High hydraulic risk is linked with high phosphorus availability across a broad range of tropical and subtropical species

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Abstract

N or P availability constrains plant growth in tropical and subtropical regions, and may influence plant hydraulic system that mediated forest vulnerability to drought. Although the effects of N/P availability on plant hydraulic traits have drawn much attention, most studies neglected the hydraulic failure threshold, and were limited to single species using fertilization experiments. This study aimed to fill this gap by examining how variation in the relative availability of N/P, as reflected by foliar N:P ratios, influences plant hydraulic failure threshold across a broad range of species by collecting published data and doing field experiments. The results demonstrated that increasing P availability would decrease the hydraulic safety margin (increase hydraulic failure risk) by regulating the leaf area: stem area ratio and vessel wall reinforcement. Forest droughtinduced mortality was predicted to increase with increasing temperature; however, this study suggests N deposition-driven decreases in P availability would potentially alleviate this trend.

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ABSTRACT

N or P availability constrains plant growth in tropical and subtropical regions, and may influence plant hydraulic system that mediated forest vulnerability to drought. Although the effects of N/P availability on plant hydraulic traits have drawn much attention, most studies neglected the hydraulic failure threshold, and were limited to single species using fertilization experiments. This study aimed to fill this gap by examining how variation in the relative availability of N/P, as reflected by foliar N:P ratios, influences plant hydraulic failure threshold across a broad range of species by collecting published data and doing field experiments. The results demonstrated that increasing P availability would decrease the hydraulic safety margin (increase hydraulic failure risk) by regulating the leaf area: stem area ratio and vessel wall reinforcement. Forest drought-induced mortality was predicted to increase with increasing temperature; however, this study suggests N deposition-driven decreases in P availability would potentially alleviate this trend.

INTRODUCTION

Low N and P availability limit primary productivity and plant growth rates in most tropical and subtropical regions (Koerselman & Meuleman 1996; Venterink *et al.* 2003; Vitousek *et al.* 2010; Chen *et al.* 2013), and was influenced by global change, increased atmospheric N deposition (Galloway *et al.* 2008) and conservation management (Gusewell 2004). N/P would influence patterns of carbon uptake and allocation (Christoffersen *et al.* 2016; Eller *et al.* 2018; Bittencourt *et al.* 2020). Therefore, plant hydraulic traits might change in coordination with photosynthetic capacity and plant morphology when nutrient availability patterns varying (Santiago 2015). Plant hydraulic traits determined their ability to avoid hydraulic failure (Choat *et al.* 2012) that has been considered as the most direct factor causing tree die-off under severe drought (Martinez-Vilalta *et al.* 2012; Nardini *et al.* 2013; O'Grady *et al.* 2013). Therefore, deciphering the effects of nutrition availability on plant hydraulic traits is crucial to improve the predictability of climate change and N deposition effects on vegetation productivity and forest mortality.

Many researchers have focused on the influence of nutrition availability on the plant hydraulic traits using fertilization experiments. For example, some researchers found that increase nutrient availability could significantly increase the water transport efficiency (specific conductivity of terminal stems (K_S)) (Amponsah

