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Vessel dimorphism and wood traits in lianas and trees among three contrasting environments

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Abstract

Premise: Determining how xylem vessel diameters vary among plants and across environments gives insights into different water-use strategies among species and ultimately their distributions. Here, we tested the vessel dimorphism hypothesis that the simultaneous occurrence of many narrow and a few wide vessels gives lianas an advantage over trees in seasonally dry environments.

Methods: We measured the diameters of 13,958 vessels from 15 liana species and 10,430 vessels from 16 tree species in a tropical seasonal rainforest, savanna, and subtropical evergreen broadleaved forest. We compared differences in mean and hydraulically weighted vessel diameter (MVD and D_h), vessel density (VD), theoretical hydraulic conductivity (K_t), vessel area fraction (VAF), and wood density (WD) between lianas and trees and among three sites.

Results: Nine liana species and four tree species had dimorphic vessels. From the tropical seasonal rainforest to the savanna, liana MVD, D_h and K_t decreased, and VD and WD increased, while only tree WD increased. From the tropical seasonal rainforest to the subtropical forest, six wood traits remained unchanged for lianas, while tree MVD, D_h and K_t decreased and VD increased. Trait space for lianas and trees were more similar in the savanna and more divergent in the subtropical forest compared to the tropical seasonal rainforest.

Conclusions: These results suggest that lianas tend to possess greater vessel dimorphism, which may explain how lianas grow well during seasonal drought, influencing their unique distribution across tropical rainfall gradients.

KEYWORDS
anatomy, hydraulic architecture, savanna, subtropical forest, tropical seasonal rainforest, vessel distribution pattern, woody vine

Plant vascular anatomy and morphology strongly influence the trade-off in the ability of xylem to supply water to distal leaves while, concomitantly, avoiding embolism (Hacke and Sperry, 2001). For example, narrow vessels can allow plants to avoid embolism during dry periods but constrain the speed at which they can move water to their leaves when water is abundant. By contrast, wide and long vessels have far higher hydraulic conductivity than do narrow and short vessels, which can be beneficial when water is abundant, however, plants with wide and long vessels may be more vulnerable to embolism when water is limiting or with freezing temperatures (freeze–thaw embolism; Davis

et al., 1999; Jiménez-Castillo and Lusk, 2013). Therefore, determining plant vessel structure is fundamental for further understanding vascular functioning in diverse plant groups.

One way that plants most efficiently conduct water while avoiding embolism is by adjusting their vascular design to the prevailing environmental conditions. Variations in plant xylem hydraulic traits are closely related to habitat type (Fisher et al., 2007; Wheeler et al., 2007; Medeiros and Pockman, 2014; Crivellaro and Schweingruber, 2015). For example, species in warm and moist habitats generally have larger mean vessel diameters than those of the same species in cold or dry habitats (Wheeler et al., 2007; Pfautsch

et al., 2016). However, some evidence suggests that stem length or diameter is also linked to vessel diameter variation (Olson and Rosell, 2012; Fajardo et al., 2020; Olson et al., 2020). In addition, plant vessel dimension varies with species identity beyond species-level plasticity and can be constrained by species' life-history strategy.

Another way that plants may negotiate the trade-off between water conductivity and embolism is by having a diverse range of vessel sizes within their stems. Xylem vessel dimorphism (Carlquist, 1981), that is, the co-occurrence of very narrow vessels with wide vessels in a plant's secondary xylem, may be beneficial because the wide vessels contribute to disproportionately high hydraulic conductance (e.g., Jiménez-Castillo and Lusk, 2013), while the very narrow vessels may ensure resistance to xylem embolism (Carlquist, 1981; van der Sande et al., 2019). Therefore, vessel dimorphism could be an important plant hydraulic strategy and ecological adaptation.

Lianas, a common tropical and subtropical plant growth form, tend to have exceptionally long and wide xylem vessels, which give them an efficient stem vascular system with high sapwood specific conductivity compared to trees (Ewers et al., 1990; He et al., 2020; Mello et al., 2020). Lianas also appear to have high vessel dimorphism (Rosell and Olson, 2014; Angyalossy et al., 2015, Zhu et al., 2017; Meunier et al., 2020), which may help lianas to avoid embolism, also explains why some studies reported a decoupling between liana xylem hydraulic efficiency and safety (i.e., avoiding a hydraulic safety–efficiency trade-off; van der Sande et al., 2019; Zhang et al., 2019). A wide vessel diameter range, combined with the ability of lianas to rapidly reach the top of the forest canopy may also be responsible for the notable pattern of relatively high liana abundance in highly seasonal forests and across the tropics (Schnitzer, 2005, 2018; Parolari et al., 2020).

Although most previous studies have found that lianas generally have larger vessel diameters than co-occurring trees (Jiménez-Castillo and Lusk, 2013; Zhang et al., 2021), these results may differ among vegetation types. For example, in a tropical dry forest, Werden et al. (2017) reported that lianas had smaller mean vessel diameter than co-occurring trees. By contrast, in seasonal dry forests, lianas had larger mean vessel diameters than trees (Dias et al., 2019; Medina-Vega et al., 2021). One explanation for these mixed results is that differences in xylem traits between lianas and trees are site-dependent (Medina-Vega et al., 2021) or related to large variations in vessel diameters in lianas (Crivellaro et al., 2012). However, there are few empirical comparisons on the variation in xylem vessel diameters and associated hydraulic traits between lianas and trees across different habitats (but see Dias et al., 2019). Furthermore, most comparative studies were based on mean vessel diameter values, and many did not formally test for variation in the xylem vessel dimorphism between these two growth forms.

In this study, we evaluated the variations in liana and tree vessel diameter distribution and six xylem hydraulic traits (mean vessel diameter, hydraulically weighted vessel diameter, vessel density, theoretical hydraulic conductivity, vessel area fraction, and sapwood density). We developed a theoretical model to predict how vessel diameters vary between lianas and trees and across sites (Figure 1). Given that vessel dimorphism is a common feature of lianas (e.g., Angyalossy et al., 2015; Gerolamo and Angyalossy, 2017) and most lianas have a larger maximal vessel diameter than that of trees (Zhang et al., 2019, 2021), we tested the following hypotheses: (1) Lianas have greater vessel dimorphism than trees, with many narrow vessels and fewer wide ones, across the three contrasting environments. (2) Liana vessel dimorphism increases from warm and wet
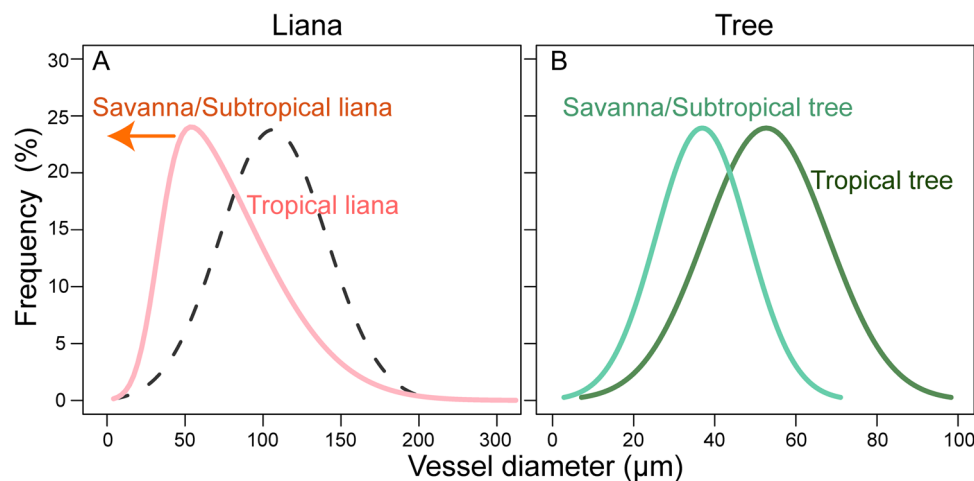
FIGURE 1 Conceptual model for patterns in vessel diameter frequency distribution of liana and tree species along environmental gradients. (A) We expected that the distribution of vessel diameter frequency in lianas would be positively skewed and that the skewness of vessel diameter frequency curves for the drier (savanna) or colder (subtropical evergreen broadleaved forest) site would shift left compared to the warm, wet site (tropical forest) (as shown by the arrow). The black dashed line represents a normal distribution. (B) We expected that vessel diameter frequency in trees would exhibit a normal distribution across the environmental gradient, with mean vessel size smaller in the drier savanna and in the subtropical forests.

