

Hydraulic properties and photosynthetic rates in co-occurring lianas and trees in a seasonal tropical rainforest in southwestern China

Shi-Dan Zhu · Kun-Fang Cao

Received: 9 September 2008 / Accepted: 23 February 2009 / Published online: 14 March 2009
© Springer Science+Business Media B.V. 2009

Abstract In this study, we examined wood anatomy, hydraulic properties, photosynthetic rate, and water status and osmotic regulation in three liana species and three tree species co-occurring in a seasonal tropical rain forest. Our results showed that the three liana species had larger vessel diameter, lower sapwood density, and consequently higher branch sapwood specific hydraulic conductivity (K_S) than the three tree species. Across species, K_S was positively correlated with leaf nitrogen concentration and maximum net CO_2 assimilation rate. However, it was also positively correlated with xylem water potential at 50% loss of hydraulic conductivity, indicating a trade-off between hydraulic efficiency and safety. Compared to the tree species, the liana species had higher predawn leaf water potential and lower osmotic adjustment in the dry season. The combination of more efficient water transport, higher photosynthetic rates, and their ability to access to more reliable water source at deeper soil

layers in the dry season in the lianas should contribute to their fast growth.

Keywords Hydraulic conductivity · Xylem cavitation · Leaf water potential · Osmotic regulation

Introduction

Lianas are important components of tropical rain forests; they usually distribute most of their leaves on the top of the canopy and cast shade on their host trees, which may reduce the growth rates and increase mortality rates of the hosts (Putz 1984a, b). Lianas can rapidly colonize the canopy gaps in the forests and proliferate in heavily disturbed forests (Putz 1984b; Schnitzer and Bongers 2002; Schnitzer et al. 2000). With the exacerbation of forest fragmentation and global environmental change, the abundance of lianas in tropical forests is increasing (Granados and Körner 2002; Wright et al. 2004; Zhu et al. 2004), which will consequently influence the species composition and ecosystem service of tropical forests.

Lianas have relatively little structural support and typically have a very high canopy: stem biomass ratio, resulting in a higher proportion of assimilating biomass than other woody plants (Schnitzer and Bongers 2002). For example, liana biomass accounts for less than 10% of total forest biomass but up to 40% of the leaf biomass of tropical rain forests in Panama (Putz 1984b). Lianas have wide and large vessels (Ewers

S.-D. Zhu · K.-F. Cao (✉)
Key Laboratory of Tropical Forest Ecology,
Xishuangbanna Tropical Botanical Garden,
Chinese Academy of Sciences, Mengla,
Yunnan Province 666303, China
e-mail: caokf@xtbg.ac.cn

S.-D. Zhu
e-mail: zhud@xtbg.ac.cn

S.-D. Zhu
Graduate University of Chinese Academy of Sciences,
19A Yuquan Road, Beijing 100049, China

et al. 1990), and thus should have high hydraulic conductivity, which should compensate hydraulically for their narrow and long stem (Chiu and Ewers 1992; Ewers and Fisher 1991; Field and Balun 2008). Since water supply influences leaf water potential and stomatal conductance, hydraulic conductance is strongly correlated with photosynthetic capacity of plants (Brodribb and Feild 2000; Brodribb et al. 2002).

The abundance of lianas increases with the rainfall seasonality in tropics (Reddy and Parthasarathy 2003; Schnitzer 2005; Swaine and Grace 2007). Schnitzer (2005) found that in seasonal tropical rain forests, lianas were able to grow significantly more than trees during the dry season relative to their growth in the wet season. Similarly, Cai (2007) found that in a seasonal rain forest of the same region as used in the present study, the photosynthesis of lianas in the dry season was less affected than the trees. In this context, we might expect that lianas suffer little from water stress during a dry season. Several morphological and physiological traits are involved in drought resistance, including rooting depth (Trifilò et al. 2004), xylem vulnerability to cavitation (Choat et al. 2007; Lopez et al. 2005; Maherali et al. 2004), and osmotic adjustment (Clayton-Greene 1983; Cao 2000). Lianas have been shown to have deep root systems (Restom and Nepstad 2004), but we know less about their xylem vulnerability to cavitation and osmotic adjustment in a dry season. Osmotic adjustment enables the maintenance of cell turgor and may serve to sustain growth and photosynthesis under a dry condition (Cao 2000).

The objectives of the present study were: (1) to compare wood anatomy, hydraulic properties, and photosynthetic rate between co-occurring lianas and trees in a seasonal tropical rain forest; (2) to evaluate their drought tolerance by comparing the xylem vulnerability to cavitation induced dehydration and osmotic regulation in response to a drought. This dataset should provide a clear understanding of the difference in ecophysiology between lianas and trees, and might provide the basis for the future comparison with the two groups.

Materials and methods

Study site and plant materials

The present study was carried out in a seasonal tropical rainforest in the Xishuangbanna Tropical

Botanical Garden (21°54'N, 101°46'E, 580 m a.s.l.), southern Yunnan, China. The climate of this region is dominated by the south-west monsoon coming from the Indian Ocean, with a distinct dry season from November to next April. Mean annual total precipitation is 1,379 mm, of which about 80% occurs in wet season (May–October). Mean annual temperature is 21.4°C.

