

Article

Savanna Plants Have a Lower Hydraulic Efficiency than Co-Occurring Species in a Rainforest

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Abstract: A plant species can have diverse hydraulic strategies to adapt to different environments. However, the water transport divergence of co-occurring species in contrasting habitats remains poorly studied but is important for understanding their ecophysiology adaptation to their environments. Here, we investigated whole-branch, stem and leaf water transport strategies and associated morphology traits of 11 co-occurring plant species in Yuanjiang valley-type savanna (YJ) with dry-hot habitats and Xishuangbanna tropical seasonal rainforest (XSBN) with wet-hot habits and tested the hypothesis that plants in YJ have a lower water transport efficiency than co-occurring species in XSBN. We found high variation in whole-branch, stem and leaf hydraulic conductance (K_{shoot} , K_{stem} and K_{leaf}) between YJ and XSBN, and that K_{stem} was significantly higher than K_{leaf} in these two sites (K_{stem}/K_{leaf} : 16.77 in YJ and 6.72 in XSBN). These plants in YJ with significantly lower K_{shoot} and K_{leaf} but higher sapwood density (WD) and leaf mass per area (LMA) showed a lower water transport efficiency regarding less water loss and the adaptation to the dry-hot habitat compared to co-occurring species in XSBN. In contrast, these co-occurring plants in XSBN with higher K_{shoot} and K_{leaf} but lower WD and LMA tended to maximize water transport efficiency and thus growth potential in the wet-hot habitat. Our findings suggest that these co-occurring species employ divergent hydraulic efficiency across YJ and XSBN so that they can benefit from the contrasting hydraulic strategies in adaptation to their respective habitats.

Keywords: dry-hot habitats; hydraulic conductance; water availability; water transport



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1. Introduction

The intensity and frequency of drought are increasing globally and will continue to rise in the future [1]. Drought, as a key environmental factor, affects plant growth and productivity, and limits their abundance and distribution [2–4], even threatening plant survival and forest health [5–7]. Plant hydraulic dysfunction is probably a primary cause of dieback and death in plants and forests [8–10]. Thus, revealing differences in the hydraulic strategies of co-occurring plants in dry habitats with low water availability and in wet environments with favorable water status can provide a better understanding of how they adapt and respond to drought with climate change.

Plant hydraulic conductance (water transport efficiency through roots, stems and leaves) is a key parameter in describing hydraulic strategies [11,12]. For example, leaves generally have lower hydraulic conductance than stems, which allows plants to maintain the water status of the high-carbon-investment stems [11], because the reduction in water loss due to low hydraulic conductance (high resistance to water transport) in leaves helps

to decrease the water stress of the stems to minimize cavitation [13–16]. Through the leaf–stem hydraulic distribution, plants can retain high plant water potentials and prevent drought-induced catastrophic hydraulic failure [11,17]. Therefore, investigating the water transport strategy in leaves and stems can provide insight into hydraulic mechanisms in predicting plant performance and in response to drought.

Plant hydraulic traits are associated with environmental conditions, i.e., dry vs. wet habitats [18–22]. Plants in dry environments generally have narrower vessels than co-occurring species in wet environments [18,23]. In the dry–hot savanna, lianas have smaller vessel diameter and thus theoretically lower hydraulic conductance compared to those in wet–hot tropical seasonal rainforests [21,22]. In addition, plants adapt to drought environments through multiple strategies due to trait syndromes [17,24,25]. On the one hand, plants employ some traits associated with low hydraulic efficiency and growth rates (such as narrow vessels, low hydraulically weighted vessel diameter and stomatal conductance, and small leaf sizes) in dry–hot habitats [21–23,26,27]. On the other hand, they also show a trait combination associated with high drought tolerance (such as high wood density, water use efficiency and leaf mass per area LMA, and low leaf water potential at leaf turgor loss) [20,21,27,28].

In contrast, plants in rainforests with wet–hot habitats generally have larger hydraulically weighted vessel diameter and leaf sizes [21]. Plants with large vessels and thus high water transport efficiency can supply enough water to leaves to meet their transpiration demand in favorable water conditions [29,30]. Plants in wet–hot environments also show low LMA [27,28], which is typically related to high leaf photosynthesis and productivity across tree species in various ecosystems [31–34]. Therefore, plants in wet habitats tend to adopt a fast-growth strategy to maximize their hydraulic efficiency, growth and productivity [34,35]. Although the above studies have revealed that plants from dry and wet habitats can have contrasting ecophysiology strategies, we still have little direct evidence of a comparison of water transport strategy based on hydraulic conductance in the same species between dry and wet environments.

In southwest China, there are two distinct ecosystem types: the Yuanjiang valley-type savanna (YJ) with low precipitation and soil water availability, and high temperature, irradiance and evaporative demand throughout the year [28,36]; and the Xishuangbanna tropical seasonal rainforest (XSBN) with relatively high precipitation and water availability (see Table 1). The YJ dry–hot and XSBN wet–hot habitats give us a good opportunity to evaluate how plants, as regards water transport strategies, respond to these two contrasting habitats. We expect that co-occurring species in YJ and XSBN should exhibit divergent water transport strategies to succeed in their respective habitats.