et al. 2004: Lovelock et al. 2004: Bucci et al. 2006: Hacke et al. 2010: Plavcova & Hacke 2012; Plavcova et al. 2013; Medeiros et al. 2016; Zhang et al. 2021). The main reason for this significant improvement in water efficiency after fertilization was an increase in vessel diameter (Hacke et al. 2010) or a change in pit structure (Choat *et al.* 2008). However, negative effects of increasing nutrient availability on K_S have also been found in some study (Faustino et al. 2015; Medeiros et al. 2016; Wanget al. 2016). Although increase nutrient availability may enhance stomatal control (reducing stomatal conductance (gs)) to avoid higher water losses, this adjustment may be insufficient to prevent a decrease in the minimum leaf water potential (Ψ_{\min}) due to the increasing ratio of leaf area: sapwood area (Bucci *et al.* 2006; Samuelson *et al.* 2008). Considering the trade-off between water transport capacity and cavitation tolerance, the effect of nutrient availability on plant hydraulic risk has also been explored by many researchers (Gleason et al. 2016). Some research has shown that nutrient availability can affect drought resistance (Hacke et al. 2001; Lens et al. 2011; Lenset al. 2013). For example, there is some evidence that cavitation resistance (-P50) might decrease with nutrient availability increasing (Harvey & vandenDriessche 1997; Harvey & van den Driessche 1999; Hacke et al. 2010) by reducing wood density (WD) (Chave et al. 2009; Savage & Cavender-Bares 2012; Reich 2014), and increasing vessel diameter and tree height (Coomes et al. 2007). Opposite responses have also been found in some studies that reported an increase in cavitation resistance with nutrient availability increasing due to changes in the traits of xylem pit membranes (Harvey & vandenDriessche 1997; Bucci et al. 2006; Villagra *et al.* 2013). The difference between Ψ_{\min} and P50, also called hydraulic safety margin, can represents the plant proximity to the point of catastrophic hydraulic dysfunction (Delzon & Cochard 2014); however, it is still unclear as to the influence of nutrient availability on safety margin. For example, the higher leaf area (Kozlowski & Pallardy 2002), larger stomatal conductance (Fangmeier et al. 1994), higher tree height (Wright et al. 2011), wider vessel diameters (Hacke et al. 2010), and thinner vessel cell wall thickness (Anttonen et al. 2002; Luo et al. 2005; Thomas et al. 2006) with nutrient availability increasing are likely to provide a narrow hydraulic safety margin and result in hydraulic failure during drought. However, increasing nutrient availability might widen safety margins by decreasing stomatal conductance (Goldstein et al. 2013), and changing pit membrane thickness and porosity (Hacke et al. 2004).

Although there has been an increasing number of controlled-manipulative experiments to investigate how plant hydraulic traits might respond to nutrient availability change, all of them are limited to a single species, and there is lack of a clear pattern on how nutrient availability affects hydraulic risk across a broad range of species and environments. Because of different experimental setups, fertilizers, fertilizing treatments, significant logistical challenges and extended response times, it is challenging to establish a universal rule by comparing various fertilization studies (Elser *et al.* 2007; Beikircher *et al.* 2019). As leaf N: P ratios have been identified useful to investigate shifts from N to P limitation and are easily determined and compared across species (Venterink *et al.* 2003; Gusewell 2004), we collected leaf N:P ratios to represent the relative availability of N and P (Koerselman & Meuleman 1996; Venterink *et al.* 2003). We tested the following hypotheses for species in tropical and subtropical regions: plants with higher nutrient availability would (1) reduce leaf water potential due to decrease in the sapwood area: leaf area ratio, and (2) reduce drought resistance due to decrease in vessel wall thickness and vessel wall reinforcement, and ultimately reduce the hydraulic safety margins.

2 MATERIALS AND METHODS

2.1 Data extraction

We searched the Web of Science using the keywords: "xylem conductivity" or "xylem vulnerability" or "xylem cavitation" or "gas exchange" or "stomatal conductance" or "safety margin" or "leaf water potential" or "plant hydraulic", and "nutrition" or "nitrogen" or "phosphorus". We chose studies in the tropical and subtropical region, where species were mainly under P limitation. Finally, we compiled nutrition data for 196 species from nine studies with corresponding K_S for 127 species, Ψ_{\min} for 105 species, safety margin for 96 species, g_S for 172 species, and P50 for 113 species (Table S1, Supplementary material). Climate data were taken from the paper in which safety margin data were published.

2.2 The field experiments

Study area and plant materials

For further researching the mechanisms of the relationships between nutrient availability and plant hydraulic systems, a field experiment was conducted in the Chenqi watershed $(1.3 \text{ km}^2, 25^{\circ}15' \text{ N}, 105 \text{deg46' E})$, Southwest China. The region is characterized as a typical subtropical monsoon climate, with a mean annual temperature of 15.1 and an annual average precipitation of 1140 mm (Puding climate station, 19 km away from Chenqi watershed), with 80% of the annual precipitation occurring during the wet season (from May to October). The main lithology is limestone and dolomite of the Guanling Formation of the middle Triassic, intercalated with gypsum strata. The main vegetation type is deciduous broad-leaved forest including 9 woody species (Table 1).