Because of the inconvenience in accessing the canopy, we restricted the study to three liana species, *Combretum latifolium* BL. (Combretaceae), *Quisqualis indica* Linn. (Combretaceae), and *Millettia pachycarpa* Benth. (Papilionaceae), as well as three tree species, *Bauhinia variegata* Linn. var. *candida* (Roxb.) Voigt. (Caesalpiniaceae), *Baccaurea ramiflora* Lour. (Euphorbiaceae), and *Syzygium szemaense* Merr. et Perry (Myrtaceae). *Bauhinia variegata* is deciduous, which sheds all of its leaves in February, and flush new leaves near the end of April. *C. latifolium* and *Q. indica* are brevi-deciduous, which exchange all their leaves during a short period (Brodribb et al. 2002) in the mid-dry season but are never completely leafless. The others are evergreen. These species are important components of the local forest; especially, *C. latifolium* and *M. pachycarpa* are currently increasing their abundance in the forests of the present region (Tang et al. 1997). All sampled plants grew in flat sites along the paths. If the trees carry lianas, some ecophysiological traits would be changed, for example, leaf water potential would be lowered (Pérez-Salicrup and Barker 2000); therefore, we selected the tree species that did not carry any lianas. Collections of branches and leaves and gas exchange measurements were made on the upper canopy (the height was >10 m) of trees along the paths with the help of a crane loaded on a truck.

Stem hydraulic conductivity and vulnerability curve

Because of the large difference in the distance to the apex between the two growth forms, terminal branches with similar diameters (7–10 mm) close to the canopy from five individuals per species were collected early in the morning during the wet season. These branches were sealed in black plastic bags and were transported to the laboratory. Maximum vessel lengths for each species were measured preliminarily by using the method described by Brodribb and Feild

(2000). Air at 0.05–0.1 MPa pressure was blown into the cut end of branches while cutting the branch tips under water. Bubbles were blown through when the branch length was shorter than the longest vessel. The lengths of stem segments used for hydraulic conductivity measurements were 10% larger than the longest vessel length measured. This ensured no presence of open vessels and small variation in branch length within species. The length of branches segments in this study were 30–50 cm for the tree species and 80–110 cm for the liana species.

The stem hydraulic conductivity (K_h) was determined using the steady-state flow-meter method. A total of 10 mol m⁻³ oxalic acid could prevent long-term decline in conductivity caused by microbial growth within the vessels (Sperry et al. 1988) and was considered as a suitable perfusion fluid in measuring hydraulic conductivity (Blake and Li 2003; Zhai et al. 2002). The branch segments were cut underwater with a fresh razor blade and then flushed at a pressure of 0.1 MPa for 10 to 20 min to remove air embolisms. The hydraulic conductivity per unit pressure gradient (K_h) equals the ratio between water flux (F , kg s⁻¹) through an excised stem segment and the pressure gradient (dP/dx , MPa m⁻¹) causing the flow, $K_h = F/(dP/dx)$. Sapwood specific conductivity (K_s , kg m⁻¹ s⁻¹ MPa⁻¹) was obtained by dividing K_h by the sapwood cross-section area. Leaf specific conductivity (K_L , kg m⁻¹ s⁻¹ MPa⁻¹) was calculated as the ratio of K_h to the leaf area, which is a measure of the hydraulic sufficiency of the stem to supply water to leaves distal to the stem (Cruziat et al. 2002). Huber value (HV) is defined as sapwood cross-section area divided by the leaf area distal to the stem.

Stem vulnerability curves were determined by measuring percentage loss of hydraulic conductivity (PLC) due to embolism over a range of xylem water potential (Ψ_x) reached during dehydration by the bench drying method (Tyree and Sperry 1989). For these measurements, at predawn in the wet season, a number of branches were cut from five individuals of each species. The branches were immediately wrapped in plastic bags to prevent further desiccation, brought to the laboratory, and were allowed to dry on the bench over different periods until the desired water potentials were approximately reached. Then, the branches together with some wet tissue papers were wrapped in plastic bags to equilibrate for 1–2 h. The water potential was measured on two to

three leaves or small twigs with a pressure chamber (SKPM 1400, Skye Instruments Ltd, Powys, UK) and one stem segment was cut under water and connected to tubing apparatus. After the initial hydraulic conductivity (K_0) was measured, the segment was flushed with the solution with 0.1 MPa pressure for 10 to 60 min to remove embolisms, and then maximum hydraulic conductivity (K_{max}) was measured. PLC was calculated as $100 \times (K_{max} - K_0)/K_{max}$. The vulnerability curve was generated as the function of PLC on xylem water potential and was fitted by the equation described by Pammenter and Vander Willigen (1998). Xylem water potential at 50% loss of hydraulic conductivity (P50) was used to estimate the xylem vulnerability to cavitation.

Xylem anatomy and sapwood density

The vessel diameters (D_v) and sapwood density (ρ_{sapwood}) were measured from branches used for hydraulic conductivity measurements (Kocacinar and Sage 2004). Transverse sections of xylem were made using a sliding microtome, and vessel lumen diameters were measured using a light microscope equipped with an ocular micrometer. After removing the bark and pith, the fresh sapwood was immersed in tap water overnight to saturate the samples. The volume of sapwood was then determined by water displacement method, and its dry mass was weighted after being oven-dried at 80°C for 72 h. The sapwood density was calculated as ratio of dry mass to fresh volume.

Leaf water potential

Predawn leaf water potential (Ψ_{pd}) and midday leaf water potential (Ψ_{md}) in the wet (August) and dry seasons (November) were measured with the pressure chamber. For these measurements, one leaf-bearing twig per stem was covered with a plastic bag for 1 h prior to excision to ensure equilibration between leaf water potential and xylem water potential of the shoots. Leaf samples were taken between 04:00–06:00 h and 12:00–14:00 h (solar time). For each of the six species, five sun leaves from five different individuals were cut with a sharp razor blade and sealed immediately in small plastic bags with moist tissue papers in them and kept briefly in a cooler until balancing pressures were determined in the laboratory.