to dry and cold sites because vessel dimorphism offers protection against embolism (Figure 1). (3) Both lianas and trees have smaller mean vessel diameter, hydraulically weighted vessel diameter, theoretical hydraulic conductivity, and vessel area fraction and higher vessel density and sapwood density from warm and wet habitat to dry-hot and/or cold habitats because of constraints of drought and subzero-temperature stresses.

MATERIALS AND METHODS

Study site and species

This study was carried out in the Xishuangbanna (XSBN) tropical seasonal rainforest, Yuanjiang savanna (YJ), and Ailaoshan (ALS) subtropical evergreen broadleaved forest in Yunnan Province, Southwest China. The climate of the study region is influenced by the southwestern monsoon and the Tibetan Plateau, and >80% of the precipitation occurs during the rainy season (May–October) in all three sites (Table 1).

We chose 15 liana species and 16 tree species from three sites in September–October 2019 when the growing season generally ends in these sites (Appendix S1). We sampled seven, six, and five liana species in the XSBN tropical

seasonal rainforest, YJ savanna, and ALS subtropical evergreen broadleaved forest, respectively, and six tree species in each site. Among the selected species, three liana species and two tree species occur in both XSBN tropical seasonal rainforest and YJ savanna. The selected species represent a wide range of taxonomic and phylogenetic diversity (Appendix S1). The wood type of all selected species is diffuse-porous. We sampled three to six individuals for each species for a total of 210 individuals from the three sites.

Measurement of xylem traits

For each of the three to six individuals per species, we selected one terminal branch that was 1 to 2 cm in diameter to measure vessel diameter and other wood traits. One stem segment for each terminal branch was fixed in FAA solution (900 mL 70% alcohol, 50 mL formalin, 50 mL 17.5 mol/L glacial acetic acid). Stem transverse sections (10–25 μm thick) were cut with a rotary microtome (Leica Microsystems, Leica RM2245, Wetzlar, Germany). Sections were bleached with sodium hypochlorite solution, stained with a mixture of 1% w/v safranin O and 0.5% w/v astral blue, dehydrated in an ethanol series (50%, 70%, 85%, 95%, and 100%), then

TABLE 1 Basic information about the study sites.

Site	Xishuangbanna (XSBN)	Yuanjiang (YJ)	Ailaoshan (ALS)
Vegetation type	Tropical seasonal rainforest	Savanna	Subtropical evergreen broadleaved forest
Coordinates	21°41′N, 101°25′E	23°28′N, 102°10′E	24°32′N, 101°01′E
Elevation (m a.s.l.)	580	481	2450
Mean annual precipitation (mm)	1447	733	1778
Mean annual temperature (°C)	22.7	24.7	11.3
Temperature range (minimum–maximum, °C)	2.0 – 40.5	3.6 – 45.0	−8.0 – 26.9
Soil type	Latosol	Dry-red soil	Yellow-brown soil
Soil pH	5.41	7.88	4.24
Organic matter (mg g^{-1})	46.91	87.73	170.4
Total N (mg g^{-1})	3.07	3.96	5.64
Total P (mg g^{-1})	0.69	1.3	0.97
Total K (mg g^{-1})	10.84	12.72	9.46
Available N (mg kg^{-1})	126.9	206.9	51.17
Available P (mg kg^{-1})	4.22	13.28	11.10
Available K (mg kg^{-1})	88.2	576.3	185.4

permanently mounted on slides with Neutral Balsam Mounting Medium (BBI Life Sciences, Shanghai, China). We mounted at least three slides for each individual. For some species with stiff wood such as *Tamarindus indica*, *Bridelia stipularis*, *Castanopsis wattii*, *Vaccinium duclouxii*, and *Lirianthe henryi*, we soaked the samples in 1:1 70% ethanol and glycerin for 1 to 2 weeks to soften the wood. For some species with vessels that were difficult to distinguish from other cells, we made longitudinal and tangential sections.

At least 5–10 images for each slide were photographed at 100× and 200× magnification with a light microscope (Leica Microsystems Ltd., Leica DM2500, Wetzlar, Germany) equipped with a digital camera (2560 × 1920 pixels). All anatomical traits were analyzed using images at 100× magnification, except for *Vaccinium duclouxii*, *Schima noronhae*, and *Jasminum seguinii* at 200× magnification. We used these images to quantify the number of vessels per standardized area for all species. For some species with very few vessels in an image, we combined multiple images to increase the number of vessels that we measured. Finally, we measured a minimum of 18 vessels in an image (1.12 mm^2) and a minimum of 155 vessels for species (*Argyreia osyrensis* var. *cinerea*). To better distinguish vessels from other tissues, we processed and sharpened images of transverse sections with Photoshop CC 2019 (Adobe, San Jose, CA, USA).

For each of 3–6 individuals per species, one representative image was chosen to measure vessel traits with ImageJ software (National Institutes of Health, Bethesda, MD, USA). Vessels were excluded when they had incomplete edges and less than half of their area was visible. The diameter (D) of each vessel (i) was calculated using the equation of Meunier et al. (2020):

$$D_i = 2\sqrt{\left(\frac{A_i}{\pi}\right)},$$

where A_i (μm^2) represents the area of vessel i, and π is the circular constant, 3.14. In total, we measured the diameter of 24,388 vessels (13,958 and 10,430 vessels for lianas and trees, respectively). We calculated mean vessel diameter (MVD; μm) per individual by summing all vessel diameters and dividing them by the number of vessels. The hydraulically weighted vessel diameter (D_h; μm) per individual was calculated as described by Poorter et al. (2010):

$$D_h = \left[\left(\frac{1}{n}\right)\sum_{i=1}^{n} D_i^4\right]^{\frac{1}{4}}.$$

Vessel density (VD; no. mm^{-2}), defined as the number of vessels per unit stem cross-sectional area, was estimated by counting the number of vessels on a subset of the whole stem cross-section. Vessel area fraction (VAF; %) was calculated as the percentage of cross-sectional area occupied by vessels. The theoretical hydraulic conductivity (K_t; kg

m^{-1} s^{-1} MPa^{-1}) was calculated using the Hagen–Poiseuille principle (Poorter et al., 2010):

$$K_t = \left(\frac{\pi\rho}{128\eta}\right) \times VD \times D_h^4,$$

where π is the circular constant of 3.14, ρ is the water density (998.2 kg m^{-3} at 20°C), η is the water viscosity (1.002 × 10^{-9} MPa s at 20°C).

