Fully exposed canopy tree and liana branches in a tropical forest differ in mechanical traits but are similar in hydraulic traits

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Large lianas and trees in the forest canopy are challenged by hydraulic and mechanical failures and need to balance hydraulic conductivity, hydraulic safety and mechanical safety. Our study integrates these functions in canopy branches to understand the performance of canopy trees and lianas, and their difference. We sampled and measured branches from 22 species at a canopy crane in the tropical forest at Xishuangbanna, SW China. We quantified the hydraulic conductivity from the xylem-specific hydraulic conductivity ($K_S$), hydraulic safety from the cavitation resistance ($P_{50}$) and mechanical safety from the modulus of rupture (MOR) to evaluate trade-offs and differences between lianas and trees. We also measured a number of anatomical features that may influence these three functional traits. Our results suggest the following: trade-offs between hydraulic conductivity, hydraulic safety and mechanical safety are weak or absent; liana branches better resist external mechanical forces (higher MOR) than tree branches; and liana and tree branches were similar in hydraulic performance ($K_S$ and $P_{50}$). The anatomical features underlying $K_S$, $P_{50}$ and MOR may differ between lianas and trees. We conclude that canopy branches of lianas and trees diverged in mechanical design due to fundamental differences in wood formation, but converged in hydraulic design.

Keywords: anatomy, canopy, hydraulic conductivity, hydraulic safety, mechanical safety, trade-off.

Introduction

In tropical forests, trees and lianas grow to tall statures to display their leaves for light capture in the exposed upper forest canopy. Lianas are known to increase at the cost of trees in many tropical forests (Schnitzer and Bongers 2011), but the mechanisms related to the canopy branches are poorly explored (Schnitzer 2018, Schnitzer and van der Heijden 2019). These branches can achieve high carbon gain under full light exposure, but this comes with risks for structural stability and high water losses via transpiration (Givnish 1988), especially under dry conditions. Tall woody plants have more negative water potentials in branches and leaves, and bigger conduits, than smaller plants to maintain the passive water flow driven by a water potential gradient from roots to leaves (Petit et al. 2016, Sterck and Zweifel 2016), but this comes at the risk of drought-induced cavitation (Hacke et al. 2000, Olson et al. 2018). Tall woody plants then should maintain a water conductive system that is safe against both cavitation and mechanical failure. Possible trade-offs between these functions have been put forward in the literature but remain highly uncertain (Pittermann et al. 2006, Gleason et al. 2016; Table 1) and are hardly studied for tall individuals of trees and lianas (van der Sande et al. 2013, De Guzman et al. 2016). Here we fill this knowledge gap by comparing hydraulic conductivity, hydraulic safety and mechanical safety between canopy dwelling trees and lianas in a tropical forest.
Table 1. Selected studies of trade-offs between hydraulic conductivity ($K_S$), hydraulic safety (drought-induced cavitation, $P_{50}$) and mechanical safety (MOR) in angiosperms. Only studies focused on one (or more) of our studied trade-offs are shown. Total species and/or family number used in corresponding studies are given. MAP: mean annual precipitation; MAT: mean annual temperature; MDTmax: mean daily maximum temperature. A question mark '?' refers to unknown total species or family numbers. A square root symbol ‘√’ represents studies with a significant correlation found between two traits. A capital letter 'X' represents studies that found no significant correlation between two traits. ‘Weak’ represents studies that found a significant trade-off under certain conditions or within a certain species group. Ranges of variables in each work are given when the units are the same as our study.