Pressure–volume curve

Pressure–volume (P–V) curves for leaves or terminal shoots provide a promising tool for estimating desiccation tolerance of plants (Kyriakopoulos and Richter 1981; Lenz et al. 2006). The relationship between leaf water potential (Ψ_L) and relative water content (RWC) was quantified using bench drying technique (Lenz et al. 2006; Brodribb and Holbrook 2003) in mid-wet season (August) and early dry season (November). Terminal branches were harvested from five different individuals for each species, re-cut the broken ends underwater, and rehydrated until leaf water potential being greater than -0.05 MPa, after which leaves were detached for P–V curve determination. Leaf weight and water potential were measured periodically during slow desiccation of the sample leaves in the laboratory. The leaf desiccation continued until the leaf water potential stopped falling or began to rise due to cell damage. Osmotic potential at full turgor (π^{100}) and turgor loss point (π^0) were calculated from the analysis of the regression between $1/\Psi_L$ and RWC. The leaf weight at full turgor and dry mass were also measured to calculate the ratio of leaf dry weight to saturated fresh weight (DW/SW).

Net CO₂ assimilation rate and leaf nitrogen concentration

In the wet season, maximum net CO₂ assimilation (A_{\max}) were measured from fully-expanded, healthy sun leaves on consecutive sunny days (08:00–11:00 solar time) in the field with a photosynthesis system (Li-6400, LiCor, Lincoln, Nebraska, USA) from three to five individuals each species. The photosynthetic photon flux density (PPFD) of 1,000 to 1,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was used for the measurements, which was photosynthetically saturated for all species. Leaf nitrogen concentration was determined according to the Kjeldahl method by the Biogeochemical Laboratory of the Xishuangbanna Tropical Botanical Garden.

Statistical analysis

We conducted *t*-tests to compare the differences for each variable between lianas and trees as two groups, and to compare mean values of Ψ_{pd} , Ψ_{md} , DW/SW, π^{100} , and π^0 for each species between the wet and dry

season. Two-way ANOVA was used to test the effect of growth form and season and their interaction on leaf water potential and parameters from the P–V curves. The relationships between leaf traits were analyzed by linear regression analysis.

Results

Taken as a group, the three liana species had relatively wider D_v and lower ρ_{sapwood} compared to the three tree species (Table 1). The mean K_S value of the three liana species was twice as high as that of three tree species. Because of their substantially lower HV, the liana species showed similar K_L compared to the tree species. Compared with the trees, the three liana species showed higher N concentrations and A_{\max} . On the other hand, the three liana species had significantly higher P50 values compared to the three tree species (Fig. 1), indicating more vulnerability of the lianas' xylem to cavitation. PLC in the three liana species increased more rapidly with decreasing water potential than the tree species, indicating narrower safety margin in the lianas. Combining the data together from the six species studied, P50 was correlated positively with vessel diameter and negatively with sapwood density, while K_S were correlated positively with vessel diameter and P50 and negatively with sapwood density (Fig. 2a–e). Leaf N concentration and A_{\max} were positively correlated with K_S across species (Fig. 3).

In the dry season, Ψ_{pd} and Ψ_{md} decreased significantly for all species except Ψ_{pd} in the liana *Millettia pachycarpa* (Table 2), while the values of π^{100} and π^0 were significantly reduced and DW/SW values were significantly increased for the three tree species. The π^{100} values were also reduced for two of the three liana species. However, there was no significant difference in π^0 between the two seasons for all of the three liana species (Table 2). Taken as two groups, the lianas and trees did not differ significantly in all variables except for π^0 in the wet season. In the dry season, the lianas showed higher Ψ_{pd} , π^{100} and π^0 and lower DW/SW, but the two groups did not differ significantly in Ψ_{md} (Table 2). Two-way ANOVA revealed the significant effects of growth form on Ψ_{pd} , DW/SW and π^{100} , and season on Ψ_{pd} , Ψ_{md} , π^{100} and π^0 , as well as the interaction of growth form and season on all of these variables except for Ψ_{md} (Table 3).

Table 1 Sapwood specific hydraulic conductivity (K_S), leaf specific hydraulic conductivity (K_L), Huber value (the ratio of sapwood cross-section area to the leaf area distal to the stem, HV), vessel diameter (D_v), sapwood density (ρ_{sapwood}), maximum net CO₂ assimilation rate (A_{max}), and nitrogen concentrations (N) of the three liana and three tree species measured in the wet season

Species	K_S ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$)	$K_L \times 10^{-4}$ ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$)	HV $\times 10^{-4}$	D_v (μm)	ρ_{sapwood} (g cm^{-3})	A_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	N (g kg^{-1})
Lianas							
<i>Combretum latifolium</i>	3.14 ± 0.20	4.83 ± 0.63	1.54 ± 0.17	212 ± 5	0.46 ± 0.01	10.85 ± 0.49	19.93 ± 0.18
<i>Millettia pachycarpa</i>	3.13 ± 0.52	3.77 ± 1.18	1.10 ± 0.21	165 ± 6	0.49 ± 0.01	12.05 ± 0.94	36.96 ± 0.22
<i>Quisqualis indica</i>	3.07 ± 0.24	4.44 ± 0.34	0.87 ± 0.24	173 ± 13	0.50 ± 0.02	10.50 ± 0.34	35.14 ± 0.05
Trees							
<i>Bauhinia variegata</i>	2.07 ± 0.11	6.33 ± 0.39	3.06 ± 0.11	126 ± 5	0.51 ± 0.01	7.84 ± 0.63	20.88 ± 0.04
<i>Syzygium szamaoense</i>	1.64 ± 0.20	5.33 ± 0.52	3.34 ± 0.15	97 ± 2 d	0.52 ± 0.01	10.36 ± 1.93	12.22 ± 0.22
<i>Baccaurea ramiflora</i>	0.74 ± 0.03	3.70 ± 0.38	5.02 ± 0.50	79 ± 1 d	0.56 ± 0.02	4.97 ± 0.99	14.93 ± 0.05
Liana means	3.11*	4.34	1.17*	183*	0.48*	11.13*	30.68*
Tree means	1.48	5.12	3.81	101	0.53	7.72	16.01