Sapwood density was determined for 3–6 individuals per species using stem segments 3–5 cm long after removing pith and bark. Fresh volume was measured with the water displacement method (Hacke et al., 2000). Wood dry mass was determined after wood was oven-dried for at least 48 h at 80°C. Sapwood density (WD; g cm^{-3}) was calculated as dry mass divided by fresh volume.

Statistical analyses

For each site, we calculated the mean number of vessels per area for all species separately and for all liana species and for all tree species using all individuals of each group. We grouped vessels in 10-μm-diameter classes from 10 to 300 μm, and all vessels >300 μm in diameter were grouped together. The relative contribution of each vessel diameter class to total hydraulic conductivity was calculated as the sum of the fourth power of the vessel diameter within the class divided by the sum of the fourth power of the vessel diameter (Jiménez-Castillo and Lusk, 2013). Vessel dimorphism was defined by the skewness of the frequency distribution of the vessel diameters. The skewness was calculated as follows:

$$skewness = \left(\frac{1}{n}\right)\sum_{i=1}^{n}\left(\frac{D_i - MVD}{s}\right)^3,$$

where s is standard deviation, n is the vessel number. If skewness was >0.5 or <−0.5, then vessels were dimorphic; if skewness was between −0.5 and 0.5, then vessel diameter frequency was normally distributed (Carlquist, 1985; Meunier et al., 2020). In addition, we compared the difference in skewness between lianas and trees using an independent-samples t-test.

We used a linear mixed-effects model (LMM) to test for the effects of growth form and site on wood traits, with species as a random factor, using the lmer function in the R package lme4 package (Bates et al., 2015). We also used LMM to determine differences in the six wood traits in either lianas or trees among the three sites and between lianas and trees in the same site. For the XSBN tropical and YJ savanna sites, we examined differences in the six wood traits for the five shared species using an independent-samples t-test.

We used Pearson's correlation to investigate the linkages between traits of lianas and trees. A principal component

analysis (PCA) was used to evaluate how these traits of all liana and tree species were associated using the pca function in the R package FactoMineR (Lê et al., 2008). All data were log$_{10}$-transformed before analysis to improve the normality and homogeneity of variance. R v.4.0.3 (R Core Team, 2020) was used for all analyses.

RESULTS

Lianas generally had larger vessel diameters than trees across all three study sites (Figures 2, 3). As an extreme example, in the XSBN tropical seasonal rainforest the maximum vessel diameter of the liana *Gnetum montanum* reached 424.7 µm, whereas the maximum vessel diameter of the tree *Castanopsis indica* in that forest was only 140.2 µm. Similar to trees, lianas also had many narrow vessels. In addition, the large vessels of liana species such as *Bauhinia championii* were often surrounded by copious parenchyma tissue (Figure 2A).