[Please insert Table 1 here]

[Please insert Figure 1 here]

Soil, leaf, and stem traits

Photosynthetic parameters

We used a LI-6400 (Li-Cor, Lincoln, Nebraska, USA) to measure stomatal conductance (g_S , mmol m⁻² s⁻¹) of the most recently and fully expanded leaves during August 2017, between 9:00 and 11:00 am. Six to eight sun-exposed mature leaves from 3–5 individuals per species were measured under ambient CO₂ concentration (about 400 mmol m⁻²s⁻¹). Because different plant species have variable light saturation points, the photosynthetic photon flux density (PPFD) was set from 1200 to 1500 mmol m⁻²s⁻¹. All photosynthetic parameters were measured *in-situ*. The leaf to air vapor pressure deficit was <1.6 kPa.

Leaf nutrients and structure

After measuring photosynthetic parameters, 15–20 sun-exposed mature leaves at the same position were collected for leaf nutrient and structure measurements. The leaves with rachis removed were oven-dried at 70 degC for 48 hours and then ground and homogenized for subsequent analyses. Plant total N concentrations based on mass (N_{mass} , mg g⁻¹) and area (N_{area} , g m⁻²) were determined using the Kjeldhal method. Total P concentrations based on mass (P_{mass} , mg g⁻¹) and area (P_{area} , g m⁻²) were determined using carbon isotope ratio atomic absorption spectrum photometry at the Key Laboratory of Agro-ecological Processes in Subtropical Regions, Institute of Subtropical Agriculture, Chinese Academy of Sciences.

Leaf water potential

Leaf water potential was measured with a pressure chamber (PSM-1505D, USA) on single fascicles from the mid-canopy of the trees. The predawn leaf water potential (Ψ_{predawn} , MPa) and min leaf water potential (Ψ_{min} , MPa) were measured at 5:00–6:00 and 13:00–14:00 in the later period of extreme drought events, respectively. For each species, 5-6 terminal shoots from different individual were excised and immediately placed in a black plastic bag with moist paper towel and kept in a cooler to stop transpiration. All leaf water potential measurements were taken within 10 min after removal from the tree. The hydraulic safety margin (MPa) is defined as the difference in water potential between the minimum value experienced in the field and the value at either 50% loss of leaf or stem xylem hydraulic conductivity (Ψ_{min} , P50) (Johnson*et al.* 2011).

Stem traits

We used a long-reach pruner to collect at least ten middle canopy branches (about 10 mm in diameter, one-year-old branches) from three to five mature tall plants of each species early in the morning (5:30–6:30 am) on a rainy day. The branches were sealed in black plastic bags with a moist towel and immediately transported to the laboratory. The detached branches were recut about 10–20 cm from the ends under water immediately after harvesting to preserve xylem water continuity; the resulting length of the stem segments was 40–90 cm. These stem segments were then used to determine the specific conductivity of terminal stems using the method described by Sperry *et al.*(1988). In an air-conditioned laboratory (26 °C), branch segments

were flushed with 0.1 mol L⁻¹ KCl solution at a pressure of 0.1 MPa for 25 min to remove air embolisms. Hydraulic conductivity per unit pressure gradient (K_h , Kg m s⁻¹ MPa⁻¹) was calculated using Eq. (1):

where F is the water flux rate (F), dp is the pressure drop along the length of the segment (dx, m), and dp/dx is the pressure gradient (MPa m⁻¹) (Santiago*et al.* 2004).

The specific conductivity of terminal stems (K_S , kg m⁻¹ s⁻¹ MPa⁻¹) is equal to the value of K_h divided by *the* sapwood cross-section area as defined by Eq. (2):

$$K_{\rm S} = \frac{K_{\rm h}}{A_{\rm SW}} \tag{2}$$

where Asw is the average sapwood area of the segment (m²).

The dehydration method was used to establish xylem vulnerability curves (Sperry *et al.* 2012). In the early morning, 30–50 branches from 10–20 mature individuals (1-year-old branches of approximately 10 mm in diameter) were collected, and the cut end of each branch was immediately wrapped in parafilm, and the entire branch was covered in black plastic bags to prevent excessive evaporation. In the laboratory, the branches were exposed to various states of dehydration untill a target dehydration condition was reached. We sealed the branches in black plastic bags and waited for the water potential to equilibrate. We measured two ends of the leaf for water potential (p), and the average water potential of the leaves was used to represent the xylem water potential (the difference between the leaves was <0.3 MPa). The corresponding xylem water conductivity (K_i) and maximum xylem water conductivity (K_{max}) were measured to calculate the percentage loss of xylem conductivity (PLC) using Eq. (3):

PLC (%) = 100 ×
$$(1 - \frac{K_h}{K_{\text{max}}})$$
 (3)

For each branch, the relationship between PLC and xylem water pressure was fitted with Eq. (4):

$$PLC = \frac{100}{1 + e^{a \times (p-b)}} \tag{4}$$

where PLC is the percentage loss of hydraulic conductivity (%), p is the xylem water potential (MPa), and a and bare the estimated parameters of the PLC curve— b represents P50, which is negatively related to cavitation resistance, and a is the slope of the vulnerability curve.