Data are means ± SE for each species, $n = 5$. * Indicates significant differences between lianas and trees as two groups ($P < 0.05$, t -test)

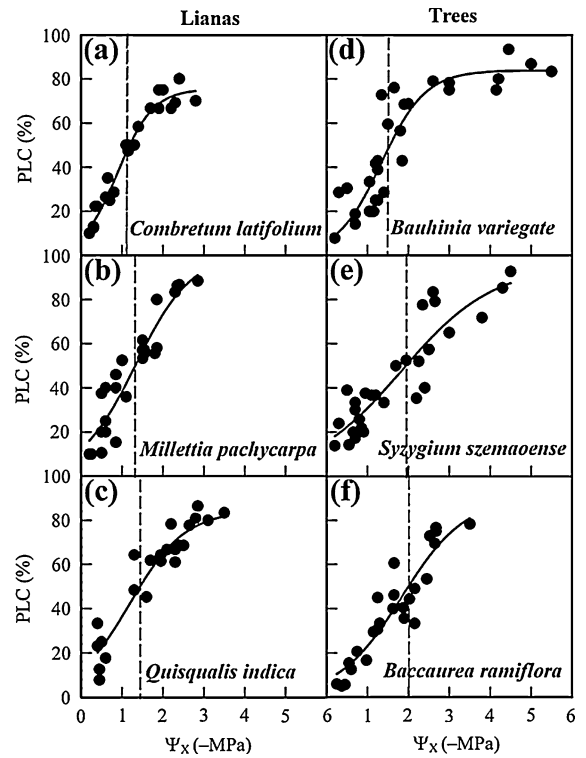


Fig. 1 The curves of vulnerability to cavitation of terminal branches for each species measured in the wet season. Ψ_x is xylem water potential. PLC is percent loss of hydraulic conductivity. $P < 0.001$ for all the regression lines. The vertical dashed lines indicate the xylem water potential at 50% loss of hydraulic conductivity (P50)

Discussion

Compared to the three tree species, the three liana species showed substantially higher K_S , which was mainly contributed by their larger vessels (Fig. 2), since theoretical K_h is proportional to vessel diameter to the fourth power according to Hagen-Poiseuille equation (Tyree and Ewers 1991; Zimmermann 1983). By having wider vessels, lianas can transport water more efficiently and may compensate hydraulically for their narrow stems (Chiu and Ewers 1992; Ewers and Fisher 1991; Field and Balun 2008). On the other hand, the lianas had much lower HV (Table 1), indicating that the lianas could support more leaves with the same cross-section sapwood area. Due to their lower HV values, K_L of the liana species was similar to that of the trees, indicating that individual leaves could get similar water supply across the liana and tree species, consistent with the

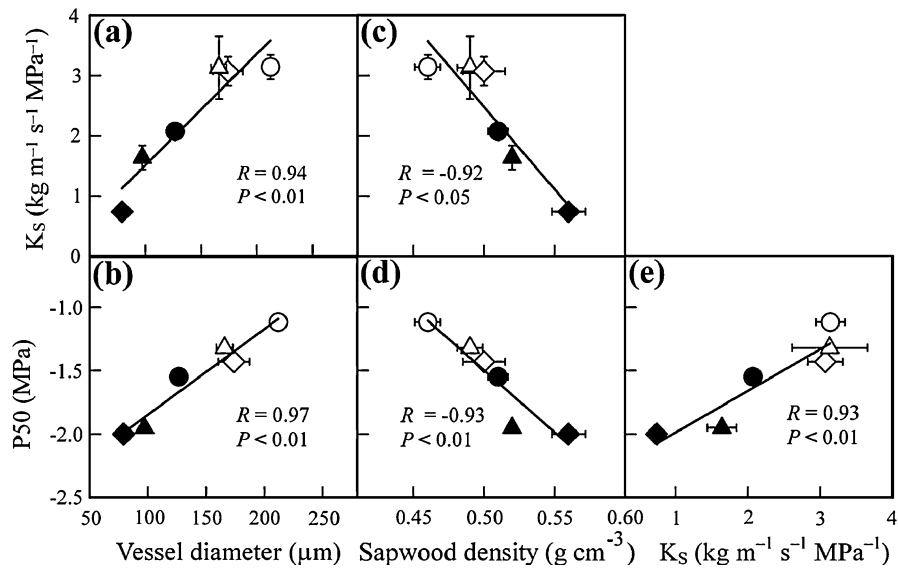


Fig. 2 Hydraulic conductivity and xylem vulnerability to cavitation as a function of xylem traits (a–d), and correlation between hydraulic conductivity and xylem vulnerability (e) across the three liana species (open) and three tree species (filled). These characteristics were measured in the wet season. K_S = sapwood specific hydraulic conductivity; P50 = xylem

water potential at 50% loss of hydraulic conductivity. Data are means \pm SE, $n = 5$. The different symbols represent different species: *Combretum latifolium* (open circles), *Millettia pachycarpa* (open triangles), *Quisqualis indica* (open diamonds), *Bauhinia variegata* (filled circles), *Syzygium szamaense* (filled triangles), and *Baccaurea ramiflora* (filled diamonds)