Lianas had greater vessel dimorphism than trees. Nine liana species and only four tree species exhibited skewness >0.5 or <−0.5 across the three sites (Appendices S2–S4), and the skewness between lianas (0.77) and trees (−0.02) differed significantly among the three sites ($t = 3.74$, $P < 0.001$). The proportion of lianas with dimorphic vessels decreased from
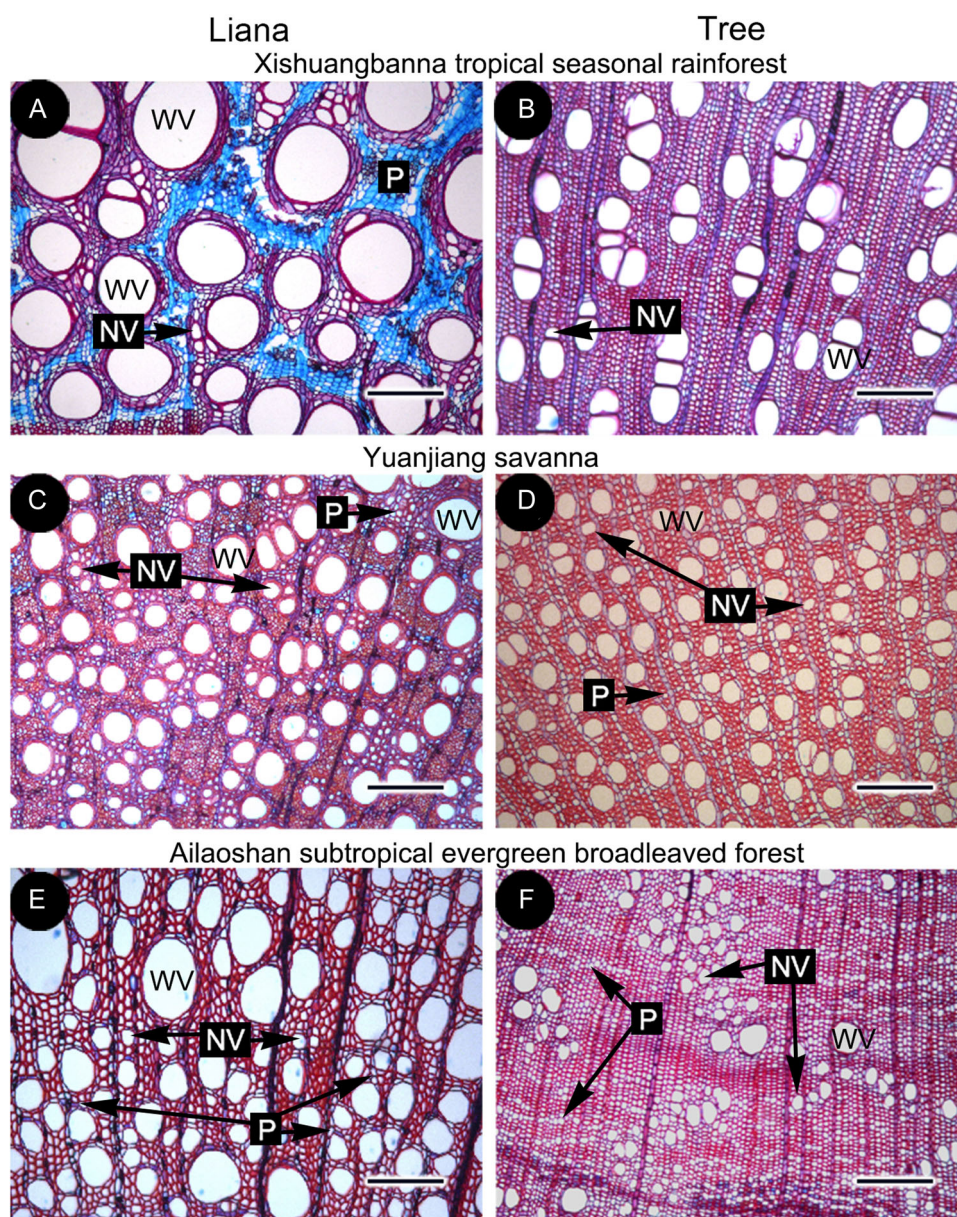
FIGURE 2 Light micrographs of stem transverse sections of six species from three sites in Southwest China. (A) *Bauhinia championii* (liana) and (B) *Adina pilulifera* (tree) are from the XSBN tropical seasonal rainforest; (C) *B. championii* (liana) and (D) *Haldina cordifolia* (tree) are from the YJ savanna; and (E) *Kadsura heteroclita* (liana) and (F) *Castanopsis wattii* (tree) are from the ALS subtropical evergreen broadleaved forest. WV, wide vessels; NV, narrow vessels; P, parenchyma tissues. In all images, the outer xylem is toward the top, and the inner xylem is toward the bottom. Scale bar = 200 µm.
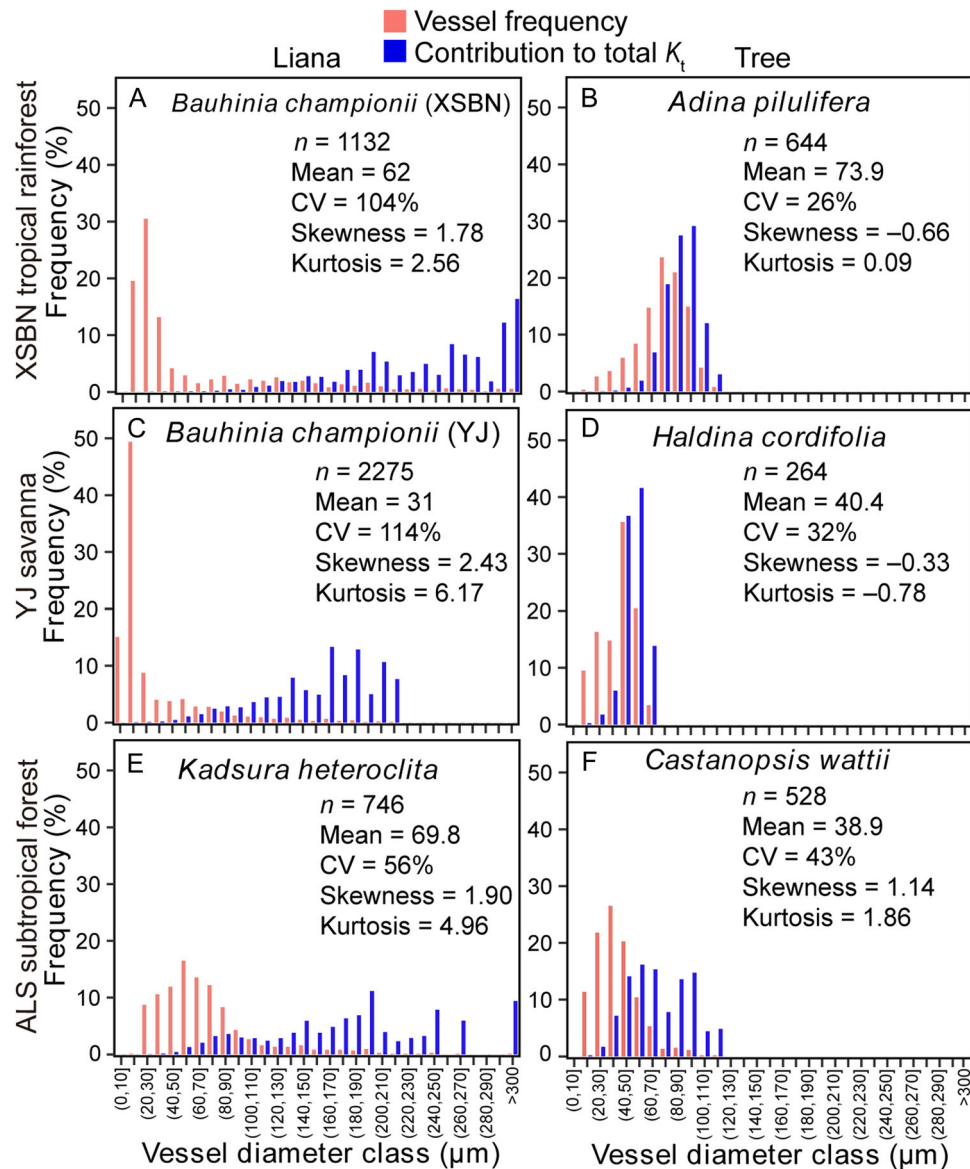
FIGURE 3 Frequency distribution of vessel diameter and their relative contributions to total hydraulic conductivity of three representative liana species and three representative tree species (from Figure 2) in tropical seasonal rainforest, savanna, and subtropical evergreen broadleaved forest, in Southwest China. (A) *Bauhinia championii* (liana), (B) *Adina pilulifera* (tree), (C) *B. championii* (liana), (D) *Haldina cordifolia* (tree), (E) *Kadsura heteroclita* (liana), (F) *Castanopsis wattii* (tree).

the tropical rainforest (five of the seven lianas had dimorphic vessels) to savanna (two of the six) and subtropical forest (two of the five) (Appendices S2–S4). Liana species with dimorphic vessels had a few wide vessels and many narrow ones; these wide vessels, however, contributed a high proportion of total hydraulic conductivity in lianas (Figure 3).

Lianas had wider range in vessel diameters (6–424.7 μm) than trees did (10.5–140.2 μm). Compared to trees, lianas in the three sites had higher mean vessel diameter (MVD), hydraulically weighted vessel diameter (D_h), theoretical hydraulic conductivity (K_t), and vessel area fraction (VAF), but lower vessel density (VD) and wood density (WD) (Table 2, Figure 4). Among the three sites, XSBN tropical

lianas had similar MVD, D_h, VD, K_t, and WD compared to ALS subtropical lianas ($p > 0.05$), but significantly higher MVD, D_h, and K_t and lower VD and WD than the YJ savanna lianas ($P < 0.05$). By contrast, XSBN tropical trees had similar MVD, D_h, VD, and K_t compared to YJ savanna trees ($P > 0.05$), but significantly higher MVD, D_h, and K_t and lower VD than in the ALS subtropical trees ($P < 0.05$; Figure 4).

Two of the same liana species had higher MVD, D_h, and K_t and lower VD and WD in the XSBN tropical seasonal rainforest than in the YJ savanna ($P < 0.05$; Figure 5). There were no significant differences in the six wood traits for the two shared tree species in these two contrasting sites ($P > 0.05$), except for increased WD in *Phyllanthus emblica*

TABLE 2 Results of linear mixed-effects models with stem traits as response variables.