The Huber value (HV) was calculated as the ratio of wood cross-section per unit leaf area attached (sapwood area: leaf area ratio). The same branches used for hydraulic conductivity measurements were cut into small segments to measure sapwood density (WD, g cm⁻³) and anatomical measurements, which represents the ratio of dry mass to fresh volume. We removed the bark or pith and immersed the fresh sapwood in distilled water (12 h) to saturate the sample (Zhu *et al.* 2013). The volume of sapwood was determined by water displacement, and its dry mass was determined after oven-drying at 70 °C for 72 h.

Anatomical measurements

The segment samples were conserved in formalin-acetic acid-alcohol (FAA) for 1 month. Then we measured the anatomical characteries at Guangxi University, China; 5–6 segments from 3–5 individuals per species were selected for anatomical measurements. Then, 25-um-thick cross-sections were cut using a sliding microtome (SM2010R; Nusslock, Germany). A mixture of polystyrene and ethyl acetate was brushed on the sample's exposed surface to prevent the sections from deforming before cutting (Barbosa *et al.* 2010). Then we fixed the section to the slide with an adhesive that consists of glycerinate egg albumin, and stained the sections

with Safranin-Alcian blue and mounted in Canadian balsam medium. Finally, microphotographs of crosssections were taken at $\times 40$ or $\times 20$ using a light microscope with a camera (Leica DM 3000 LED; Wetzlar, Germany) and stacked with Leica APPLICATION SUITE (v.4.11; Switzerland) (Figure S2, Supplementary material). The vessel diameter and wall were identified using the tool in IMAGEJ software (Zieminska *et al.*2013). Vessel wall reinforcement (t/b) was the ratio of the thickness of the double wall of adjacent vessel (t) to the mean diameter (b) of adjacent vessel. Note that the samples of *Platycarya longipes* was missing with anatomical measurements.

2.3 Statistical analysis

We used the Kolmogorov–Smirnov test to quantify the normal distribution of sample data; then right/leftskewed data were log-transformed to reduce skewness. To examine the associations between leaf N:P and hydraulic and leaf traits across species, we first tested weather the variables were approximately normally distributed. Then, we fit bivariate relationships using Pearson correlation analyses. The partial correlation coefficients between leaf N:P and hydraulic traits with significant levels (p < 0.05) were also determined across species with IBM SPSS Statistics.

We performed path analysis in SmartPLS 3. Path analysis was used to determine the possible influence pathways between traits, and a simplified model of best fit was established to show significant correlation pathways, and the redundance (Q^2) , path coefficient (r) and its significant level (P) and goodness of fit (R^2) were calculated with this software.

3 RESULTS

3.1 The patterns of nutrition status

The leaf N:P ratio varied considerably among species (Figure 1); 68% of plants had a higher leaf N:P ratio than 16, while only 16% of plants had a lower leaf N:P ratio than 14, indicating that most plants are under P limitation.

3.2 Relationships between leaf N: P and plant hydraulics

In terms of the collected data from literatures (Figure 2), leaf N:P ratio was significantly negatively correlated with the hydraulic conductivity of stems (Ks, Figure 2a, r = -0.37, p < 0.01), stomatal conductance (gs, Figure 2b, r = -0.20, p < 0.05) and cavitation vulnerability (P50, Figure 2d, r = -0.21, p < 0.05), but positively correlated with minimum leaf water potential (Ψ_{min} , Figure 2c, r = 0.36, p < 0.01) and hydraulic safety margin (Figure 2e, r = 0.49, p < 0.01). Note that Ks, gs, Ψ_{min} , and P50 were log-transformed to reduce skewness. Moreover, given the potential influence of climate variability on the safety margin, a partial correlation analysis was carried out among leaf N:P, safety margin, and Arid Index (AI), and the results showed that the N:P-safety margin relationship remained significant after accounting for covariation with the AI (Figure 2e, r = 0.42, p < 0.01).