Table 1. Information of the two study sites: Yuanjiang valley-type savanna (YJ) and Xishuangbanna tropical seasonal rainforest (XSBN).

Variables	Site	
	YJ	XSBN
Geographical location	23°28' N, 102°11' E	21°54' N, 101°46' E
Elevation	481 m	570 m
Vegetation type	valley-type savanna	tropical seasonal rainforest
Soil type	ferralic cambisol	latosol
Soil water content	7.22 cm ³ cm ^{−3}	25.2 cm ³ cm ^{−3}
Mean annual temperature	25.0 °C	22.7 °C
Extreme maximum temperatures	45 °C	40.5 °C
Mean annual precipitation	732.8 mm	1504.6 mm
Potential evaporation	2220 mm	1507 mm
Aridity index	0.33	0.96
Soil N	3.96 mg g ^{−1}	3.07 mg g ^{−1}
Soil P	1.30 mg g ^{−1}	0.69 mg g ^{−1}
Soil K	12.72 mg g ^{−1}	10.84 mg g ^{−1}

Therefore, the aim of this study was to evaluate how co-occurring woody plants between these two habitats with contrasting water availability differ in their branch and leaf water transport strategies. Specifically, the question and the corresponding hypothesis are as follows: Do woody plants in the valley-type savanna employ a lower water transport efficiency than co-occurring species from the rainforest? Given the water stress of the valley-type savanna, we hypothesize that the valley-type savanna plants have a lower hydraulic efficiency than co-occurring species from the rainforest; that is, savanna plants have lower whole-branch, stem and leaf hydraulic conductance, but higher sapwood density, petiole mass and leaf mass per area than co-occurring species from the tropical seasonal rainforest.

2. Materials and Methods

2.1. Study Site

This experiment was conducted at two contrasting sites in Yunnan Province, Southwest China: the Yuanjiang valley-type savanna (YJ) and the Xishuangbanna tropical seasonal rainforest (XSBN). The YJ and XSBN are characterized by dry-hot and wet-hot climate conditions, respectively [27]. The YJ site is in the Yuanjiang valley-type savanna ecosystem (23°28' N, 102°11' E; 481 m asl.), Southwest China (Table 1), which is a typically dry-hot habitat with high light and heat resources but low vegetation coverage. The XSBN site is located on the northern edge of the tropical region in Southeast Asia (21°41' N, 101°25' E; 570 m asl.), Xishuangbanna, Southwest China (Table 1), which is characterized by a wet-hot habitat with high vegetation coverage.

The mean annual air temperature and extreme high temperature are 25.0 °C and 45.0 °C, respectively [36], which are 2.3 °C and 4.5 °C higher than in the XSBN (Table 1). The YJ also shows a lower aridity index than that of XSBN, which indicates a drier habitat in YJ. The mean annual precipitation in YJ is 732.8, which is only approximately half of that of the XSBN. The total soil N, P, and K in YJ were 3.96, 1.30, and 12.72 mg g^{−1}, respectively [21], which were higher than in XSBN (Table 1).

2.2. Plant Materials and Sampling

In this study, we selected 11 co-occurring woody species (Table 2) from these two sites (YJ and XSBN). These species included three different leaf habits (evergreen, semi-deciduous and deciduous) [7,25]. During June and September (growing season) in 2023, we collected the branch samples of these co-occurring woody species similar diameter at breast height in YJ and XSBN. Six branches measuring 7–12 mm in diameter and 0.8–2 m in length for each species in each site were sampled randomly. A total of 66 branches were collected for each site. Hydraulic conductance was measured using a high-pressure flow meter (HPFM Gen3; Dynamax Corp., Elkhart, IN, USA). After the measurements of hydraulic traits, the associated morphological traits of these samples were determined (Table 3).

Table 2. List of 11 co-occurring species from these two study sites (YJ and XSBN).

Latin Name	Family	Leaf Habit
<i>Bauhinia brachycarpa</i> Wall. ex Benth.	Fabaceae	Semideciduous
<i>Broussonetia papyrifera</i> (L.) L'Hér. ex Vent.	Moraceae	Deciduous
<i>Cipadessa baccifera</i> (Roth) Miq.	Meliaceae	Deciduous
<i>Garuga forrestii</i> W. W. Sm.	Burseraceae	Deciduous
<i>Huberantha cerasoides</i> (Roxb.) Chaowasku	Annonaceae	Semideciduous
<i>Jatropha curcas</i> L.	Euphorbiaceae	Deciduous
<i>Mangifera indica</i> L.	Anacardiaceae	Evergreen
<i>Murraya exotica</i> L.	Rutaceae	Evergreen
<i>Phyllanthus emblica</i> L.	Phyllanthaceae	Deciduous
<i>Pistacia weinmannifolia</i> J. Poiss. ex Franch.	Anacardiaceae	Evergreen
<i>Tamarindus indica</i> L.	Fabaceae	Semideciduous

Table 3. Traits measured in this study.