Traits	Fixed effects									Random effects			
	Site			Growth form			Site × growth form			Species		Residual	
	SS	F	P	SS	F	P	SS	F	P	Variance	SD	Variance	SD
MVD	0.116	10.387	**<0.001**	0.083	14.779	**0.001**	0.067	5.944	**0.005**	0.022	0.147	0.006	0.075
D_h	0.095	9.264	**<0.001**	0.173	33.898	**<0.001**	0.054	5.269	**0.009**	0.019	0.139	0.005	0.072
VD	0.539	12.634	**<0.001**	0.083	3.873	0.060	0.180	4.224	**0.021**	0.106	0.326	0.021	0.146
K_t	0.293	3.023	0.058	3.093	63.743	**<0.001**	0.334	3.444	**0.04**	0.102	0.32	0.049	0.220
VAF	0.005	0.273	0.762	0.314	31.349	**<0.001**	0.008	0.385	0.683	0.018	0.134	0.010	0.100
WD	0.216	32.944	**<0.001**	0.021	6.535	**0.017**	0.0354	5.403	**0.008**	0.009	0.094	0.003	0.057

Note: Sites (Xishuangbanna, Yuanjiang, and Ailaoshan) and growth forms (lianas and trees) are fixed factors and species is the random factor. Sum of squares (SS), F and P values of fixed effects, variance and standard deviation (SD) of random effects are reported, $\alpha = 0.05$.

Abbreviations: D_h, hydraulically weighted vessel diameter; K_t, theoretical hydraulic conductivity; MVD, mean vessel diameter; VAF, vessel area fraction; VD, vessel density; and WD, sapwood density.

from the XSBN tropical seasonal rainforest to YJ savanna ($t = -3.52$, $P = 0.006$; Figure 5). Growth form had a greater impact on variation in MVD, D_h, K_t, and VAF across lianas and trees studied ($P \leq 0.001$), except for VD and WD, for which variation was more affected by the site ($P < 0.001$; Table 2).

With increasing K_t, the vessel skewness increased for all liana and tree species ($R = 0.52$, $P = 0.001$); however, the vessel skewness decreased with increasing WD for all liana and tree species ($R = -0.4$, $P = 0.017$; Figure 6). For lianas, there was a positive correlation between K_t and VAF ($R = 0.55$, $P = 0.018$) and a negative correlation between K_t and WD ($R = -0.75$, $P < 0.001$; Figure 7). These correlations, however, were absent for trees (Figure 7). There was a significant positive correlation between K_t and VAF and a negative correlation between K_t and WD for combined lianas and trees in the same site ($P < 0.05$; Figure 7; Appendix S5).

The first two axes of PCA for XSBN tropical seasonal rainforest, YJ savanna, and ALS subtropical evergreen broadleaved forest explained 93.32%, 93.01%, and 92.11% of the variation, respectively (Figure 8). The first axis of the three sites consistently showed strong positive associations with MVD, D_h, K_t, and VAF related to lianas and negative linkages with VD and WD related to trees. The second axis showed a positive association for VD and VAF. Lianas and trees were clearly separated in XSBN and ALS, whereas they overlapped in YJ.

DISCUSSION

We found that lianas had greater vessel diameter, vessel area fraction, dimorphism, theoretical hydraulic conductivity, and lower sapwood density than trees. Furthermore, these differences were consistent among contrasting forest types. Vessel dimorphism in lianas was of particular interest because it may explain the ability of lianas to thrive in highly seasonal forests and in treefall gaps (Schnitzer, 2005, 2018). Lianas grow well in treefall gaps and during the dry season in seasonal forests, when light is abundant, but water stress can limit growth (Schnitzer and van der Heijden, 2019). Lianas appear to utilize the large vessels for the majority of stem water movement when water is available and the smaller vessels for protection from embolism when water availability is low (see also Jiménez-Castillo and Lusk, 2013). This vessel dimorphism was consistent across the three contrasting sites, from XSBN tropical seasonal rainforest, to YJ savanna, to ALS subtropical forest. By contrast, we found that trees had consistently conservative hydraulic traits, with relatively small diameter vessels and low vessel dimorphism due to the lack of large vessels. The difference in liana and tree hydraulic traits may explain why lianas and trees tend to have different distributions and relative abundances across tropical environments.

Vessel dimorphism

Theoretically, liana species would benefit from vessel dimorphism conferred by both a few wide and many narrow vessels (Gutiérrez et al., 2009). Few but wide vessels contribute disproportionately to high hydraulic conductivity for lianas, especially during warm and wet seasons (Jiménez-Castillo and Lusk, 2013) and thus a high photosynthetic rate and stem elongation (Schnitzer, 2005; Wyka et al., 2013). However, if these wide vessels become cavitated due to extreme drought or frost stress, the remaining multiple narrow vessels could still maintain limited hydraulic conductance (Carlquist, 1985; Ewers et al., 1990; Jiménez-Castillo and Lusk, 2013; Gerolamo and Angyalossy, 2017).

Indeed, we found that more liana species in the three sites displayed obvious dimorphic vessel frequency distribution pattern, supporting our first hypothesis that lianas possess greater vessel dimorphism than trees. This result suggests that vessel dimorphism is taxon-specific, occurring disproportionately in certain liana families, genera, or species, such as Nepenthaceae (Carlquist, 1981), Bignoniaceae (Gerolamo and Angyalossy, 2017), *Paullinia* of Sapindaceae (Chery et al., 2020) and *Bauhinia* of Fabaceae (Ewers et al., 1990; Zhu et al., 2017). By contrast, trees tend to be hydraulically conservative and have significantly smaller vessel diameter than lianas at the same site (Zhu et al., 2017; Zhang et al., 2021). Compared to liana species, tree species generally have a higher fiber content in their xylem, which supports their stature, along with consistently small vessels that are relatively resistant to
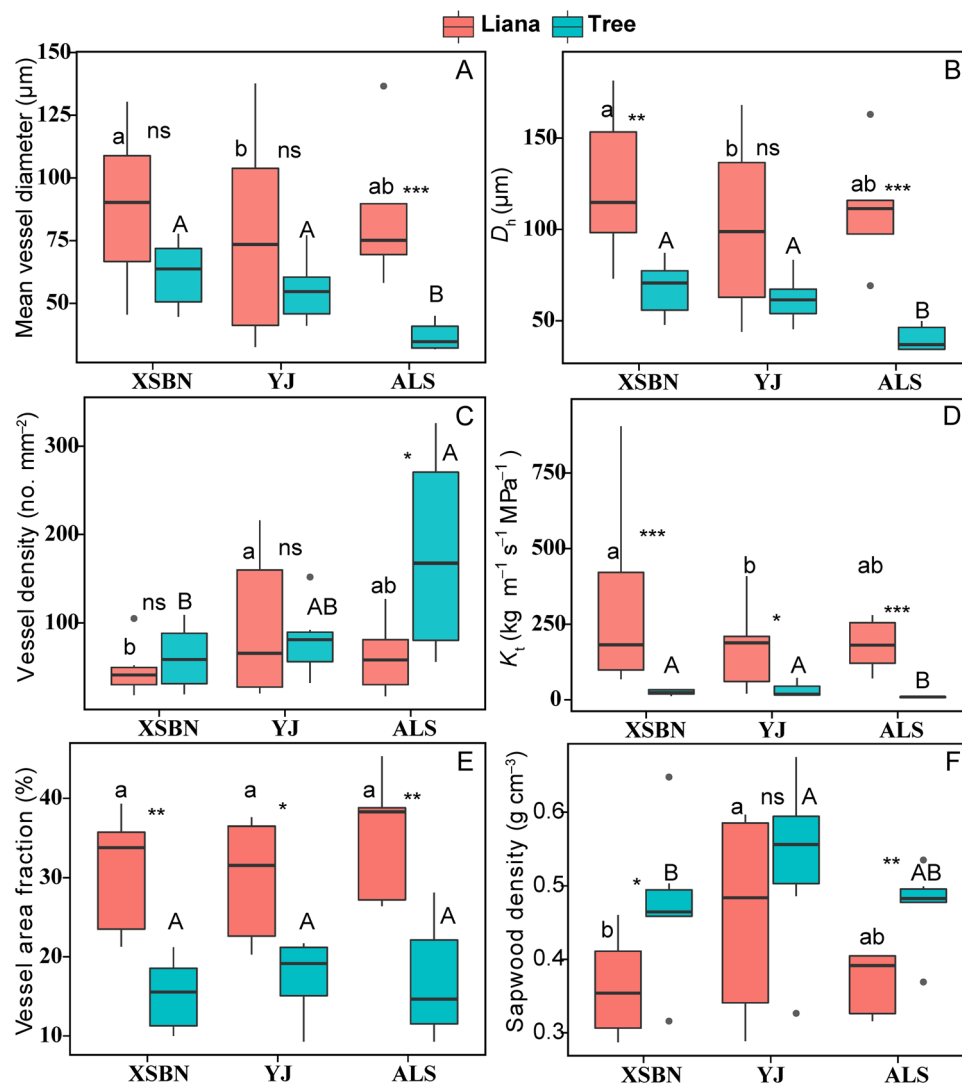