[Please insert Figure 1 here]

[Please insert Figure 2 here]

In terms of the field survey data, Figure 3 shows that the leaf N:P ratio was significantly positively correlated with Ψ_{\min} (Figure 3a, r = 0.68, p < 0.01) and safety margin (Figure 3c, r = 0.84, p < 0.01), but negatively correlated with P50 (Figure 3b, r = -0.79, p < 0.01). These patterns were generally similar with the results of the collected data analysis, except that the leaf N:P ratio was not significantly related with Ks or gs for the field survey data (Figure 3d and 3e, p > 0.05).

[Please insert Figure 3 here]

3.3 Physiological mechanistic linkage between leaf N:P and xylem hydraulics

To determine the physiological mechanic linkage between nutrient availability and plant hydraulic traits, the HV, WD, and xylem anatomy structure were measured in this study. As shown in Figure 3, the leaf N:P

ratio was significantly correlated with the HV (Figure 3f, r = 0.79, p < 0.01), vessel wall thickness (t, Figure 3g, r = 0.77, p < 0.01) and vessel wall reinforcement (t/b, Figure 3h, r = 0.85, p < 0.01), but not with WD (Figure 3i, p > 0.05). A priori conceptual framework was established by the path analysis model in terms of the known relationships of the aforementioned two hypotheses; The results showed that nutrient availability controlled the safety margin by regulating the HV or vessel wall reinforcement (t/b) (Figure 4).

[Please insert Figure 4 here]

4 DISCUSSION

Nutrient availability plays a key role in plant growth, photosynthesis rate carbon allocation and so on (Maire *et al.* 2015), and these plant processes are tightly correlated with leaf water potential, stem cavitation resistance (Santiago *et al.* 2004), which potentially affect the risk degree of hydraulic failure. We identified the relationships between nutrient availability and the plant's hydraulic traits based on data collected from tropical and subtropical regions. We used the foliar N:P ratio to represent the relative availability of N and P. To our knowledge, this is the first study to reveal how nutrient availability influence the plants hydraulic safety margin, especially across a broad range of species.

4.1 Increasing P availability decrease safety margin via reducing t/b

More than two thirds of the plants in this study were under P limitation (leaf N:P >16, Figure 1), and only 16% of plants were under N limitation (leaf N:P <14), which was attributed to the substrate age and higher rates of leaching associated with higher rainfall in tropical and subtropical regions (Reich & Oleksyn 2004; Peltzer *et al.* 2010). As expected, increasing P availability resulted in a considerable decrease in the plant hydraulic safety margin in both the collected data from publications and field survey of this study (Figures 2e and 3c), which suggests that plants have higher hydraulic risk with higher P availability. According to the definition of the safety margin, this result can be explained by the change in P50 and/or Ψ_{\min} with nutrient availability variation (Figures 2c, 2d, 3a, and 3b).

In both the data collection and field survey analyses, P50 decreased with decreasing P availability (Figures 2d and 2b, P < 0.05), which was similar to the results from fertilization experiments (Harvey & vandenDriessche 1997; Harvey & van den Driessche 1999; Hackeet al. 2010); these previous studies showed that improving P availability decrease cavitation resistance by decreasing the WD as a consequence of the faster growth rate (Harvey & vandenDriessche 1997; Ewers et al. 2000). However, in this study, nutrient availability had no significant relationships with WD in this study (Figure 3i, p > 0.05), while vessel wall thickness (t) and vessel wall reinforcement (t/b) significantly decreased with increasing P availability (Figure 3e and 3f, p < 10.01). Several previous studies also reported that increasing nutrient availability would improve the xylem growth rate resulting in a decreased cell wall thickness (Anttonen et al. 2002; Luo et al. 2005; Thomaset al. 2006), and a thinner cell wall thickness potentially resulted in a thinner and more porous pit membranes (Jacobsen et al. 2005; Wheeler et al. 2005; Li et al. 2016), which is essential for determining xylem embolism resistance (Hacke et al. 2001; Li et al. 2016). Moreover, the weaker vessel wall reinforcement will weaken the deflection of walls and potentially damage to pit membranes. Thus, we made a hypothesis that increasing P availability reduces the vessel wall reinforcement, and then reduces the hydraulic cavitation resistance (-P50) and safety margin; this hypothesis, for the first time, was confirmed with the path analysis mode (Figure 4a). Although previous research showed that alleviating nutrition limitation can increase the availability of sugars for xylem embolism repair to offset the narrow safety margin (Zwieniecki & Holbrook 2009; Sala et al. 2010; Gessler et al. 2017), refilling does not represent an effective escape strategy for mitigating the effects of severe and persistent drought (Choat et al. 2012). Therefore, increasing P availability could decrease safety margin via reducing t/b, and potentially increase the forest drought-induced mortality rate.