Traits	Abbreviation	Units
Whole-branch hydraulic conductance	K_{shoot}	$\times 10^{-4} \text{ kg s}^{-1} \text{ MPa}^{-1} \text{ m}^{-2}$
Stem hydraulic conductance	K_{stem}	$\times 10^{-4} \text{ kg s}^{-1} \text{ MPa}^{-1} \text{ m}^{-2}$
Leaf hydraulic conductance	K_{leaf}	$\times 10^{-4} \text{ kg s}^{-1} \text{ MPa}^{-1} \text{ m}^{-2}$
Ratio of stem to leaf hydraulic conductance	$K_{\text{stem}}/K_{\text{leaf}}$	
Sapwood density	WD	g cm^{-3}
Leaf mass per area	LMA	g m^{-2}
Ratio of petiole mass to lamina mass	PM/LM	
Petiole mass	PM	g

2.3. Measurements of Hydraulic Conductance

We measured the whole-branch, stem and leaf hydraulic conductance using the HPFM (Figure S1). This method was described in previous studies [25,36]. Briefly, we generally sampled branches at dawn and the branch end was immediately re-cut underwater. We then took the branches to the laboratory. Then, a sample branch underwater was connected to the HPFM to measure the whole-branch hydraulic conductance (K_{shoot}). After the K_{shoot} values became stable, the K_{shoot} was determined. Then, all leaves (including laminae and petioles) were rapidly removed to determine the stem hydraulic conductance (K_{stem}). After that, leaf hydraulic conductance (K_{leaf}) was calculated as $1/(1/K_{\text{shoot}} - 1/K_{\text{stem}})$. After finishing these hydraulic conductance measurements, we used a scanner, CanoScan 9000F Mark II (CANON, Tokyo, Japan), to scan the cut leaves, and used the ImageJ 1.52a (National Institutes of Health, Bethesda, MD, USA) to calculate leaf area (LA, m^2). Finally, K_{shoot} , K_{stem} and K_{leaf} were standardized by LA. $K_{\text{stem}}/K_{\text{leaf}}$ was calculated as the ratio of K_{stem} to K_{leaf} (Table 3).

2.4. Measurements of Morphological Traits

After the measurements of hydraulic conductance, sample branches were used to measure sapwood density (WD, g cm^{-3}). A small segment measuring 3–5 cm length of the branch was peeled to remove the bark and pith; the fresh sapwood volume was determined using the water displacement method. Then, the segment without bark and pith was placed in an oven at 80 °C for over 48 h and weighed using a precision balance with a ten-thousandth resolution. The WD was calculated as the ratio of the dry weight to sapwood volume. In addition, all laminae and petioles cut from the sample branches were placed in an oven at 80 °C for over 48 h, and the dry weight for laminae and petioles (LM and PM, g) was measured using a precision balance with a ten-thousandth resolution. Leaf mass per area (LMA, g m^{-2}) was calculated as the ratio of the dry weight of leaves to leaf area, and the ratio of petiole mass to lamina mass (PM/LM) was calculated as the ratio of the dry weight of petioles to the dry weight of leaves.

2.5. Statistical Analyses

The differences in eight traits between YJ and XSBN for 11 co-occurring species were analyzed by an independent sample *t*-test using the *t.test* function in the ‘stats’ package. In multiple comparisons, we used the method of Benjamini and Hochberg (1995) to adjust the *p*-values (Adjusted *p*) [37]. Then, Pearson’s correlation analysis was carried out to test the bivariate relationships between these traits between YJ and XSBN with the “corr.test” function in the “Psych” package. In addition, principal component analysis (PCA) was used to test the correlations among these traits and the position of 11 co-occurring species in YJ and XSBN in the trait space. All analyses were conducted in R v.4.0.3 [38].

3. Results

3.1. Trait Differences in Co-Occurring Species Between the Yuanjiang Valley-Type Savanna (YJ) and Xishuangbanna Tropical Seasonal Rainforest (XSBN)

There were large differences in stem and leaf hydraulic conductance between YJ and XSBN, and stem hydraulic conductance (K_{stem}) was significantly higher than leaf hydraulic conductance (K_{leaf}) in both sites (Figure 1, Table 4). Woody plants in YJ had lower whole-branch hydraulic conductance (K_{shoot}) and leaf hydraulic conductance (K_{leaf}), but a higher ratio of stem to leaf hydraulic conductance ($K_{\text{stem}}/K_{\text{leaf}}$) than the co-occurring species from XSBN (Table 4). For example, the K_{shoot} and K_{leaf} of plants in the YJ were only about half those of the co-occurring species in the XSBN (Table 4). And the $K_{\text{stem}}/K_{\text{leaf}}$ of plants in the YJ was 2.5 times as high as that of the XSBN (Table 4).