FIGURE 4 Differences in (A) mean vessel diameter, (B) hydraulic weighted vessel diameter (D_h), (C) vessel density, (D) theoretical hydraulic conductivity (K_t), (E) vessel area fraction, and (F) sapwood density between lianas and trees among three sites. Individual values for traits were analyzed using linear mixed-effects models. The line in the boxplot represents the median. Significant differences in six traits between lianas and trees are shown: ns, $P > 0.05$; *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$. Different lowercase letters above means indicate a significant difference in the trait between the sites for lianas, and different uppercase letters above means indicate a significant difference in the trait between the sites for trees (Tukey's HSD post hoc test, $P \leq 0.05$). The XSBN = Xishuangbanna tropical seasonal rainforest, YJ = Yuanjiang savanna, and the ALS = Ailaoshan subtropical evergreen broadleaved forest.
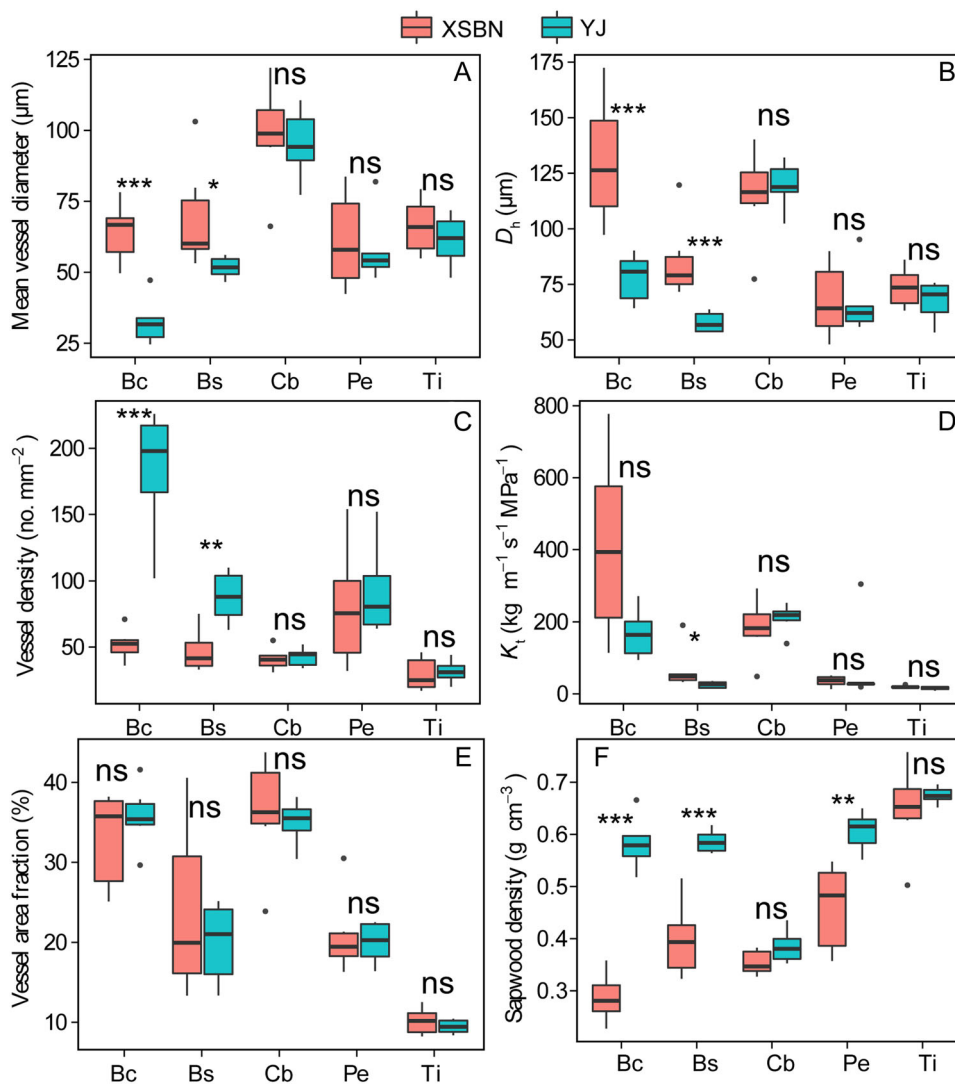
FIGURE 5 Differences in six traits of the same species between Xishuangbanna (XSBN) tropical seasonal rainforest and Yuanjiang (YJ) savanna. The line in the boxplot represents the median value. D_h: hydraulically weighted vessel diameter; K_t: theoretical hydraulic conductivity. Lianas: Bc, *Bauhinia championii*; Bs, *Bridelia stipularis*; Cb, *Cryptolepis buchananii*. Trees: Pe, *Phyllanthus emblica*; Ti, *Tamarindus indica*. ns, $P > 0.05$; $*P \leq 0.05$; $**P \leq 0.01$; $***P \leq 0.001$. Theoretical hydraulic conductivity of *Bauhinia championii*: $P = 0.057$.
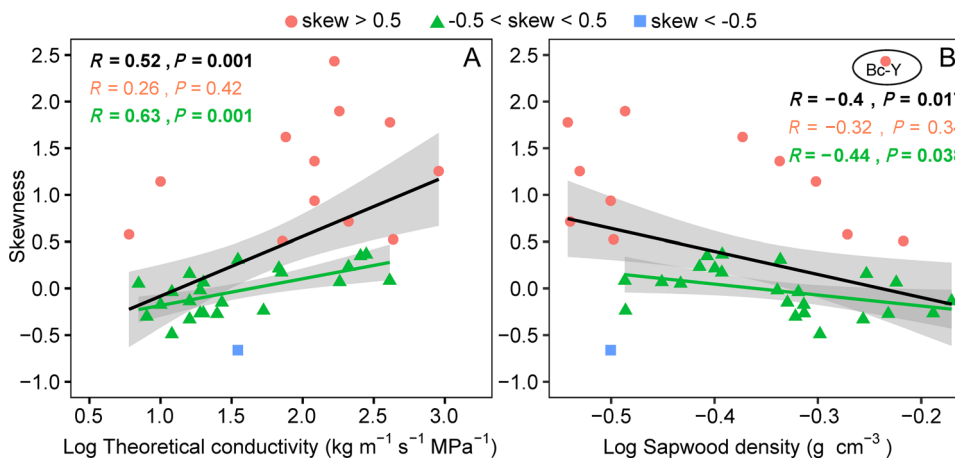
FIGURE 6 Relationships of (A) theoretical hydraulic conductivity and (B) sapwood density with vessel diameter distribution pattern (skewness). Black line: regression line for all species. *Bauhinia championii* in Yuanjiang savanna (Bc-Y) was excluded from the regression analysis.