<table>
<thead>
<tr>
<th>Literature</th>
<th>$K_S - P_{50}$</th>
<th>$P_{50} - $MOR</th>
<th>MOR - $K_S$</th>
<th>Lifeform</th>
<th>Species no.</th>
<th>Location</th>
<th>Condition</th>
<th>Trait range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult/branch</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Sperry and Sullivan (1992)</td>
<td>X</td>
<td></td>
<td></td>
<td>Broadleaves, conifer</td>
<td>5 (5)</td>
<td>W USA</td>
<td>Temperate zone; elevation: 1370–2825 m</td>
<td>$K_S: 0, 20; P_{50}: -10, 0$</td>
</tr>
<tr>
<td>Tyree et al. (1994)</td>
<td></td>
<td></td>
<td></td>
<td>Tree, shrub</td>
<td>15 (8)</td>
<td>S USA</td>
<td>Elevation: 1036 m; MAP: 310 mm; MDTmax: 32 °C</td>
<td>$K_S: 0, 4; P_{50}: -12, 0$</td>
</tr>
<tr>
<td>Pockman and Sperry (2000)</td>
<td>√</td>
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<tr>
<td>Jacobsen et al. (2005)</td>
<td>X</td>
<td></td>
<td></td>
<td>Shrub</td>
<td>6 (4)</td>
<td>W USA</td>
<td>Elevation: 480 m</td>
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</tr>
<tr>
<td>Jacobsen et al. (2007)</td>
<td>√</td>
<td>X</td>
<td></td>
<td>Shrub</td>
<td>17 (9)</td>
<td>South Africa</td>
<td>Elevation: 540–1160 m; MAP: 315–600 mm</td>
<td></td>
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<tr>
<td>Choa et al. (2007)</td>
<td>X</td>
<td></td>
<td></td>
<td>Tree, shrub</td>
<td>9 (1)</td>
<td>USA, Panama, Costa Rica</td>
<td>MAP: 1250–4200 mm</td>
<td>$K_S: 0, 14; P_{50}: -4, 0$</td>
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<tr>
<td>De Guzman et al. (2016)</td>
<td>√</td>
<td></td>
<td></td>
<td>Weak</td>
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<tr>
<td>Gleason et al. (2016)</td>
<td></td>
<td></td>
<td></td>
<td>Tree, liana Angiosperm, gymnosperm</td>
<td>12 (11)</td>
<td>Panama</td>
<td>MAP: 1865 mm</td>
<td>$K_S: 0, 12; P_{50}: -1.5, 0$</td>
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<td></td>
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<td>335 (10)</td>
<td>Global</td>
<td>—</td>
<td>$K_S: 0, 16; P_{50}: -14, 0$</td>
</tr>
<tr>
<td>Zhang et al. (this study)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>Tree, liana</td>
<td>22 (17)</td>
<td>SW China</td>
<td>Tropical forest; MAP: 1493 mm; MAT: 21.8 °C</td>
<td>$K_S: 0, 10; P_{50}: -3, 0; MOR: 0, 170$</td>
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<tr>
<td>Adult/stem</td>
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<tr>
<td>Martínez-Vilalta et al. (2002)</td>
<td>√</td>
<td></td>
<td></td>
<td>Tree, shrub</td>
<td>9 (8)</td>
<td>NE Spain</td>
<td>Mediterranean; MAP: 537 mm; MAT: 10 °C</td>
<td>$K_S: -; P_{50}: -7, 0$</td>
</tr>
<tr>
<td>Pratt et al. (2007)</td>
<td>X</td>
<td></td>
<td></td>
<td>Shrub</td>
<td>9 (1)</td>
<td>W USA</td>
<td>Elevation: 480 m</td>
<td>$K_S: 0, 2.5; P_{50}: -10, 0; MOR: 0, 275$</td>
</tr>
<tr>
<td>Jacobsen et al. (2009)</td>
<td>√</td>
<td></td>
<td></td>
<td>Shrub</td>
<td>15 (9)</td>
<td>W USA</td>
<td>Elevation: 540–660 m; 850–1020 m; MAP: 315 mm; 420 mm</td>
<td></td>
</tr>
<tr>
<td>Adult/sapling/branch/stem</td>
<td></td>
<td></td>
<td></td>
<td>Angiosperm, gymnosperm</td>
<td>167 (50)</td>
<td>Global</td>
<td>—</td>
<td>$K_S: 0, 8; P_{50}: -16, 0$</td>
</tr>
<tr>
<td>Maherali et al. (2004)</td>
<td>X</td>
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<td>Sapling</td>
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<tr>
<td>van der Sande et al. (2019)</td>
<td>√</td>
<td></td>
<td></td>
<td>Tree, liana</td>
<td>55 (?)</td>
<td>Panama</td>
<td>MAP: 2311–3203 mm</td>
<td>$K_S: -; P_{50}: -5, 0$</td>
</tr>
</tbody>
</table>
lowland rainforest. We aim to show whether trade-offs between these functions are manifested among species, and whether lianas and trees differ as groups in such functions. Such group differences are expected for mechanical stability since trees stand alone while lianas do not, but the possible implications of such mechanical differences for hydraulic conductivity and safety are not clear.

Hydraulic conductivity and hydraulic safety are two functions that reflect the hydraulic performance of plants. Hydraulic conductivity can be quantified by specific hydraulic conductivity ($K_S$), which is the water transport ability standardized by branch length and xylem area (Sperry et al. 1988). The hydraulic safety is often quantified by proxies for cavitation resistance (the occurrence of air bubbles in the transport system) such as $P_{50}$, which is the xylem tension that causes 50% conductivity loss by cavitation. Several studies suggest that plants cannot maximize both hydraulic conductivity (high $K_S$) and hydraulic safety (negative $P_{50}$) because large conduits that provide more efficient water transport (Tyree et al. 1994) contain larger pit pores and are therefore more sensitive to air-induced cavitation through those pores (Tyree et al. 1994, Hacke et al. 2000, Pockman and Sperry 2000, Martinez-Vilalta et al. 2002). As lianas are known to have wider vessels (Ewers and Fisher 1991, Gartner 1991a, 1991b, Wagner et al. 1998), we expect that lianas have a higher $K_S$ but a lower cavitation resistance (less negative $P_{50}$) than trees (Zhu and Cao 2009, Johnson et al. 2013).