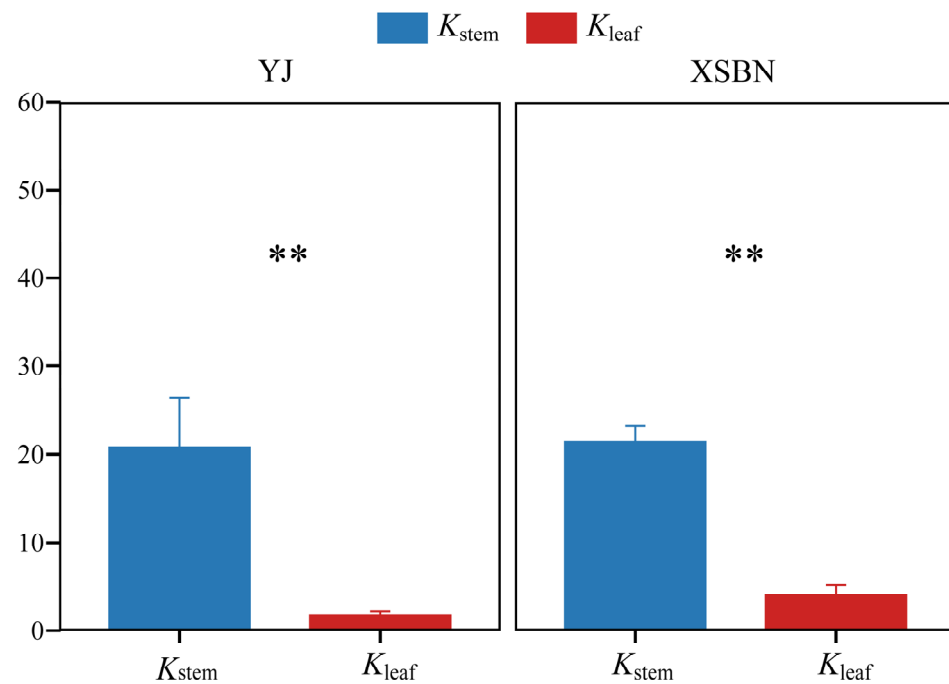


Figure 1. Comparisons of stem hydraulic conductance (K_{stem} , $\times 10^{-4}$ kg s⁻¹ MPa⁻¹ m⁻²) and leaf hydraulic conductance (K_{leaf} , $\times 10^{-4}$ kg s⁻¹ MPa⁻¹ m⁻²) in these two sites: YJ and XSBN. **: $p < 0.01$.

Table 4. Means $\pm$ SE of eight traits of 11 co-occurring woody species between these two sites (YJ and XSBN). The t , p and adjusted p of independent sample t -test were given (*: $p < 0.05$, **: $p < 0.01$). See Table 2 for trait abbreviations.

Trait	Mean $\pm$ Standard Error		t	p	Adjusted p
	YJ (n = 11)	XSBN (n = 11)			
K_{shoot}	1.402 $\pm$ 0.359	2.788 $\pm$ 1.282	3.43	0.001 **	0.0032 *
K_{stem}	20.756 $\pm$ 10.837	21.362 $\pm$ 14.810	0.138	0.89	0.8900
K_{leaf}	1.767 $\pm$ 0.488	3.940 $\pm$ 2.387	3.617	0.001 **	0.0026 *
$K_{\text{stem}}/K_{\text{leaf}}$	16.768 $\pm$ 4.189	6.724 $\pm$ 1.715	−4.355	0.000 **	0.0003 **
WD	0.594 $\pm$ 0.017	0.528 $\pm$ 0.019	−2.477	0.015 *	0.0255 *
LMA	76.505 $\pm$ 15.943	61.574 $\pm$ 13.961	−2.463	0.015 *	0.0255 *
PM/LM	0.182 $\pm$ 0.021	0.193 $\pm$ 0.064	0.474	0.636	0.7951
PM	4.819 $\pm$ 1.020	4.418 $\pm$ 1.096	−0.759	0.449	0.6416

In addition, woody plants in the YJ had higher sapwood density (WD) and leaf mass per area (LMA) than the co-occurring species in the XSBN (Table 4). However, these co-occurring species had comparable stem hydraulic conductance (K_{stem}), petiole mass (PM), and ratio of petiole mass to lamina mass (PM/LM) between the YJ and XSBN (Table 4).