embolism, which provide hydraulic safety (Gerolamo and Angyalossy, 2017; Zhu et al., 2017).

Our results do not support the second hypothesis that the proportion of lianas with vessel dimorphism would increase from warm and wet forest to cold and dry forest. In fact, we found the opposite result: five of the seven liana species had vessel dimorphism in the tropical seasonal rainforest, whereas only two species had vessel dimorphism in the savanna and subtropical forest. This finding suggests that anatomical properties other than vessel size differentiation, such as vessel groupings, presence of vasicentric tracheids, and abundant parenchyma cells around vessels, may play important but largely unexplored roles in the adaptation of lianas to adverse environments (Carlquist, 1984, 1985; Angyalossy et al., 2015).

Two liana species (*Bridelia stipularis* and *Jasminum seguinii*) possessed only narrow vessels (Appendix S4c,f) in the hot and dry savanna in YJ, Southwest China. In this site, *B. stipularis* grows as a scandent shrub (having a long self-supporting phase). Zhang et al. (2021) found that scandent shrubs usually have smaller vessels than true lianas, strengthening their resistance to freezing conditions in a subalpine cold temperate forest. Vessels of *J. seguinii* are even smaller than that of most other lianas and co-existing trees. A number of previous studies have shown that small vessels are resistant to drought-induced embolism (Pfautsch et al., 2016; Janssen et al., 2020). Such vessel anatomy presumably explains why *J. seguinii* is evergreen throughout the year in hot and dry savanna habitat.

Interestingly, we found that the vessel skewness increased with increasing theoretical hydraulic conductivity but decreased with increasing wood density (Figure 6). This relationship implies that species with greater skewness (and thus a combination of large and small vessels) also have light wood. Such phenomenon should be true for lianas, which tended to have wide vessels and low wood density in both this study and others (e.g., Ewers et al., 1990; Zhu et al., 2017; Dias et al., 2019; Meunier et al., 2020). However, the relationship between high vessel skewness and low wood density was not true for all liana species in our study. *Bauhinia championii*, a liana species distributed in the XSBN tropical rainforest and the YJ savanna, had extremely large vessel skewness with both large and small vessels and high wood density, suggesting that not all liana species with high hydraulic conductivity have light wood. Instead, the relationship between hydraulic conductivity and wood density may depend more on the number of fibers in the xylem and the thickness of fiber and vessel cell walls (Carlquist, 1981; Zhu et al., 2017; van der Sande et al., 2019).

Different responses of lianas and trees to contrasting environments

We found that lianas had higher hydraulic conductivity and lower hydraulic safety than trees across the three sites. Moreover, in the hot and dry savanna ecosystem, lianas and
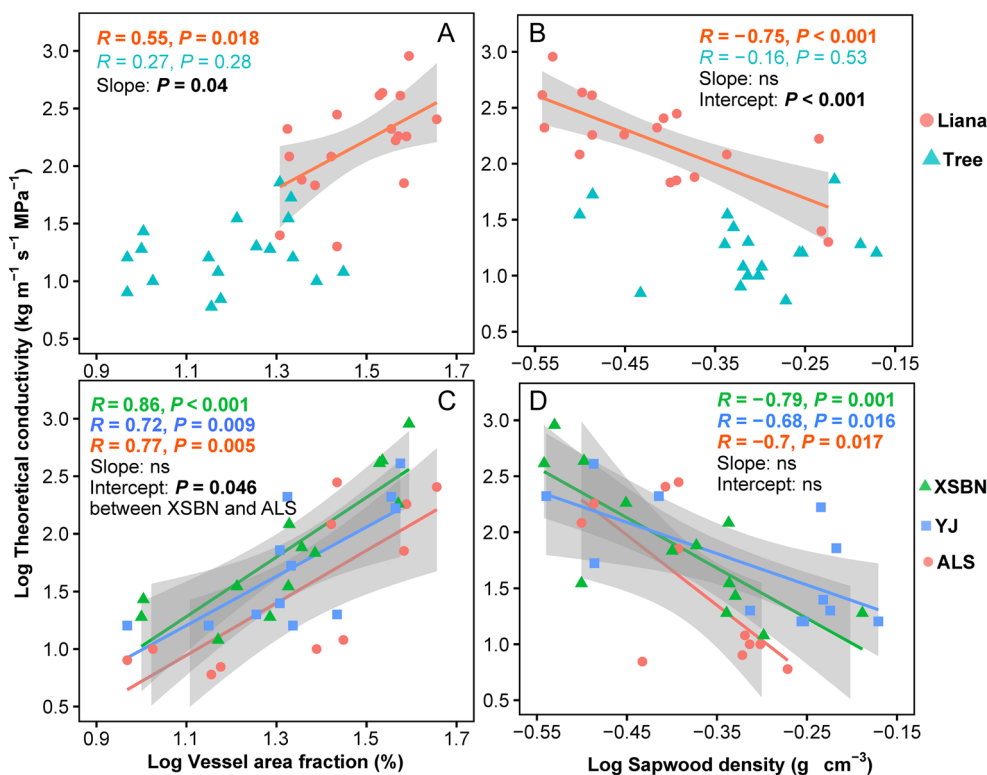
FIGURE 7 Relationships of theoretical hydraulic conductivity with (A, C) vessel area fraction and with (B, D) sapwood density in lianas and trees in the Xishuangbanna (XSBN) tropical seasonal rainforest, Yuanjiang (YJ) savanna, and Ailaoshan (ALS) subtropical evergreen forest.
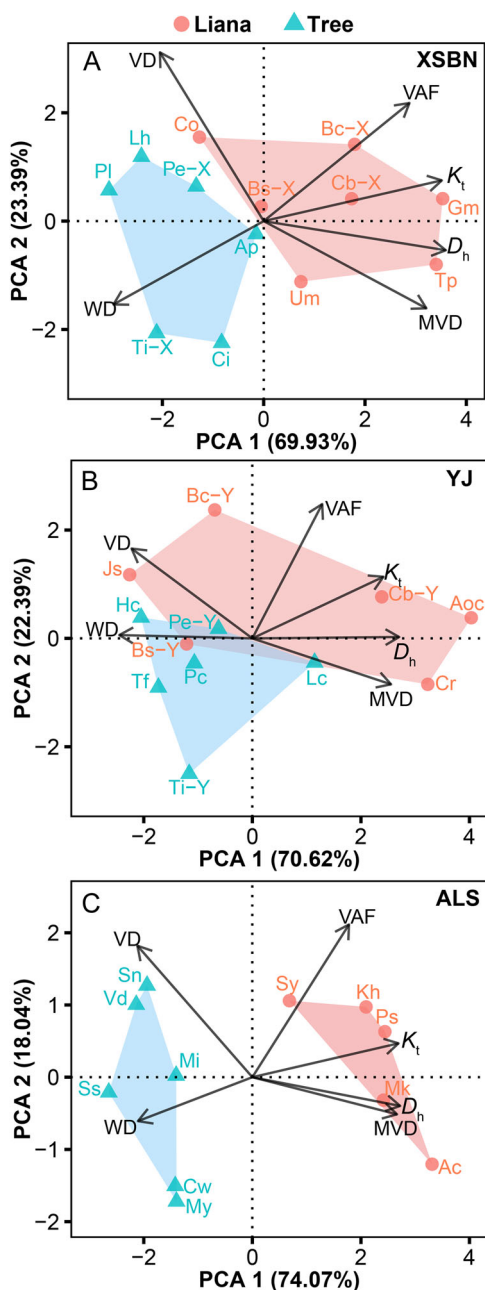
FIGURE 8 Principal component analysis for six traits from 31 species. Among the selected species, three liana species and two tree species occurred in both the Xishuangbanna (XSBN) tropical seasonal rainforest and the Yuanjiang (YJ) savanna. ALS stands for Ailaoshan subtropical evergreen forest. See the text for trait abbreviations and Appendix S1 for species codes.