4.2 Increasing P availability decrease safety margin via reducing HV

In both the data collection and field survey analyses, Ψ_{\min} increased with P availability decreasing (Figures 2c and 3a, p < 0.05), which is similar to the results from some fertilization experiments (Clearwater & Meinzer 2001; Bucci *et al.* 2006; Domec *et al.* 2009). This might be that nutrient availability changes the carbon

allocation by mediating cytokinins, then reduce the ratio between sapwood area and leaf area (HV) (Forde 2002; de Groot *et al.* 2003) for enhancing light and CO₂capture (Cannell & Dewar 1994). When P availability increased, the total leaf area increased, but sapwood area did not increase proportionally; therefore, it still cannot fully compensate for the greater transpiration demand, causing an imbalance between water uptake and supply to the leaves, and leading to a lower Ψ_{\min} and safety margin (Enquist *et al.* 2000; Bucci *et al.*2006). The path analysis model partly confirmed that increasing P availability would reduce the hydraulic safety margin via the HV (Figure 4b), and there was a significant relationship between the leaf N:P ratio and Ψ_{\min} . However, we did not find a linkage between HV and Ψ_{\min} , and the physiological mechanism still requires further research. For example, belowground growth was not measured in the present study, but we speculate that alleviating nutrition limitation may influence the Ψ_{\min} via a greater increase in aboveground biomass than in belowground carbon allocation or deeper root depth, which would then result in an unbalanced leaf water potential (Stape *et al.* 2008; Novaes *et al.* 2009).

The collected data showed that increasing P availability increased the Ks and gs (Figure 2a, P < 0.05), which is similar to the results of previous research that were attributed to the increasing vessel diameter after fertilization (Bucci *et al.* 2006; Hacke *et al.* 2010; Plavcova & Hacke 2012; Plavcova *et al.* 2013; Medeiros*et al.* 2016). Although stem hydraulic conductivity increases with increasing P availability, this adjustment is insufficient to prevent an increase in the water deficit (water potential and safety margin becoming more negative) due to the decreasing stomatal control (increasing stomatal conductance, Figure 2). However, the significant relationship between the leaf N:P ratio and Ks did not exist in the field survey analysis, and we speculate that this is because the contribution of genetics to the observed phenotypic variation in Ks was higher than that of the environment.

The present study suggested that, except for water stress, the increasing P availability would reduce the sapwood area:leaf area ratio and the vessel wall reinforcement, and then reduce the hydraulic safety margin (Figure 4b), and led to the variable hydraulic risk across a broad range of species. These findings provide new insights into why safety margins are largely independent of mean annual precipitation (Choat *et al.* 2012); predictions on the vulnerability of forests to drought might be improved by the inclusion of N/P availability in community and ecosystem models.

Conclusions

Significant correlations between the nutrient availability and plant hydraulic traits (Ψ_{\min} , P50, and safety margin) were found across a broad range of species; this suggests that increasing P availability universally increases the leaf water deficit and aggravates the risk of hydraulic failure by influencing carbon investment (HV and vessel wall reinforcement) in tropical and subtropical region. Our results highlight that the effects of nutrition balance change on plant hydraulic systems should be adequately considered to assess the vulnerability of forests to drought under future global change.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article

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Table 1 Characteristics of the 9 woody species tested in the present study

| Species Family | | Code | Canopy height (m) | | |
|------------------------|--------------|---------------|-------------------|--|--|
| Eucommia ulmoides | Eucommiaceae | Eu | 5-6 | | |
| Pyrus pyrifolia | Rosaceae | Рp | 5-6 | | |
| Catalpa bungei | Bignoniaceae | Cb | 8-9 | | |
| Toona sinensis | Meliaceae | Ts | 11 - 13 | | |
| Quercus fabri | Fagaceae | Qf | 9-10 | | |
| Populus Adenopoda | Salicaceae | Pa | 10 - 13 | | |
| Kalopanax septemlobus | Araliaceae | Ks | 11 - 12 | | |
| Platycarya strobilacea | Juglandaceae | \mathbf{Ps} | 7–8 | | |
| Platycarya longipes | Juglandaceae | Pl | 5 - 6 | | |