3.2. Correlations Between Stem and Leaf Hydraulic Traits Between YJ and XSBN

For woody plants in the YJ, K_{leaf} and K_{stem} were positively associated with K_{shoot} , but K_{leaf} was not associated with K_{stem} (Figure 2; Table 5). The K_{shoot} and K_{leaf} were negatively related to WD, but K_{stem} was not associated with WD (Figure 3; Table 5). In addition, LMA was positively associated with WD (Figure 4; Table 5). In contrast, for co-occurring species in the XSBN, K_{leaf} and K_{stem} were positively associated with K_{shoot} , and K_{leaf} was also positively associated with K_{stem} (Figure 2). The K_{shoot} , K_{stem} , and K_{leaf} were negatively related to WD (Figure 3). However, LMA was not related to WD (Figure 4).

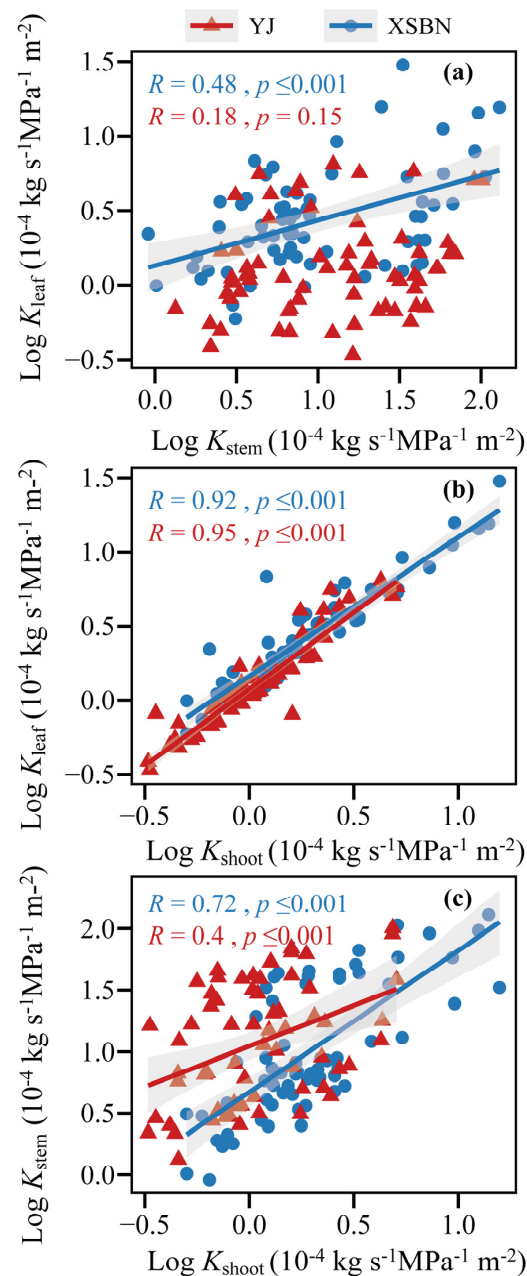


Figure 2. The log–log relationships of (a) leaf hydraulic conductance (K_{leaf}) with stem hydraulic conductance (K_{stem}), (b) leaf hydraulic conductance (K_{leaf}) with whole-branch hydraulic conductance (K_{shoot}), (c) stem hydraulic conductance (K_{stem}) with whole-branch hydraulic conductance (K_{shoot}) across the XSBN (blue circle) and the YJ (red triangle). The absence of lines indicates the correlation is not significant ($p > 0.05$).

Table 5. Coefficients of Pearson’s correlation between pairs of stem and leaf traits in the Yuanjiang valley-type savanna (YJ: the lower left corner) and Xishuangbanna tropical seasonal rainforest (XSBN: the upper right corner). See Table 3 for trait abbreviations. *: $p < 0.05$, **: $p < 0.01$.

	K_{shoot}	K_{stem}	K_{leaf}	K_{stem}/K_{leaf}	WD	LMA	PM/LM	PM
K_{shoot}		0.723 **	0.924 **	0.151	−0.781 **	0.348 **	0.278 *	−0.058
K_{stem}	0.398 **		0.476 **	0.780 **	−0.585 **	0.175	0.171	−0.039
K_{leaf}	0.947 **	0.18		−0.179	−0.704 **	0.390 **	0.237	−0.045
K_{stem}/K_{leaf}	−0.209	0.804 **	0.440 **		−0.153	−0.082	0.023	−0.012
WD	−0.277 *	−0.199	−0.309 *	0.005		−0.212	−0.16	0.121
LMA	0.073	−0.205	0.088	−0.24	0.567 **		−0.228	−0.058
PM/LM	0.400 **	0.136	0.386 **	−0.109	−0.097	−0.015		0.704 **
PM	−0.083	0.067	−0.119	0.133	0.17	0.181	0.771 **	