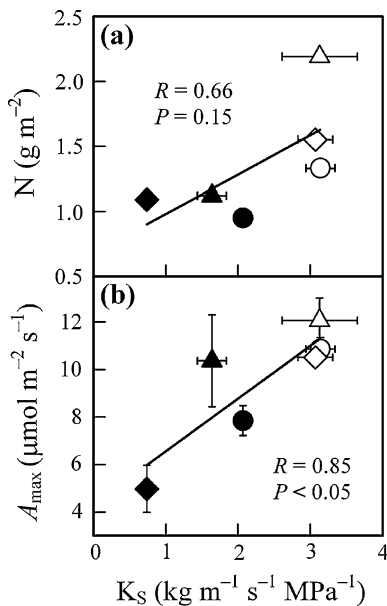


Fig. 3 Leaf N concentration (N) and maximum net CO_2 assimilation rate (A_{max}) as a function of sapwood specific hydraulic conductivity (K_S). Leaf N concentration and A_{max} were measured in the wet season. Data are means \pm SE, $n = 3$ –5. See Fig. 2 for indications of the symbols for the species

finding of Ewers et al. (1989). On the other hand, the three liana species showed higher N concentration and A_{max} than the three tree species (Fig. 3), which were consistent with the findings of other studies (Cai 2007; Salzer et al. 2005). By having relatively cheap (lower wood density) but hydraulically efficient xylem and more efficient leaves, the lianas should have an advantage over the trees on carbon assimilation and growth in favorable habitats.

The hydraulic architecture in woody plants is consistent with the maximization of transport efficiency operating within mechanical constraints (McCulloh and Sperry 2005). Lianas could escape this trade-off because they are structural parasites, ascending to the canopy with mechanical support of the host plants. They do not need to develop as much fibre as in trees for mechanical support. Therefore, lianas have higher hydraulic conductivity per sapwood area and support more leaves with a narrower stem by packing larger vessels in a smaller xylem area (Table 1). Furthermore, lianas allocate more biomass to photosynthesis tissues by reducing biomass investment to the supporting structures. Both higher proportion of photosynthetic biomass and

Table 2 Average leaf water potentials and parameters from the P–V curves in the three liana and three tree species in the wet and dry season

Species	Seasons	Ψ_{pd} (MPa)	Ψ_{md} (MPa)	DW/SW ($g\ g^{-1}$)	π^{100} (MPa)	π^0 (MPa)
Lianas						
<i>Combretum latifolium</i>	Wet	$-0.26 \pm 0.03^*$	$-0.51 \pm 0.05^*$	0.32 ± 0.02	$-0.72 \pm 0.10^*$	-1.16 ± 0.26
	Dry	-0.41 ± 0.02	-1.28 ± 0.05	0.31 ± 0.01	-1.16 ± 0.08	-1.42 ± 0.09
<i>Millettia pachycarpa</i>	Wet	-0.20 ± 0.01	$-0.63 \pm 0.69^*$	$0.40 \pm 0.01^*$	-1.12 ± 0.09	-1.55 ± 0.10
	Dry	-0.23 ± 0.02	-1.29 ± 0.03	0.34 ± 0.03	-1.34 ± 0.03	-1.49 ± 0.06
<i>Quisqualis indica</i>	Wet	$-0.26 \pm 0.01^*$	$-0.97 \pm 0.05^*$	$0.30 \pm 0.02^*$	$-0.92 \pm 0.12^*$	-1.37 ± 0.11
	Dry	-0.34 ± 0.02	-1.48 ± 0.05	0.26 ± 0.01	-1.32 ± 0.05	-1.43 ± 0.04
Trees						
<i>Bauhinia variegata</i>	Wet	$-0.26 \pm 0.01^*$	$-0.76 \pm 0.07^*$	$0.33 \pm 0.01^*$	$-1.03 \pm 0.01^*$	$-1.15 \pm 0.04^*$
	Dry	-0.79 ± 0.08	-1.71 ± 0.03	0.37 ± 0.01	-1.52 ± 0.07	-1.70 ± 0.11
<i>Syzygium szemaoense</i>	Wet	$-0.27 \pm 0.03^*$	$-0.73 \pm 0.02^*$	$0.36 \pm 0.01^*$	$-1.00 \pm 0.07^*$	$-1.28 \pm 0.07^*$
	Dry	-0.34 ± 0.05	-1.35 ± 0.09	0.39 ± 0.01	-1.56 ± 0.03	-1.77 ± 0.03
<i>Baccaurea ramiflora</i>	Wet	$-0.16 \pm 0.01^*$	$-0.54 \pm 0.31^*$	$0.31 \pm 0.03^*$	$-0.74 \pm 0.02^*$	$-1.00 \pm 0.07^*$
	Dry	-0.41 ± 0.04	-1.20 ± 0.02	0.35 ± 0.01	-1.40 ± 0.13	-1.56 ± 0.14
Liana means	Wet	-0.24	-0.74	0.34	-0.92	-1.36*
Tree means		-0.22	-0.68	0.33	-0.93	-1.14
Liana means	Dry	-0.32*	-1.35	0.31*	-1.27*	-1.45*
Tree means		-0.63	-1.44	0.37	-1.50	-1.68