Trees and lianas obviously differ in mechanical requirements, since the former are stable while standing alone and the latter use and hang on trees (and/or on other lianas) to reach the canopy. Mechanical safety can be quantified by the modulus of rupture (MOR), which is the force required to break a branch or stem, standardized by length and cross-sectional area (Sterck et al. 2006). Mechanical safety is expected to be positively related to hydraulic safety because strong, dense wood, known to convey greater mechanical safety (van Gelder et al. 2006, Chave et al. 2009), can contribute to avoid conduit collapse under negative pressures (Hacke et al. 2001, Sperry et al. 2006, Domec et al. 2009, Arbello et al. 2012). In line with this, mechanical safety is expected to decrease with higher hydraulic conductivity, also because stronger wood requires denser wood with fewer and/or narrower vessels, which reduces hydraulic conductivity. From these functional trait relations, we predict that lianas have a lower mechanical stability (MOR) than trees.

Differences in these three functional traits ($K_S$, $P_{50}$ and MOR) across species or species groups (such as lianas versus trees) are expected to result from differences in anatomical features, which can be observed in the stem or branch cross sections (Figure 1). $K_S$ depends on the total transporting area and vessel diameter. $K_S$ may increase with the area occupied by ray and axial parenchyma since parenchyma provides capacity for water storage and may contribute to $K_S$ (Angyalossy et al. 2012, Pratt and Jacobsen 2017), but may also decrease when parenchyma area comes at the cost of the area occupied by vessels. Cavitation resistance may increase ($P_{50}$ becomes more negative) with a higher wall–lumen ratio (WLR) and wood density (Hacke et al. 2001, but see Powell et al. 2017 and Rosas et al. 2019) because the resultant stronger cell wall strength lowers the risk of wall micro-fractures, which causes air-seeding and cavitation (Sterck and Bongers 1998, Jacobsen et al. 2005, van Gelder et al. 2006). Species that are more vulnerable to cavitation (less negative $P_{50}$) may require more ray and axial parenchyma to store sugars that contribute to embolism repair (Brodersen et al. 2010, Ogasa et al. 2013, Klein et al. 2018, Zeppel et al. 2019). Finally, MOR depends on wood density (van Gelder et al. 2006), WLR (Hacke et al. 2001) and the total area of fibers, with higher MOR resulting from higher values of such traits. Overall, relations between these three focal functional traits and underlying anatomical traits involve possible trade-offs, but those are still poorly tested for canopy trees and lianas.

Here we evaluate the existence of hydraulic and mechanical trade-offs between liana and tree species dwelling in the same tropical forest upper canopy. Instead of addressing entire individuals, we focussed on exposed branches in the upper canopy: (i) with the high irradiation and temperature during the day, these branches potentially gain most carbon but face high transpiration demands and can thus act as bottlenecks for the hydraulic integrity and carbon gain of the entire individual; (ii) in canopy branches, standardized branches length can be easily controlled for diminishing the tapering effects of vessels and their related functionalities (Becker et al. 2000, Petit and Anfodillo 2009); and finally (iii) it is practically more feasible to study branches than entire individuals, certainly the large ones that dwell in the forest canopy. In our study, we addressed three main questions. (i) How do canopy branch traits differ between lianas and trees? (ii) Do lianas and trees show trade-offs between hydraulic conductivity, hydraulic safety and mechanical safety in canopy distal branches? (iii) How do underlying anatomical features influence trait values and trade-off among traits?

**Materials and methods**

**Study site**

The study was carried out in a crane site in a seasonal tropical lowland rain forest located in the core area of National Nature Reserves in the Bubeng region, Xishuangbanna (Xishuangbanna Tropical Botanical Garden; XTBG), Yunnan Province, SW China ($21^\circ36'N 101^\circ35'E$). The altitude of the crane site is $\sim780$ m. The area has a typical monsoon climate with distinguishable wet and dry seasons. A wet season starts from May and lasts until October, and a dry season characterizes the period from November to April. The average annual temperature is...
21.8 °C with mean monthly temperature ranging from 15 °C in December to 25 °C in June. The average annual precipitation is 1493 mm, of which 1256 mm (84%) falls between May and October (Cao et al. 2006).

**Field work**

Canopy branches of trees and lianas were collected using a canopy crane with a height of 80 m and a radius of 60 m. A total of 44 individuals of 22 species (10 tree and 12 liana species, all evergreen broad-leaved angiosperm species) were randomly selected. Species information is given in Table S1 (available as Supplementary Data at Tree Physiology Online). All the sampling work was conducted in the early morning before sunrise (during 07:00–09:00h) in the wet season of 2016. Three 1.5-m long (from branch tip) canopy branches from each tree individual and three 3-m long (from branch tip) branches from each liana individual were cut for subsequent hydraulic and mechanical measurements. All tree branches selected were self-supporting ones that were not hanging on other branches. All liana branches selected were non-self-supporting ones hanging on other branches. All branches were immediately treated: (i) side twigs were cut off leaving ~10 cm base in order to avoid cavitation by cutting; (ii) the whole remaining branch was wrapped with wet towels to reduce desiccation; and (iii) each branch was put into a black plastic bag, which was closed to avoid further water loss. Afterwards, the branches were transported to the XTBG lab for subsequent hydraulic and mechanical measurements. Additionally, for all individuals, a 50-cm long sun-exposed canopy branch was cut, of which the basal 10-cm branch segment was cut and preserved in Formaldehyde-acetic acid alcohol solution for subsequent anatomical analysis.