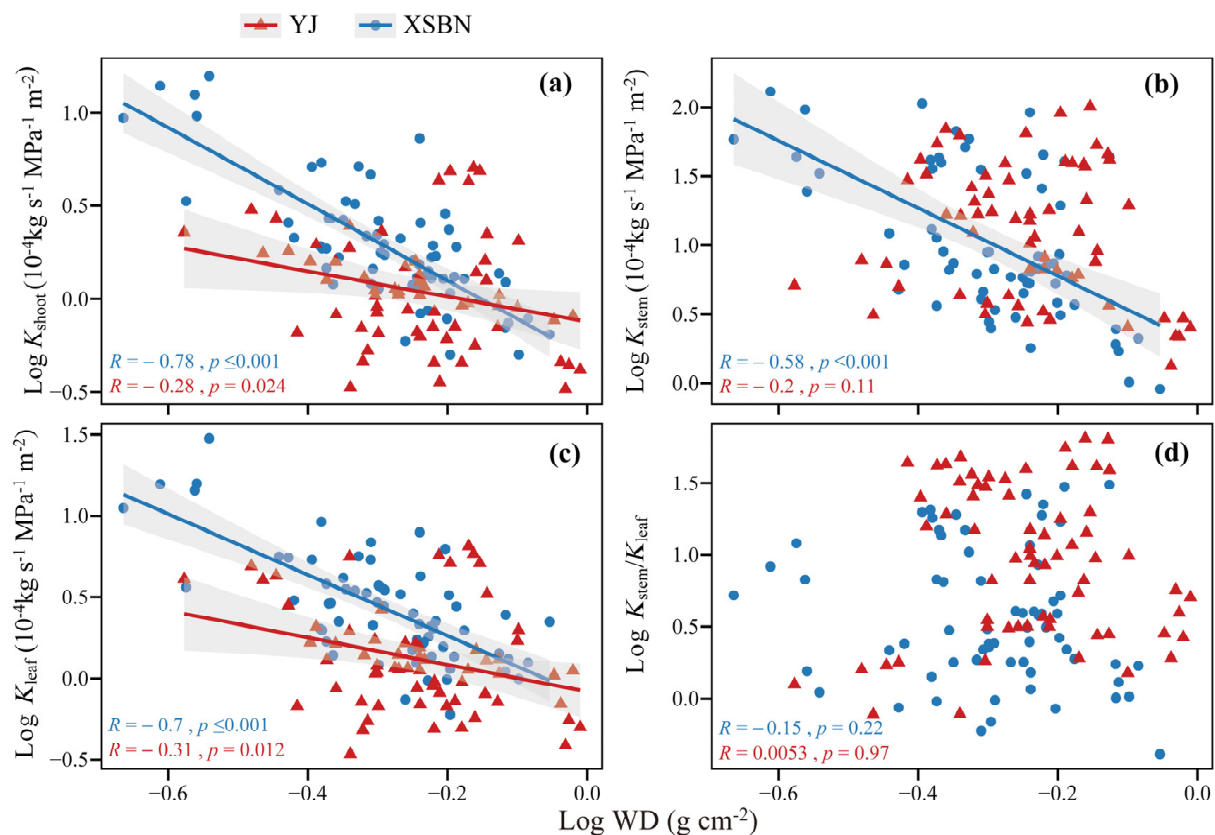


Figure 3. The log–log relationships between sapwood density (WD) and (a) whole-branch hydraulic conductance (K_{shoot}), (b) stem hydraulic conductance (K_{stem}), (c) leaf hydraulic conductance (K_{leaf}), and (d) ratio of stem to leaf hydraulic conductance (K_{stem}/K_{leaf}) in these two sites (YJ: red triangle; XSBN: blue circle). Lines depict parameters of linear regressions, and shaded areas represent 95% confidence intervals. The absence of lines indicates the correlation is not significant ($p > 0.05$).

Based on the PCA results for 8 traits of the 11 co-occurring woody species in the YJ and XSBN, the PC1 and PC2 explained 37.2% and 22.9% trait variance, respectively. In addition, these co-occurring plants showed partial overlap between the YJ and XSBN in the trait space (Figure 5).