 ${\bf Table \ 2} \ {\rm Characteristics \ of \ leaf \ and \ stem \ traits \ measured}$

| Parameter | Parameter | Abbreviation | Unit | Average |
|--|------------------------------|------------------------------|--|---------|
| Leaf nitrogen unit dry mass | N _{mass} | N _{mass} | mg g ⁻¹ | 19.64 |
| Leaf nitrogen unit leaf area | N_{area} | N_{area} | $g m^{-2}$ | 1.67 |
| Leaf phosphorus unit dry mass | $\mathbf{P}_{\mathrm{mass}}$ | $\mathbf{P}_{\mathrm{mass}}$ | $mg g^{-1}$ | 1.06 |
| Leaf phosphorus unit leaf area | $\mathbf{P}_{\mathrm{area}}$ | $\mathbf{P}_{\mathrm{area}}$ | $\mathrm{g}~\mathrm{m}^{-2}$ | 0.09 |
| Leaf nitrogen / phosphorus ratio | N:P | N:P | None | 21.06 |
| Predawn leaf water potential | $\Psi_{ m predawn}$ | $\Psi_{ m predawn}$ | MPa | -0.16 |
| Min leaf water potential | $\Psi_{ m min}$ | $\Psi_{ m min}$ | MPa | -2.03 |
| Stomatal conductance | $g_{\rm S}$ | $g_{\rm S}$ | mmol m ⁻² s ⁻¹ | 0.21 |
| Specific conductivity of terminal stems | K_S | $ m K_S$ | $\mathrm{Kg}~\mathrm{m}^{-1}\mathrm{s}^{-1}~\mathrm{MPa}^{-1}$ | 5.85 |
| Xylem water potential at 50% loss of hydraulic conductivity | P50 | P50 | MPa | -2.25 |
| Wood density | WD | WD | ${ m g~cm^{-3}}$ | 0.56 |
| Hydraulic safety margin | \mathbf{SM} | \mathbf{SM} | MPa | 0.23 |
| Huber value | HV | HV | $\times 10^{-4}$ | 1.260 |
| Vessel wall thickness | \mathbf{t} | t | μm | 2.20 |
| Vessel wall reinforcement | t/b | t/b | $\mu m \mu m^{-1}$ | 0.04 |



Figure 1.



Figure 2.



Figure 3 .



Figure 4.

FIGURE CAPTIONS

Figure 1. The relationship between mass-based leaf P concentrations (P_{mass}) and leaf N concentrations (N_{mass}) . Gray lines represent the N:P ratios of 14 and 16. Points above the N:P = 16 line indicate P limitation; points below the N:P = 14 line indicate N limitation.

Figure 2. The relationships between leaf nutrient and hydraulic architecture with collection data. Data points represent the individual species values. Ks, specific conductivity of terminal stems; Ψ_{\min} , min leaf water potential; P50, xylem water potential at 50% loss of hydraulic conductivity; SM, hydraulic safety margin; AI, aridity index; the r(AI) in Figure 2e represents the partial correlation between the leaf N:P ratio and SM but with controlled AI.

Figure 3. The relationships between leaf nutrient and hydraulic architecture with field survey data. Data points represent the individual species values. Ks, specific conductivity of terminal stems; Ψ_{\min} , min leaf water potential; P50, xylem water potential at 50% loss of hydraulic conductivity; t, vessel wall thickness; t/b, vessel wall reinforcement.

Figure 4. Path analysis model of how the leaf N:P ratio influences the safety margin for nine select species in the field survey analysis (Q²>0). Path coefficients and their level of significance are given. *, p < 0.05; **,

p < 0.01, ^{ns}, p > 0.05. The red line shows a positive correlation. The blue line shows a negative correlation. N:P, leaf nitrogen: phosphorus ratio; HV, Huber value; t/b, vessel wall reinforcement; Ψ_{\min} , min leaf water potential; P50, xylem water potential at 50% loss of hydraulic conductivity; SM, hydraulic safety margin; t/b, vessel wall reinforcement.