**Hydraulic measurements**

In the laboratory, we measured xylem-specific hydraulic conductivity (KS) and the vulnerability curve to get cavitation resistance (P50). KS is the maximal water flow per area standardized by length. P50 is the xylem potential at which 50% of maximum hydraulic conductivity is lost (as defined by Domec and Gartner 2001). Before we started those measurements, we did a preliminary survey on the maximum vessel length (MVL; values for each species are provided in Table S1, available as Supplementary Data at Tree Physiology Online) to determine the branch length to be taken from trees and lianas for all the species collected in this study. We used an air-injection method (Ewers and Fisher 1989) to estimate the MVL. Long branches were harvested in the field and brought to the lab. The distal parts of branches were cut and connected with a 100 kPa compressed air, while the upstream parts of the branch segments were immersed under water. Segments were shortened at a 1-cm interval until the first air bubble emerged. The MVL amounted to the remaining length of the segment plus 0.5 cm.

**Xylem-specific hydraulic conductivity (KS, kg m⁻¹ s⁻¹ MPa⁻¹)**

We determined KS using a water flow meter system (Sperry et al. 1988). Branch samples were shorted to ~1.5 times the length of MVL under water in the lab. The remaining branches were flushed with 10 mM degassed KCl solution at 100 kPa pressure for 1 h to reach the maximum flow rate. The upstream parts were connected to ~5 kPa KCl solution (same as above). The distal part of a segment was connected to a pipette. A steady flow rate was obtained after 3–5 min equilibrium. The KS was then calculated as follows:

$$KS = FL / (\Delta P A_x)$$

where $F$ (kg s⁻¹) is the water flux, $L$ is the segment length (m) and $\Delta P$ is the pressure difference between the two ends of a segment (MPa). Xylem area ($A_x$, cm²) was then measured by using a micro-caliper.

**Cavitation resistance (P50, −MPa)**

To obtain $P_{50}$, a xylem vulnerability curve was constructed at species level. This curve shows the loss in branch hydraulic conductivity with decreasing negative pressure. We used the air-pressurization method to induce embolism (Cochard et al. 1992). Branches were flushed under 100 kPa pressure with degassed KCl solution for 1 h to reach a maximal conductance ($K_{max}$) first. Then a series of imposed, increasing pressures were applied in 8–12 steps of 0.5 or 1.0 MPa (see Figure S3 available as Supplementary Data at Tree Physiology Online) using a pressure chamber (PMS1505D-EXP, PMS Instruments, Albany, OR, USA) until the branch was fully cavitated. Each pressurization was maintained for 15 min (see Cochard et al. 1992) and then the pressure was released for 20–240 min until a stable conductance ($K$) was reached. The percentage loss of hydraulic conductivity (PLC, %) at each pressurization step was calculated as follows:

$$PLC = 100\% \times (K_{max} - K) / K_{max}.$$  

We used a three-parameter sigmoid function to fit the vulnerability curves

$$PLC = 100 / (1 + \exp (a \times (\Psi_s - X_0)))$$

where $a$ is the maximum slope of the curve, and $X_0$ is the pressure at the 50% loss of hydraulic conductivity ($P_{50}$).

**Mechanical and density measurements**

To estimate mechanical safety, we measured the MOR by using a laboratory technique that is used to measure the maximum load-carrying capacity in bending (Green et al. 1999). We used a three-point measurement with a span length ($L$, mm):diameter ($D$, mm) ratio of 15 to estimate MOR. A 30-cm long branch segment cut from the above described long branch was used. The branch segment was horizontally placed on two supports
(span length, \(L\)). Subsequently, a vertical, downward-orientated load was applied under a constant speed (\(\sim 1\) mm s\(^{-1}\)) at the midpoint of the branch using a SUNDOO SIY-500 test stand. A portable electronic scale was used to measure the load \((P_{\text{max}}; N)\) at the moment of branch breakage. The MOR \((\text{N mm}^{-2})\) was then calculated as \((\text{Sterck et al. 2006})\) follows:

\[
\text{MOR} = \left(\frac{M_{\text{max}}}{R}\right) / I = \left(\frac{1}{4 P_{\text{max}} L \cdot R}ight) / \left(\frac{1}{4 R^4}\right),
\]

where \(M_{\text{max}}\) is the maximum bending moment, \(I\) is the second-order moment of area and \(R\) is the radius in a circle cross section.

After measuring MOR, one 10-cm branch segment was cut and fresh volume \((V, \text{cm}^3)\) was determined using the water displacement method. The branch segment was then dried in an oven (PH240A) at 65 °C for 48 h and weighed \((\text{DW}, \text{g})\), and dry wood density \((\text{WD}, \text{g cm}^{-3})\) was calculated as follows:

\[
\text{WD} = \frac{\text{DW}}{V}.
\]