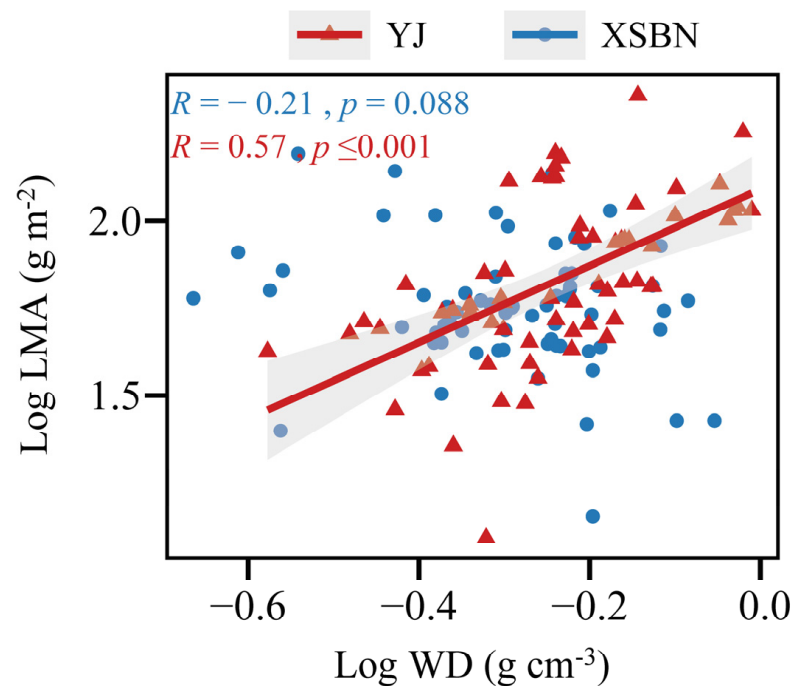


Figure 4. The log–log relationship between sapwood density (WD) and leaf mass per area (LMA) in these two sites (YJ: red triangle; XSBN: blue circle). Lines depict parameters of linear regressions, and shaded areas represent 95% confidence intervals. The absence of lines indicates the correlation is not significant ($p > 0.05$).

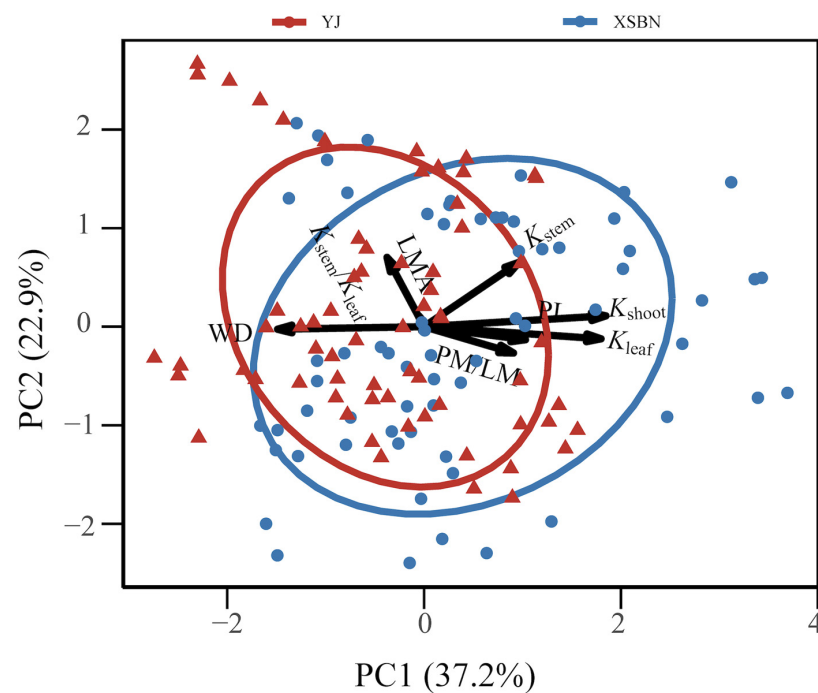


Figure 5. Principal component analysis (PCA) using log-transformed data for 8 traits of 11 co-occurring species between these two sites (YJ: red triangle; XSBN: blue circle). Whole-branch hydraulic conductance (K_{shoot}), stem hydraulic conductance (K_{stem}), leaf hydraulic conductance (K_{leaf}), ratio of stem to leaf hydraulic conductance (K_{stem}/K_{leaf}), sapwood density (WD), leaf mass per area (LMA), ratio of petiole mass to lamina mass (PM/LM), petiole mass (PM).

4. Discussion

Consistent with our hypothesis, plants in the Yuanjiang valley-type savanna (YJ) have a lower water transport efficiency than co-occurring species in the Xishuangbanna tropical seasonal rainforest (XSBN). These woody plants in the YJ had significantly lower leaf and whole-branch hydraulic conductance (K_{leaf} and K_{shoot}) compared to the co-occurring species in the XSBN. The low K_{leaf} (higher hydraulic resistance in leaves) of the YJ plants growing in a dry-hot habitat can decrease their water loss, which helps to sustain predawn leaf water potential [39]. The previous study showed that savanna species are more buffered and take longer for the predawn leaf water potentials to drop to critical values (such as turgor loss points) than the congeneric forest species [39]. Therefore, the leaves with less water loss due to the lower leaf water transport efficiency help keep a higher water potential in upstream stems [11,40], which can act as a bottleneck or ‘safety valve’ to help decrease water stress of the more carbon-costly stems and to keep their hydraulic integrity [17,36,41–43].