trees overlapped more in trait space compared to the high-elevation subtropical forest and tropical seasonal rainforest. Previous studies also found that drought might allow species with distinct growth forms to be more convergent (e.g., Crivellaro et al., 2012; Zhang et al., 2022). Our data suggest that xylem trait differences between growth forms are affected by environmental conditions and, for lianas, may be related to large vessel diameter variation (dimorphism; Crivellaro et al., 2012; Medina-Vega et al., 2021).

Lianas also responded to environmental constraints differently from trees, partly consistent with our prediction that both lianas and trees have lower hydraulic conductivity and higher hydraulic safety in a dry-hot, cold habitat than in a warm, wet habitat due to constraints of drought and subzero-temperature stresses. For instance, lianas adjusted their wood traits from the warm, wet habitat to the hot, dry habitat, but without regulation of wood traits in the colder habitat at high elevation. This difference suggests that adjustment in liana wood hydraulic traits was driven mainly by reduced precipitation rather than by low temperature at high elevation (Crivellaro et al., 2012).

By contrast, coexisting trees from the XSBN tropical seasonal rainforest and the YJ savanna had similar hydraulic properties, with significantly lower vessel diameters and hydraulic conductivity and higher wood density in the colder ALS subtropical evergreen forest at high elevation. These results suggest that low temperature at high elevation rather than reduced precipitation strongly affects tree wood traits (Fisher et al., 2007). Small vessels or decline in vessel diameters in a subzero temperature habitat may help trees decrease the risk of freeze–thaw cavitation (Davis et al., 1999; Hacke and Sperry, 2001; Medeiros et al., 2019).

Ecological implications and conclusions

Our results have three important implications. First, vessel dimorphism might provide an anatomical explanation for the seasonal-drought growth advantage of lianas (Schnitzer, 2005, 2018; Medina-Vega et al., 2021). Lianas with dimorphic vessels can grow particularly well during dry periods (Schnitzer and van der Heijden, 2019), which might further explain why lianas thrive in highly seasonal tropical forests (Schnitzer, 2005; Parolari et al., 2020). Even though we did not find greater vessel dimorphism in the exceedingly dry savanna habitat than in the tropical rainforest, lianas might be able to employ other strategies such as leaf shedding in the dry season and small vessels to adapt to extremely dry environments (Werden et al., 2017). By contrast, the greater vessel dimorphism likely facilitates tropical rainforest lianas to adapt the seasonal climate (Zhu et al., 2017). Additional studies relevant to liana vessel anatomy and physiology are needed to further elucidate the adaptation of lianas to adverse environments.

Second, liana xylem traits were predictable with their distinct distribution among the three sites. In the savanna site, liana vessel diameter decreased and wood density increased, both of which enhance the resistance to drought stress and thus allow lianas to establish in the hot and dry habitat (Zhang et al., 2022). These characteristics also likely explain why lianas are abundant but small in savanna ecosystem (Zhang et al., 2020). In a high-elevation subtropical forest, lianas still maintained wide vessels, which enable high hydraulic conductivity but are also vulnerable to freeze–thaw embolism (Hacke and Sperry, 2001; Jiménez-Castillo and Lusk, 2013;

Schnitzer, 2018). The vulnerability of lianas to freeze–thaw embolism may explain why liana abundance decreases sharply in forests subject to freezing temperatures (Schnitzer, 2005, 2018; Bai et al., 2022).

Third, with global climate change, the severity and frequency of drought have been rising and will continue to increase in the future (IPCC, 2019). Given that lianas tend to have greater vessel dimorphism and reduced vessel diameter in many tropical ecosystems, they may be able to capitalize on slight reductions in future precipitation if it increases seasonality without becoming too dry (Schnitzer and Bongers, 2011; but see Willson et al., 2022).

To conclude, our results suggest that lianas possess large vessels, even in dry and cold habitats. A dimorphic vessel pattern may enable lianas to grow well when water is available and also to reduce their risks of embolism when water becomes limiting, ensuring both high hydraulic efficiency and safety, which may contribute substantially to liana occurrence and survival in seasonal, dry, cold habitats. The dimorphic vessel patterns reported in lianas was seldom found in co-occurring trees; most trees exhibited small vessels with normal or nearly normal distribution patterns, indicating that they have a more conservative hydraulic strategy. These findings give insights into different adaptive mechanisms of lianas and co-occurring trees across common environmental gradients in terms of stem vessel variation and the potential xylem anatomical modifications that could help plants cope with global climate change.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. List of species studied.

Appendix S2. Frequency distribution of vessel diameters and their relative contributions to total hydraulic conductivity of liana and tree species in the Xishuangbanna tropical seasonal rainforest.

Appendix S3. Frequency distribution of vessel diameters and their relative contributions to total hydraulic conductivity of liana and tree species in the Yuanjiang savanna.

Appendix S4. Frequency distribution of vessel diameters and their relative contributions to total hydraulic conductivity of liana and tree species in the Ailaoshan subtropical evergreen broadleaved forest.

Appendix S5. Coefficients of Pearson's correlation between skewness and six wood traits across lianas and trees in three sites.