### Anatomical measurements

Permanent cross sections were made using the paraffin embedding method. One 1- to 1.5-mm thick branch piece was cut with a razor blade from each 10 cm branch segment, after being embedded in an FAA solution. These pieces were dehydrated with a series of 50–96–100% ethanol. After this, they were infiltrated with limonene at air temperature and then with melted paraffin at 65 °C in an oven (PH240A). Afterwards, we embedded these pieces into paraffin blocks using a Leica EG1150H Paraffin Embedding Station. After paraffin blocks got hard, we cut a 6- to 10-μm thick cross section per piece using a Leica RM2235 rotary microtome. Then we removed the paraffin from the cross sections with limonene and dehydrated the pieces again by 50–96–100% ethanol series. Following dehydration, all cross sections were stained in a safranin/astra blue solution and fixed in Neutral Balsam. After the Neutral Balsam was air dried, photographs of entire cross sections were taken with a digital camera (DFC 320; Leica, Cambridge, UK) mounted on a microscope (DM2500; Leica) using Leica imaging software (v.3.6.0). To obtain a photograph of the entire cross section, sequential photographs were stitched using PTGUIPRO (v.9.1.8; New House Internet Services BV, Rotterdam, The Netherlands). Pith area, xylem area and phloem area of cross sections were measured firstly by using ImageJ software (v.1.44; http://rsb.info.nih.gov/ij; developed by W. Rasband, National Institutes of Health, Bethesda, MD, USA). Their fractions were calculated. Then detailed tissue areas were measured using the pie-method (Zhang et al. 2016): we selected four pie-shaped areas in four directions of a cross section along rays, including a ray along one side and excluding it on the other. Vessel lumen area, ray area and axial parenchyma area were measured. Mean vessel lumen diameter (MVD) was calculated. From these areas, we calculated the surface percentages in the xylem for each of these tissues per pie and for the whole cross section. In addition, the largest 20 vessels were selected, and their lumen area, lumen diameter and vessel wall thickness were measured for each cross section. The WLR was calculated by dividing wall thickness by vessel lumen diameter. We added those measures for the largest vessels because they are expected to contribute most strongly to hydraulic conductivity and also cause the greatest risks for cavitation and mechanical failure. Tracheids were not considered in our study because our coloring method did not allow one to separate tracheids from fibers. For our species samples, Carlquist (1985) mentioned the presence of vasicentric tracheids in Combretum latifolium and Strychnos angustiflora, but no such information was provided for any other species.

### Statistics

Full names of tested variables, their abbreviations and units are given in Table 2. Differences between lianas and trees in tissue sizes, functional traits and underlying anatomical traits were tested using a linear mixed model with 44 individuals from 22 species. \(K_S, \text{MOR}, \text{WD}, \text{MVD}, \text{biggest vessel lumen diameter (BVD)}, \text{WLR}, \text{parenchyma%}, A_{pi}, A_x, \text{and } A_{aph}\) were log\(_{10}\) transformed to achieve normality. Species was set as a random factor to account for multiple observations within species.

Standardized major axis (SMA) regression was used to test trade-offs between \(K_S, P_{50}\) and \(\text{MOR}\), as well as relationships among vessel%, parenchyma% and fiber%. Standardized major axis regression allows us to test differences in slopes among different groups. To meet the normality assumption for these regressions, \(K_S\) and \(\text{MOR}\) were log\(_{10}\) transformed. Lifeform was

<table>
<thead>
<tr>
<th>Variables</th>
<th>Abbreviations</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Functional traits</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Xylem-specific conductivity</td>
<td>(K_S)</td>
<td>(\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1})</td>
</tr>
<tr>
<td>Cavitation resistance</td>
<td>(P_{50})</td>
<td>(-\text{MPa})</td>
</tr>
<tr>
<td>Modulus of rupture</td>
<td>(\text{MOR})</td>
<td>(\text{N mm}^{-2})</td>
</tr>
<tr>
<td>Tissue properties</td>
<td></td>
<td></td>
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<tr>
<td>Dry wood density</td>
<td>(\text{WD})</td>
<td>(\text{g cm}^{-3})</td>
</tr>
<tr>
<td>Mean vessel lumen diameter</td>
<td>(\text{MVD})</td>
<td>(\text{μm})</td>
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<tr>
<td>Mean biggest vessel lumen diameter</td>
<td>(\text{BVD})</td>
<td>(\text{μm})</td>
</tr>
<tr>
<td>Wall-lumen ratio</td>
<td>(\text{WLR})</td>
<td>(\text{μm}^{-1})</td>
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<tr>
<td>Tissue proportions</td>
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<tr>
<td>Vessel lumen area percentage</td>
<td>(\text{Vessel}%)</td>
<td>(%)</td>
</tr>
<tr>
<td>Ray and axial parenchyma area percentage</td>
<td>(\text{Parenchyma%})</td>
<td>(%)</td>
</tr>
<tr>
<td>Fiber area percentage</td>
<td>(\text{Fiber}%)</td>
<td>(%)</td>
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<tr>
<td>Tissue areas</td>
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</tr>
<tr>
<td>Pith area</td>
<td>(A_{pi})</td>
<td>(\text{cm}^2)</td>
</tr>
<tr>
<td>Xylem area</td>
<td>(A_x)</td>
<td>(\text{cm}^2)</td>
</tr>
<tr>
<td>Phloem area</td>
<td>(A_{aph})</td>
<td>(\text{cm}^2)</td>
</tr>
</tbody>
</table>

Table 2. The list of plant variables measured for this study. We present abbreviations used in the text and their units.
Figure 1. Conceptual model of trade-offs between hydraulic conductivity (quantified by the xylem-specific hydraulic conductivity, $K_S$), hydraulic safety (quantified by the cavitation resistance, $P_{50}$) and mechanical safety (quantified by the MOR) in branches of woody plants, and their underlying anatomical features. Parenchyma includes ray and axial parenchyma in xylem. Tissue percentages (vessel%, fiber% and parenchyma%) are the relative areas occupied in the xylem cross-sectional areas. Double-headed arrows represent expected correlations between two functional traits. Single-headed arrows represent expected causal factors. A plus sign ‘+’ means positive effects or correlations, and a minus sign ‘−’ means negative effects or correlations.

