^{-1} or higher). Furthermore, the N addition experiment in JGS had been carried out for only 2 years, which might not be long enough to cause significant changes. In addition, the decrease of water use following N addition treatment could be a combined result of hydraulic and light mediated effects on water use. As high N addition could increase leaf surface area (the mean leaf area index (LAI) values for CK, UN25, and UN50 were 3.69 ± 0.42, 3.58 ± 0.40, and 4.21 ± 0.53, respectively), the induced greater leaf surface area would increase canopy self-shading, decrease PAR per unit leaf area and influence stomatal sensitivity to fluctuating irradiance in different locations within the canopy (Domec et al., 2009; Will & Teskey, 1997). Long-term monitoring of water transport under low-N versus high-N addition was necessary for further investigation.

We found that N addition significantly changed the response of water transpiration to VPD. Response of water transpiration to VPD changed significantly with N addition in the wet period (maple, in August) and slightly but also significantly decreased in the dry condition (in May; Figure 4, $p < .05$). The result was consistent with the study of Ward et al. (2015). In addition, the different responses of Q_s to VPD of cork oak under different N treatments indicated that the high N addition has a greater potential to weaken the sensitivity of tree water use to VPD than the low N addition. The observed decreases in daily mean Q_s following increased VPD may be ascribed to the changes in stomatal regulation. Because we did not observe significant changes in LAI and stem sapwood area, this shift in stomatal responses cannot be simply attributed to changes in the ratio of sapwood to leaf area. Previous studies proposed that structural adjustments or physiological changes, such as root biomass or distribution, explained the differences in water transport associated with fertilization (Chen, Yang, & Robinson, 2013; Domec et al., 2009;

Ward et al., 2015). To be specific, Domec et al. (2009) proposed that roots contributed the majority to total tree resistance for the water transport, even under high water availabilities, and would largely decrease the conductivity under dry conditions. Therefore, less biomass and nutrients allocation to roots compared with leaves following N addition could lead to the larger changes in the root area or root hydraulic conductivity, and finally affected the water transport of trees. More data related to some hydraulic and physiological traits are required to examine this hypothesis. In terms of tree species difference, the response of stomatal regulation (indicated by the Q_s-VPD relationship) to different water condition is indicative of water strategy under water stress for the ring- and diffuse-porous species. It has been hypothesized that the stress-induced mortality of isohydric species (ring porous) might be due to long-term stomatal closure rather than cavitation-caused hydraulic failure, leading to the sharp reduction of carbohydrate and then the starvation (McDowell et al., 2008; Sevanto, McDowell, Dickman, Pangle, & Pockman, 2014). Mitchell et al. (2013) have also revealed this mechanism in drought-induced mortality of *Pinus radiata*, and contrasted it with that of *Eucalyptus* species (diffuse porous) that were more likely to die from hydraulic failure. Therefore, N addition may not have the similar effect on the species that exhibit different xylem traits or stomatal regulation under drought condition, as also reflected by the different water transpiration responses of maple and oaks to N addition in this study.

5 | CONCLUSION

This study aimed to investigate the effect of N addition on water use of codominant ring- and diffuse-porous tree species in a temperate natural deciduous broadleaf forest, as well as their response to evaporative demand (VPD). The diffuse-porous *L. formosana* (maple) showed higher water transpiration than the ring-porous *Q. variabilis* (cork oak), and *Q. acutissima* (sawtooth oak). N addition reduced the average midday water transpiration for maple and sawtooth oak in the growth seasons but induced no significant change of water transport for cork oak compared to the control treatment. A linear relationship with much steeper slope was found between Q_s and VPD for diffuse-porous species, suggesting a weaker stomatal regulation under dry condition compared to the ring-porous species. In addition, the response of water transpiration to VPD for maple trees showed a significant difference after N addition under wet period. It was also noticeable that the Q_s of all three tree species decreased when the VPD value was higher than 1.80 kPa in August after N addition. N addition may not have similar effect on the tree species with different xylem traits or stomatal regulation as reflected by the different transpiration responses of maple and oaks to VPD.

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