Despite lower K_{leaf} in the YJ plants, stem hydraulic conductance (K_{stem}) in the YJ plants was comparable to that of the co-occurring XSBN species (Table 4). The comparable K_{stem} and significantly lower K_{leaf} in the YJ plants led to a higher ratio of stem to leaf hydraulic conductance ($K_{\text{stem}}/K_{\text{leaf}}$) compared to that of co-occurring XSBN species, which means that the YJ plants employ a higher stem hydraulic redundancy. The higher stem hydraulic redundancy indicates that leaves may act as hydraulic control valves for species with high stem hydraulic conductance, and indirectly improve water transport safety in the stem and leaves [17]. In the YJ environment with high temperatures, evaporative demand and potentially low soil water availability, the lower K_{leaf} in the YJ plants may partly lead to less water supply via leaf xylem to stomata and thus lower stomatal conductance and photosynthetic rates [36,44–46], but it helps them to improve hydraulic safety and to tolerate the dry-hot habitat. In contrast, the co-occurring species with higher K_{leaf} and K_{shoot} in the XSBN showed higher hydraulic efficiency. The high efficiency of water transport can decrease water loss induced by high transpiration [29,30]. In addition, a strong xylem hydraulic coordination between the stem and leaf hydraulic system was found in these co-occurring species in XSBN with the strong positive correlations between K_{leaf} and K_{stem} (Table 5). The hydraulic coordination between the stem and downstream leaves improves the whole-branch water transport efficiency [34]. The high whole-branch hydraulic efficiency potentially contributes to high leaf stomatal conductance, photosynthetic rates and thus fast growth, as commonly observed [34,47,48]. In the present wet-hot environment with favorable water availability, the high water transport efficiency of the co-occurring species in XSBN helps them to maintain a greater growth advantage and to compete for more water and light resources.

In addition, sapwood density (WD) was negatively related to hydraulic conductance in the YJ, and the YJ plants employed higher WD than co-occurring species from the XSBN. A recent study also found that the wood density of woody vines (lianas) and trees from the YJ is higher than that of those in the XSBN [21]. Wood density as a central wood trait helps us understand plant hydraulic safety of the xylem water transport system [49–51]. Higher wood density is generally associated with higher resistance to vessel implosion to cope with low water availability [52–54], because high-wood-density species generally have greater mechanical stability and higher drought tolerance under water stress [54]. In addition, plants with high wood density can tolerate lower water potential using limited soil water [55,56], and resist cavitation induced by drought [54,57], but these tend to have a slow-growth strategy [58]. Therefore, plants in the YJ can benefit from high wood density to adapt to the dry-hot stress. In contrast, the co-occurring species in the XSBN showed lower WD compared to the YJ plants. These low-wood-density species generally have a higher hydraulic conductance to favor their fast growth with favorable water availability [35,58].

Furthermore, plants in the YJ had higher LMA than co-occurring species in the XSBN, and LMA was positively related to high sapwood density in the YJ. The higher LMA of woody plants in the valley-type savanna than in tropical seasonal forests is also found

in previous studies [27,39]. The LMA, as leaf dry mass investment per leaf area, is a key indicator of ecological strategies [59–61]. Plants with high LMA tend to have slow growth rates but tolerate drought stress [32,35,62,63]. The high-LMA species also have higher leaf tissue densities and a competitive advantage on water-poor soils [64,65]. Therefore, the combination of high LMA and WD in the YJ plants suggests that they adapt to the dry-hot habitat with significantly low precipitation and high temperatures by high leaf and stem matter investment per area [27]. In contrast, low LMA is typically associated with short diffusion paths from stomata to chloroplasts, and thus high water transport efficiency and photosynthetic rates [31–33,35], which indicates that these co-occurring species with low LMA in XSBN adopt a fast-growth strategy to speed up their productivity at high water availability.

5. Conclusions

In the YJ environment with high evaporative demand and potentially low soil water availability, plants under the stronger selective pressure employed a lower water transport efficiency than co-occurring species in the XSBN. The combinations of lower K_{leaf} and K_{shoot} and higher WD and LMA could play an important role in enabling them to succeed in the dry-hot environment despite them sacrificing their hydraulic efficiency. In contrast, co-occurring species in the XSBN with high K_{leaf} and K_{shoot} and low WD and LMA showed high hydraulic efficiency to potentially maximize their growth in favorable water habitats. Our findings suggest that the divergence in hydraulic efficiency of these co-occurring plants across different habitats helps them better adapt to their respective environments.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f15111912/s1>, Figure S1. (a) Hydraulic conductance measurements using a high-pressure flow meter (HPFM Gen3; Dynamax Corp., Elkhart, Indiana, USA), (b) the sample branch was used to measure hydraulic conductance, and (c) data records of hydraulic conductance.

Author Contributions: X.P.: Writing—Original Draft, Writing—Review and Editing, Visualization, Investigation, Formal Analysis, Data Curation, Conceptualization. D.Y.: Writing—Original Draft, Writing—Review and Editing, Investigation, Funding Acquisition, Formal Analysis, Data Curation, Conceptualization. Q.W.: Data Curation. Y.T.: Investigation. K.Y.: Data Curation. Y.Z.: Data Curation. S.Y.: Supervision, Writing—Review and Editing. J.Z.: Writing—Review and Editing, Supervision, Project Administration, Funding Acquisition, Conceptualization. All authors have read and agreed to the published version of the manuscript.

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