Ψ_{pd} predawn leaf water potential, Ψ_{md} midday leaf water potential, DW/SW the ratio of leaf dry weight to saturated fresh weight, π^{100} osmotic potential at full turgor, π^0 water potential at turgor loss point

Data are means \pm SE, $n = 5$. * indicate significant seasonal differences within the same species and significant differences between the lianas and trees as two groups in the same season ($P < 0.05$, t -test)

Table 3 F values (P values) for the two-way ANOVA on leaf water potential and parameters from the P–V curves

Variable	Growth form	Season	Growth form \times Season
Ψ_{pd}	6.39*	17.69***	7.98**
Ψ_{md}	0.16 ns	151.59***	1.73 ns
DW/SW	5.89*	0.01 ns	9.99**
π^{100}	4.97*	77.60***	4.38*
π^0	0.48 ns	39.84***	22.50***

See Table 2 for indications of the abbreviations for the variables. ns no significant at $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

higher photosynthetic capacity of the liana leaves must result in fast growth, enabling them to occupy canopy quickly.

The curves of vulnerability to cavitation revealed that the lianas were more susceptible to dehydration-induced cavitation compared to the trees (Fig. 1). This should be related to their larger vessels and lower sapwood density (Fig. 2b, d), which are

vulnerable to cavitation under large negative pressure (Hacke et al. 2001). There is usually a trade-off between hydraulic efficiency and vulnerability to cavitation (Hacke et al. 2006). The lianas maximized their hydraulic efficiency, thus enhancing their water transportation and growth, with the cost of hydraulic safety (Fig. 2e). However, if such a trade-off has an evolutionary basis, low cavitation resistance could be maintained in the habitats where high conductivity is adaptive (Maherali et al. 2004) and the sacrificial strategy of lianas might be adaptive for a habitat where water stress is generally modest (Hacke et al. 2006). Although there is a distinct dry season in a seasonal tropical rain forest, several physiological and morphological characteristics of lianas discussed below could reduce the risk of the damage from the xylem cavitation during the dry season. (1) Lianas usually have well-developed and deep root system (Fichtner and Schulze 1990; Restom and Nepstad 2004), thus they could tap soil water at depth (Andrade et al. 2005), indeed as indicated by the

high Ψ_{pd} of lianas in the dry season by this study. As Ψ_{pd} indicates soil water potential at the root zone, higher Ψ_{pd} in the lianas suggested they had deeper roots; (2) Lianas might have strong stomatal regulation (Tay et al. 2007; Forseth and Teramura 1987). A decrease of hydraulic conductivity might be a signal for stomatal closure (Brodrribb et al. 2003), which might result in maintaining stem and leaf water potential that insures the integrity of the water transport pathway upstream and avoids runaway embolism. (3) Lianas might have large stem water storage as indicated by their low sapwood density and larger difference between Ψ_{pd} and Ψ_{md} of the present study, which could significantly buffer the transpiration water loss of leaves (Goldstein et al. 1998; Meinzer et al. 2008). Having higher photosynthetic rate and maintaining higher water potential in the dry season should be particularly advantageous for the lianas because of the exposure of their leaves in upper canopy and enhancement of photosynthesis by the high irradiance in the dry season.

Osmotic regulation is an important mechanism for plants to cope with drought. The three trees showed osmotic regulation as indicated by a significant decrease in π^0 in the dry season, but there was no significant difference in π^0 between the two seasons for the three liana species (Table 2). In addition, the two brevi-deciduous liana species exchanged their leaves in the middle dry season, indicating that these liana species could get sufficient water supply even during the peak drought period. This was consistent with Putz and Windsor (1987) who found the concentration of flowering or leaf exchanging of most of lianas in a seasonal rainforest of Panama in the middle dry season.

In summary, the lianas had much lower HV, but larger vessels and higher K_S and A_{max} . During the seasonal drought, the lianas were able to maintain higher predawn leaf water potential, suggesting that they could absorb more reliable water source at deeper soil layers; the lianas invested less energy in osmotic regulation and therefore A_{max} of the lianas might be less affected. With higher proportion of leaf biomass and sustained higher A_{max} , the liana leaves should be able to fix more carbon during a year than the tree leaves.

Acknowledgments The authors are grateful to Xue-Wei Fu and Hong Ma for field assistance and Yun Fu of the

Biogeochemical Laboratory of our botanical garden for the chemical analysis, and to Ze-Xin Fan, Jiao-Lin Zhang, and Guang-You Hao for their useful suggestions and discussion. Acknowledgements are extended to the anonymous reviewers who made helpful suggestions and comments on the manuscript. This study was financially supported by a Grant (No. 2006CB403207) from a major “973” project funded by the Chinese Ministry of Science and Technology.