Firstly set as a group factor in the SMA regressions to test for differences between lianas and trees. If lifeform had no significant effect, it was removed from the model to show a single common trend for lianas and trees. Since it is impossible to add a random factor in SMA, we averaged branch data at species level (see Tables S2 and S6 available as Supplementary Data at Tree Physiology Online). For the correlation between $K_S$ and $P_{50}$, and between MOR and $P_{50}$, trends were mainly driven by the extreme values of two tree species (Allophylus cobbe and Balakata baccata), respectively (see Tables S3 and S4 available as Supplementary Data at Tree Physiology Online). We thus excluded these two species from the analysis to check for a common trend without such outliers.

Starting from the working hypothesis (see Figure 1), we built regression models and used model averaging to test for the effects of anatomical features on each functional trait ($K_S$, $P_{50}$ and MOR) for lianas and trees, separately. In these analyses, $K_S$, MOR, WD, parenchyma% and WLR were log$_{10}$ transformed to achieve normality. Then all variables were scaled to be able to directly compare their effects. In line with our working hypothesis (Figure 1), BVD, parenchyma% and vessel% were set as the explanatory variables of $K_S$; WLR, WD and parenchyma% were set as the explanatory variables of $P_{50}$; and WLR, WD and fiber% were set as the explanatory variables of MOR. In all cases, species was set as a random factor. Multicollinearity was checked (Variance Inflation Factor < 5) but played no role in our statistical models.

Afterwards, an information theory-based approach was applied to detect the best model (Burnham and Anderson 2003, Nakagawa and Freckleton 2011). The best model was generated from the smallest bias-adjusted Akaike’s information criterion (AICc). Then other models were compared to the best model by calculating the AICc difference ($\Delta$AICc), and models with $\Delta$AICc < 2 were used to perform model averaging (Burnham and Anderson 2003).

All statistical tests were conducted using RStudio (Version 0.99.903) packed with R 3.3.3 (R Development Core Team 2016). Standardized major axis (SMA) regression was performed with the sma function in the smatr package (Warton et al. 2012). Global model comparison and model averaging were performed with the dredge and model.avg function using the MuMIn package (Barton 2009).

**Phylogeny**

To control for possible phylogenetic effects on plant traits, we constructed a phylogenetic tree using the program Phylomatic (http://phyloidiversity.net/phylomatic, accessed on 22 February 2019). We constructed a species-level tree with trait values being averaged within species. Phylogenetic conservatism in all traits were then analyzed using Blomberg’s K statistic, which compares the observed signal in a trait to the signal under a Brownian motion model of trait evolution on a phylogeny (Blomberg et al. 2003). K-values closer to 0 correspond to a random or convergent pattern of evolution, while K-values greater than 1 indicate increasing strong phylogenetic signal and conservatism in trait values. To examine possible coordinated divergences in hydraulic conductivity, hydraulic safety and mechanical safety, we analyzed phylogenetic independent contrast values using Pearson product–moment correlations (Zanne et al. 2010). Phylogenetic analyses were performed...
using RStudio (Version 0.99.903) packed with R 3.3.3 (R Development Core Team 2016) including the packages APE (Paradis et al. 2004) and Picante (Webb et al. 2010).

Results

In contrast to our expectation, MOR was significantly higher in lianas than in trees (Figure 2c). Trees and lianas did not, however, significantly differ in $K_S$ or $P_{50}$ (Figure 2a and b), though mean $K_S$ was almost twice as high in lianas than in trees, but high variance occurred across liana species (Figure 2a). Trees and lianas did not differ significantly in tissue properties and neither in the tissue proportions within the branch cross sections (Figure 2d–k). Only xylem and phloem cross-sectional area was, as expected, higher in trees than in lianas (Figure 2m and n).

Thus, apart from these latter size differences, lianas and trees unexpectedly did not differ in tissue properties and proportions, nor in their functional traits, except MOR (Figure 2). For all traits, $K$-values were less than 1 with corresponding $P$-values larger than 0.05 (see Table S2 available as Supplementary Data at Tree Physiology Online). In addition, trees and lianas did not differ in anatomical structure, except for one liana species, S. angustiflora, which had included phloem (see Table S1 available as Supplementary Data at Tree Physiology Online).

We found no evidence for trade-offs between hydraulic conductivity, hydraulic safety and mechanical safety, either across liana and tree species or within liana and tree species separately (Figure 3, see Tables S3 and S4 available as Supplementary Data at Tree Physiology Online). Phylogenetic relatedness among the species evaluated, as measured using independent contrasts (see Table S5 available as Supplementary Data at Tree Physiology Online), had no significant effect on correlations between hydraulic conductivity, hydraulic safety and mechanical safety.

Lianas and trees partially differed in the underlying anatomical features that explained most variation in $K_S$, MOR and $P_{50}$ across species (Table 3). Vessel% explained variation in $K_S$, but the coefficient and importance value were higher for lianas. The BVD contributed in explaining $K_S$ differences across liana species, but only weakly. Wall–lumen ratio (WLR) or WD partially explained variation in MOR across liana and tree species, but only for trees was the effect of WD larger (Table 3). The WLR and parenchyma% partially explained the variation in $P_{50}$ in lianas, while WD partially explained the variation in $P_{50}$ in trees, but their coefficients and importance values were rather low.

Discussion

In this study, we compared hydraulics and mechanics of liana and tree branches in an upper tropical forest canopy in China. Since none of the hydraulic, mechanical and anatomical traits showed phylogenetic conservatism (see Table S2 available as Supplementary Data at Tree Physiology Online), we discuss our results here in the light of possible trade-offs in hydraulic and mechanical functional traits, the differences between lianas and trees as groups and the link with underlying anatomical traits, but irrespective of phylogenetic relations.

Do lianas and trees differ in functional traits?

As expected, liana branches were slenderer than those of trees and therefore were characterized by smaller tissue areas in the branch stem cross section. Of the functional traits, only the MOR of branches significantly differed between lianas and trees; it was significantly higher in lianas than in trees implicating a higher mechanical safety in liana branches. As lianas and trees did not significantly differ in their branch WD, vessel%, parenchyma%, fiber% and phloem% (Figure 2), these results suggest that lianas produce stronger branch stems than trees by using similar wood density and similar shares of different tissues in stem cross sections. This is consistent with the similar stem density shared by vines and shrubs within the same species (Gartner
1991c), but not with the higher stiffness observed for shrubs relative to vines. Thus, lianas should have a more efficient way, at least in their canopy branches, to build up their wood enabling them to grow longer with the same investment as tree branches, while still maintaining strong wood. A possible trait that may help lianas achieve this is microfibril orientation, which may give rise to a high flexibility and strength of liana branches (Hoffmann et al. 2000). This possibly unique anatomy and structure allows lianas to forage at low carbon costs (slender stems) without increasing risks of mechanical failure.

In contrast to our expectation, $K_S$ did not differ significantly between lianas and trees (Figure 2a). This is consistent with
results of a sapling study by van der Sande et al. (2013) and may be partially due to the large variance within lianas. As \( K_S \) depends both on the area occupied by vessels and vessel diameter (Bittencourt et al. 2016), the overlapping vessel% in lianas and trees (Figure 2h) suggests that the similar \( K_S \) is induced by similar vessel space allocation and a similar vessel diameter. This is supported by our results that BVD and MVD did not differ significantly between lianas and trees (Figure 2e and f) in the studied exposed canopy branches. Though we commonly accept that lianas generate wider vessels compared with trees in cross sections (Gartner 1991b, Chiu and Ewers 1992, Angyalossy et al. 2012), this may not be true if we scale vessel diameter by stem length (Rosell and Olson 2014). Thus, vessel diameter may be mainly driven by a general tip-to-base widening effect, rather than lifeform control. Since vessel fraction contributes to explain \( K_S \) across liana branches, but not in tree branches (Table 3), our study suggests that some liana species have a higher hydraulic efficiency in their canopy branches than other species by allocating more space for vessels rather than widening their vessels at branch tip.

We did not find significant differences in the hydraulic safety between lianas and trees (Figure 2b). The weak role of WLR and WD in both lianas and trees suggests that differences in cavitation resistance may be weakly induced by vessel wall microfractures in canopy branches. \( P_{50} \) differences across species were, however, only poorly explained by these selected anatomical features (Table 3), suggesting that other traits largely drive the variation in \( P_{50} \). Inter-conduit connection and pit geometry are important for canopy branches against cavitation (Brodersen et al. 2014, Tixier et al. 2014, Woodruff et al. 2016), but those properties were not included in our study. However, in a sapling study it was shown that trees had a higher cavitation resistance compared with lianas (van der Sande et al. 2013). Our canopy trees had a \( P_{50} \) that was similar to those of tree saplings, whereas canopy lianas had a more negative \( P_{50} \) compared with those of liana saplings (van der Sande et al. 2013). Possibly, lianas change cavitation resistance from sapling to adults. This suggests that lianas reduce xylem vulnerability at branch tips when they are tall and can thus compensate for the non-linear pressure gradient with increasing height (Couvreure et al. 2018). Thus, hydraulic strategy may shift during plant development under different mechanisms in lianas and trees. More studies are needed to understand the mechanisms that drive the difference between sapling and adult in cavitation resistance in tall woody plants (Olson et al. 2018).