References

- Andrade JL, Meinzer FC, Goldstein G, Schnitzer SA (2005) Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest. *Trees (Berl)* 19:282–289. doi:10.1007/s00468-004-0388-x
- Blake TJ, Li J (2003) Hydraulic adjustment in jack pine and black spruce seedlings under controlled cycles of dehydration and rehydration. *Physiol Plant* 117:532–539. doi:10.1034/j.1399-3054.2003.00059.x
- Brodrribb TJ, Feild TS (2000) Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests. *Plant Cell Environ* 23:1381–1388. doi:10.1046/j.1365-3040.2000.00647.x
- Brodrribb TJ, Holbrook NM (2003) Stomatal closure during leaf dehydration, correlation with other leaf physiological traits. *Plant Physiol* 132:2166–2173. doi:10.1104/pp.103.023879
- Brodrribb TJ, Holbrook NM, Gutiérrez MV (2002) Hydraulic and photosynthetic co-ordination in seasonally dry tropical forest trees. *Plant Cell Environ* 25:1435–1444. doi:10.1046/j.1365-3040.2002.00919.x
- Brodrribb TJ, Holbrook NM, Edwards EJ, Gutiérrez MV (2003) Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. *Plant Cell Environ* 26:443–450. doi:10.1046/j.1365-3040.2003.00975.x
- Cai ZQ (2007) Lianas and trees in tropical forests in south China. PhD thesis, Wageningen University
- Cao K-F (2000) Water relations and gas exchange of tropical saplings during a prolonged drought in a Bornean heath forest, with reference to root architecture. *J Trop Ecol* 16:101–116. doi:10.1017/S0266467400001292
- Chiu S-T, Ewers FW (1992) Xylem structure and water transport in a twiner, a scrambler, and a shrub of *Lonicera* (Caprifoliaceae). *Trees (Berl)* 6:216–224. doi:10.1007/BF00224339
- Choat B, Sack L, Holbrook NM (2007) Diversity of hydraulic traits in nine *Cordia* species growing in tropical forest with contrasting precipitation. *New Phytol* 175:686–698. doi:10.1111/j.1469-8137.2007.02137.x
- Clayton-Greene KA (1983) The tissue water relationships of *Callitris columellaris*, *Eucalyptus melliodora* and *Eucalyptus microcarpa* investigated using the pressure-volume technique. *Oecologia* 57:368–373. doi:10.1007/BF00377182
- Cruziat P, Cochard H, Améglio T (2002) Hydraulic architecture of trees: main concepts and results. *Ann Sci* 59:723–752. doi:10.1051/forest:2002060