Our branch study reveals the upper crown physiology and related anatomy, but the situation may change when considering the stem base (Couvreure et al. 2018) since the function of the stem base is more focused on mechanical support for the whole plant body. We call for more studies to compare canopy branch with stem base to enlarge our understanding of the physiological and underlying anatomical difference between lianas and trees.

**Do trade-offs between hydraulic conductivity, hydraulic safety and mechanical safety exist in lianas and trees?**

We hypothesized that hydraulic conductivity would trade-off against hydraulic safety. This was the case neither across both lianas and trees together, nor within lianas or trees separately (Figure 3a, see Table S4 available as Supplementary Data at Tree Physiology Online), suggesting that a high hydraulic conductivity does not necessarily connect to a low hydraulic safety in canopy branches. Support for the existence of such a trade-off varies much across studies (Table 1). Branch studies by Pockman and Sperry (2000) and De Guzman et al. (2016) showed a trade-off between \( K_S \) and \( P_{50} \) in a temperate dry vegetation and tropical seasonal dry forest. These results suggest that drought may play a role in controlling the balance between water transport and safety across species growing in the same condition. However, Choat et al. (2007; a branch study) did not find such trade-off in the genus Cordia growing at contrasting precipitation levels, and neither did Pratt et al. (2007) in a Rhamnaceae shrub stem study. This implies that phylogenetic control may weaken the response to drought
leading to the absence of such a hydraulic trade-off. Two global surveys (Maherali et al. 2004, Gleason et al. 2016) showed no evidence for a strong trade-off between $K_s$ and $P_{50}$ across stems and branches. Possibly, these weak relationships, and the lack for support of a trade-off in our study, result from species differences in underlying traits that were beyond the scope of our study, such as xylem vessel network topologies and network features, cellular arrangements, the presence of other cell types and the degree of xylem modularity (Choat et al. 2003, Wheeler et al. 2005, Loepef et al. 2007).

Against our expectation, we did not find a trade-off between hydraulic conductivity and mechanical safety across lianas and trees, nor in lianas and trees separately (Figure 3b, see Table S4 available as Supplementary Data at Tree Physiology Online). For shrub branches in a Mediterranean-type climate region, no trade-off was observed between hydraulic conductivity and mechanical safety (Jacobsen et al. 2007). These observations imply that in both dry and wet conditions, there may be no trade-off between mechanical safety and hydraulic conductivity in branches. In angiosperms, xylem tissues differentiate into vessel, parenchyma and fiber tissues, thus implying trade-offs between those tissues. Fiber%, the main supporting tissue, was however not correlated with vessel% (see Figure S1 and Table S4 available as Supplementary Data at Tree Physiology Online), suggesting that vessel area does not trade-off against fiber area in stem cross sections. This is in agreement with Fortunel et al. (2014), who found that fiber traits appeared to be independent of vessel traits. However, more studies are needed to confirm the separate development of fiber traits and vessel traits, especially in stems of tall woody plants, which may experience huge mechanical stress, and to fully understand the mechanisms that drive the relation between hydraulic and mechanical properties in angiosperm species.

Mechanical safety and hydraulic safety were decoupled as well (Figure 3c). In line with this, the underlying variables WLR in lianas and WD in trees only weakly influenced MOR and $P_{50}$. This contrasts with results from shrub studies (Table 1; Jacobsen et al. 2005, 2009, Pratt et al. 2007) showing a positive correlation between MOR and $P_{50}$ in stems/branches. These shrub studies, however, included a much wider variation in $P_{50}$ going down to minimum values close to −11 MPa, compared with −3 MPa in our study. In their studies, a negative correlation between $P_{50}$ and WD was also found, whereas we did not find such a correlation (see Figure S2b available as Supplementary Data at Tree Physiology Online). Therefore, the negative water potential in our study may not have been harsh enough to cause the structural change leading to stronger wood to avoid vessel wall micro-fractures. If the range of $P_{50}$ shown by Jacobsen et al. (2009) is narrowed to −4 MPa, the trade-off disappears.

The lack of trade-offs between hydraulic conductivity, hydraulic safety and mechanical safety did not change when considering phylogenetic dependence (see Table S5 available as Supplementary Data at Tree Physiology Online), confirming that canopy branches may reflect adaptations to the environment rather than phylogenetic constraints.

**Conclusions**

Most of our expectations on the differences between lianas and trees were not supported by our data for the studied tropical seasonal forest in SW China. The expected trade-offs between hydraulic conductivity, hydraulic safety and mechanical safety were not found. The anatomical features only partially explained the variation in functional traits. Consequently, this study mainly shows the following: (i) there are no clear trade-offs between hydraulic conductivity, hydraulic safety and mechanical safety across exposed canopy distal branches in trees and lianas; (ii) liana canopy distal branches better resist branch breakage against mechanical forces than tree canopy branches; (iii) lianas and trees are as groups similar in hydraulic performance; and (iv) the mechanisms that drive $K_s$, $P_{50}$ and MOR may differ between lianas and trees. We conclude that liana and branch traits diverged in mechanical design due to fundamental differences in wood formation, but converged in hydraulic design.

**Supplementary Data**

Supplementary Data for this article are available at Tree Physiology Online.

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**Conflict of interest**

None declared.

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