- Ewers FW, Fisher JB (1991) Why vines have narrow stems: histological trends in *Bauhinia* (Fabaceae). *Oecologia* 88:233–237. doi:[10.1007/BF00320816](https://doi.org/10.1007/BF00320816)
- Ewers FW, Fisher JB, Chiu S-T (1989) Water transport in the liana *Bauhinia fassoglensis* (Fabaceae). *Plant Physiol* 91:1625–1631. doi:[10.1104/pp.91.4.1625](https://doi.org/10.1104/pp.91.4.1625)
- Ewers FW, Fisher JB, Chiu S-T (1990) A survey of vessel dimensions in stems of tropical lianas and other growth forms. *Oecologia* 84:544–552
- Fichtner K, Schulze ED (1990) Xylem water flow in tropical vines as measured by a steady state heating method. *Oecologia* 82:355–361. doi:[10.1007/BF00317483](https://doi.org/10.1007/BF00317483)
- Field TS, Balun L (2008) Xylem hydraulic and photosynthetic function of *Gnetum* (Gnetales) species from Papua New Guinea. *New Phytol* 177:665–675
- Forseth IN, Teramura AH (1987) Field photosynthesis, microclimate and water relations of an exotic temperate liana, *Pueraria lobata*, kudzu. *Oecologia* 71:262–267. doi:[10.1007/BF00377293](https://doi.org/10.1007/BF00377293)
- Goldstein G, Andrade JL, Meinzer FC, Holbrook NM, Cavelier J, Jackson P, Celis A (1998) Stem water storage and diurnal patterns of water use in tropical forest canopy trees. *Plant Cell Environ* 21:397–406. doi:[10.1046/j.1365-3040.1998.00273.x](https://doi.org/10.1046/j.1365-3040.1998.00273.x)
- Granados J, Körner C (2002) In deep shade, elevated CO₂ increases the vigor of tropical climbing plants. *Glob Change Biol* 8:1109–1117. doi:[10.1046/j.1365-2486.2002.00533.x](https://doi.org/10.1046/j.1365-2486.2002.00533.x)
- Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126:457–461. doi:[10.1007/s004420100628](https://doi.org/10.1007/s004420100628)
- Hacke UG, Sperry JS, Wheeler JK, Castro L (2006) Scaling of angiosperm xylem structure with safety and efficiency. *Tree Physiol* 26:689–701
- Kocacinar F, Sage RF (2004) Photosynthetic pathway alters hydraulic structure and function in woody plants. *Oecologia* 139:214–223. doi:[10.1007/s00442-004-1517-3](https://doi.org/10.1007/s00442-004-1517-3)
- Kyriakopoulos E, Richter H (1981) Pressure-volume curves and drought injury. *Plant Physiol* 52:124–128. doi:[10.1111/j.1399-3054.1981.tb06044.x](https://doi.org/10.1111/j.1399-3054.1981.tb06044.x)
- Lenz TI, Wright IJ, Westoby M (2006) Interrelations among pressure-volume curve traits across species and water availability gradients. *Physiol Plant* 127:423–433. doi:[10.1111/j.1399-3054.2006.00680.x](https://doi.org/10.1111/j.1399-3054.2006.00680.x)
- Lopez OR, Kursar TA, Cochard H, Tyree MT (2005) Interspecific variation in xylem vulnerability to cavitation among tropical tree and shrub species. *Tree Physiol* 25:1553–1562
- Maherali H, Pockman WT, Jackson RB (2004) Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology* 85:2184–2199. doi:[10.1890/02-0538](https://doi.org/10.1890/02-0538)
- McCulloh KA, Sperry JS (2005) Patterns in hydraulic architecture and their implications for transport efficiency. *Tree Physiol* 25:257–267
- Meinzer FC, Woodruff DR, Domec J-C, Goldstein G, Campanello PI, Gatti MG, Villalobos-Vega R (2008) Coordination of leaf and stem water transport properties in tropical forest trees. *Oecologia* 156:31–41. doi:[10.1007/s00442-008-0974-5](https://doi.org/10.1007/s00442-008-0974-5)
- Pammenter NW, Vander Willigen C (1998) A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree Physiol* 18:589–593
- Pérez-Saliciup DR, Barker MG (2000) Effect of liana cutting on water potential and growth of adult *Senna multijuga* (Caesalpinioideae) trees in a Bolivian tropical forest. *Oecologia* 124:469–475. doi:[10.1007/PL00008872](https://doi.org/10.1007/PL00008872)
- Putz FE (1984a) How trees avoid and shed lianas. *Biotropica* 16:19–23. doi:[10.2307/2387889](https://doi.org/10.2307/2387889)
- Putz FE (1984b) The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65:1713–1724. doi:[10.2307/1937767](https://doi.org/10.2307/1937767)
- Putz FE, Windsor DM (1987) Liana phenology on Barro Colorado Island, Panama. *Biotropica* 19:334–341. doi:[10.2307/2388631](https://doi.org/10.2307/2388631)
- Reddy MS, Parthasarathy N (2003) Liana diversity and distribution in four tropical dry evergreen forests on the Coromandel coast of south India. *Biodivers Conserv* 12:1609–1627. doi:[10.1023/A:1023620901624](https://doi.org/10.1023/A:1023620901624)
- Restom TG, Nepstad DC (2004) Seedling growth dynamics of a deeply rooting liana in a secondary forest in eastern Amazonia. *For Ecol Manag* 190:109–118
- Salzer J, Matezki S, Kazda M (2005) Nutritional differences and leaf acclimation of climbing plants and the associated vegetation in different types of an Andean montane rainforest. *Oecologia* 147:417–425. doi:[10.1007/s00442-005-0294-y](https://doi.org/10.1007/s00442-005-0294-y)
- Schnitzer SA (2005) A mechanistic explanation for global patterns of liana abundance and distribution. *Am Nat* 166:262–276. doi:[10.1086/431250](https://doi.org/10.1086/431250)
- Schnitzer SA, Bongers F (2002) The ecology of lianas and their role in forests. *Trends Ecol Evol* 17:223–230. doi:[10.1016/S0169-5347\(02\)02491-6](https://doi.org/10.1016/S0169-5347(02)02491-6)
- Schnitzer SA, Dalling JW, Carson WP (2000) The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *J Ecol* 88:655–666. doi:[10.1046/j.1365-2745.2000.00489.x](https://doi.org/10.1046/j.1365-2745.2000.00489.x)
- Sperry JS, Donnelly JR, Tyree MT (1988) A method for measuring hydraulic conductivity and embolism in xylem. *Plant Cell Environ* 11:35–40. doi:[10.1111/j.1365-3040.1988.tb01774.x](https://doi.org/10.1111/j.1365-3040.1988.tb01774.x)
- Swaine MD, Grace J (2007) Lianas may be favoured by low rainfall: evidence from Ghana. *Plant Ecol* 192:271–276. doi:[10.1007/s11258-007-9319-4](https://doi.org/10.1007/s11258-007-9319-4)
- Tang JW, Zhang JH, Song QS, Feng ZL (1997) Analysis on the characteristics of *Millettia leptobotrya* community in Xishuangbanna. *Guihaia* 17:338–344. (in Chinese with English abstract)
- Tay AC, Abdullah AM, Awang M, Furukawa A (2007) Midday depression of photosynthesis in *Enkleia malaccensis*, a woody climber in a tropical rainforest. *Photosynthetica* 45:189–193. doi:[10.1007/s11099-007-0031-3](https://doi.org/10.1007/s11099-007-0031-3)
- Trifilò P, Raimondo F, Nardini A, Lo Gullo MA, Salleo S (2004) Drought resistance of *Ailanthus altissima*: root hydraulic and water relations. *Tree Physiol* 24:107–114
- Tyree MT, Ewers FW (1991) The hydraulic architecture of trees and other woody plants. *New Phytol* 119:345–360. doi:[10.1111/j.1469-8137.1991.tb00035.x](https://doi.org/10.1111/j.1469-8137.1991.tb00035.x)
- Tyree MT, Sperry JS (1989) Vulnerability of xylem to cavitation and embolism. *Annu Rev Plant Physiol Plant Mol*

- Biol 40:19–38. doi:[10.1146/annurev.pp.40.060189.000315](https://doi.org/10.1146/annurev.pp.40.060189.000315)
- Wright SJ, Calderon O, Hernandez A, Paton S (2004) Are lianas increasing in importance in tropical forests? A 17-year record from Panama. *Ecology* 85:484–489. doi:[10.1890/02-0757](https://doi.org/10.1890/02-0757)
- Zhai HB, Li JY, Jiang JP (2002) Comparative study on hydraulic architecture characteristic of *pinus tabulaeformis* and *platycladus orientalis* seedlings. *Acta Ecol Sin* 22:1890–1895. (in Chinese with English abstract)
- Zhu H, Xu ZF, Wang H, Li BG (2004) Tropical rain forest fragmentation and its ecological and species diversity changes in southern Yunan. *Biodivers Conserv* 13:1355–1372. doi:[10.1023/B:BIOC.0000019397.98407.c3](https://doi.org/10.1023/B:BIOC.0000019397.98407.c3)
- Zimmermann MH (1983) *Xylem structure and the ascent of sap*. Springer, Berlin, Heidelberg, New York