

Physiological regulation and efficient xylem water transport regulate diurnal water and carbon balances of tropical lianas

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Summary

1. Tropical lianas deploy most of their leaves towards the top of the forest canopy, whereas trees exhibit a more stratified crown. Forest canopies are often exposed to hot and windy conditions, and how lianas cope with the extremely high transpirational demands under these environments remains unknown.

2. We investigated stem hydraulic properties, leaf drought tolerance, diurnal changes in leaf and stem water potentials (Ψ_{leaf} and Ψ_{stem}), stomatal conductance (g_s), photosynthetic rate, sap flow and stem native percentage loss of conductivity (PLC) for four liana species in a tropical forest in southwest China. Five co-occurring tree species were also selected for comparison.

3. Lianas reached maximal transpiration at a relatively lower vapour pressure deficit (< 1 kPa) than did co-occurring trees, suggesting vigorous photosynthesis during the morning. However, liana g_s declined markedly over the day, with low g_s at midday and afternoon. Lianas generally had higher stem sapwood-specific conductivity and maximum sap flux density but were less tolerant to drought-induced cavitation than were evergreen trees. Both lianas and trees lost leaf turgor in the top canopy at midday, but lianas lost leaf turgor earlier (~ 2 h) than trees.

4. Seven of eight species exhibited midday increases in PLC when xylem tensions were released to -0.3 to -0.5 MPa for PLC measurements. On average, lianas experienced high PLC (35.9%), along with a greater degree of disequilibrium between leaf and stem water potentials than trees ($\Delta\Psi_{\text{stem-leaf}}$: 1.37 MPa vs. 0.75 MPa) during the day. Earlier stomatal closure and efficient water transport may help lianas maintain higher Ψ_{stem} than trees despite having similar Ψ_{leaf} .

5. Our results provide evidence that physiological regulation and efficient water transport mediate daily water relations in tropical lianas and may explain how lianas operate efficiently in tropical seasonal forests. Further studies involving a broader range of species are needed to confirm our findings.

Key-words: drought tolerance, hydraulic properties, sap flow, stomatal regulation, water relations

Introduction

Canopy plants in seasonal tropical forests experience water deficits both during the dry season, when soil water is depleted, and during the wet season, when plants are

exposed to high transpirational demands at midday. Transpiration-induced water deficits (low water potentials) can result in a strong downregulation of stomatal conductance and thus a reduction in leaf carbon gain (Simonin *et al.* 2015). Midday decline in photosynthesis, stomatal conductance and leaf-specific conductance have been observed in many plant species regardless of soil water status

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(Brodribb & Holbrook 2003, 2004; Bunce 2006; Chapotin, Razanameharizaka & Holbrook 2006; Tucci *et al.* 2010; Zufferey *et al.* 2011; Cao *et al.* 2012; Yang *et al.* 2012; Zhang *et al.* 2013; Hacke 2014). Midday reduction in leaf photosynthetic performance in response to daily water deficits reflects a trade-off between carbon fixation and hydraulic safety.

Plants depend on several different physiological adaptations that facilitate rapid response to changes in soil water availability and vapour pressure deficits (VPDs). For instance, leaf stomatal regulation plays a critical role in the balance between water loss and carbon fixation (McDowell *et al.* 2008); by regulating the stomatal aperture, plants can limit water loss and thus maintain xylem tension within a safe range, reducing the risks of xylem dysfunction (Brodribb & Holbrook 2003; Brodribb *et al.* 2003; Bucci *et al.* 2003; Johnson *et al.* 2011). Stomatal regulation can be governed by leaf and stem water potentials, VPD and ABA content (Comstock & Mencuccini 1998; Salleo *et al.* 2000; Brodribb *et al.* 2003; Bunce 2006; Chapotin, Razanameharizaka & Holbrook 2006; Tucci *et al.* 2010; Scoffoni *et al.* 2012; Zhang *et al.* 2013). Rapid stomatal response to the increases in transpirational demands reduces the risk of excessive dehydration and irreversible hydraulic dysfunction (i.e. embolism) in the vascular system; stomatal regulation thus represents an especially important adaptation for canopy plants, which frequently experience high transpirational demands. Stomatal regulation may be particularly important for lianas compared with their host trees, because lianas have a higher proportion of exposed leaves at the top of the canopy, where transpirational demand is higher (Putz 1983), and their internal stem water storage is comparatively small (Chen *et al.* 2016a).

Lianas are an important component of tropical and subtropical forests, contributing up to 35% of woody plant diversity and 40% of stem density (Gerwing & Farias 2000; Chave, Riera & Dubois 2001; Schnitzer & Bongers 2002, 2011); they are considered to be structural parasites because they commonly use the stems of other plants (mostly trees) to ascend to the forest canopy (Schnitzer & Bongers 2002). As a consequence, lianas may have a higher proportion of photosynthetic biomass per whole-plant biomass (Wyka *et al.* 2013). Trees tend to have larger internal stem water storage than lianas, enabling trees to use water stored in the top portion of their trunk to replace water lost through transpiration, whereas lianas rely primarily on soil water (Chen *et al.* 2016a). Exposure to the stressful environment of the upper forest canopy does not prevent lianas from colonizing the canopy; rather, lianas typically form a carpet-like leafy layer in the uppermost canopy in many tropical forests. Lianas generally have wider and longer vessels than trees and are reported to be hydraulically efficient but vulnerable to drought-induced cavitation (Isnard & Silk 2009; Zhu & Cao 2009; Johnson *et al.* 2013; Chen *et al.* 2014). The mechanism by which lianas balance hydraulic efficiency with safety and

the role of stomatal regulation are both poorly understood, but may be key to explaining how lianas aggressively colonize both treefall gaps and seasonally dry forests (Schnitzer 2005; Ledo & Schnitzer 2014).

Here, we examined the stem hydraulic properties, leaf drought tolerance, diurnal variations in photosynthesis and leaf stomatal conductance, leaf and stem water potentials and sap flow of four tropical lianas in south-western China. In addition, we measured the same physiological properties for five co-occurring trees (two deciduous and three evergreen trees) for the purposes of comparison with lianas. Our goal was to determine how tropical lianas cope with the extremely high transpirational demands prevalent in forest canopies. Specifically, we tested whether physiological regulation aids lianas in mediating diurnal water and carbon balances.

Materials and methods

FIELD SITE

The study was conducted at Xishuangbanna Tropical Botanical Garden (XTBG, 21°54'N, 101°46'E, 580 m a.s.l.), Chinese Academy of Sciences in south of Yunnan Province, China. A 30 × 30 m plot located in a natural flood plain forest inside XTBG was selected for the study. This region has a distinct dry season from November to April. Mean annual precipitation is approximately 1560 mm, nearly 80% of which occurs during the wet season from May to October. Mean annual temperature is 21.7 °C with a monthly mean temperature of 15.9 °C in the coldest month (December) and 25.7 °C in the hottest month (June). We used meteorological data recorded at 30-min intervals (photosynthetic photon flux density (PPFD), air temperature, relative humidity) from a weather station (Xishuangbanna Tropical Rainforest Ecosystem Station of the Chinese Academy of Sciences) located 1 km away from our study site.

DIURNAL CHANGE IN PHOTOSYNTHESIS, STOMATAL CONDUCTANCE AND LEAF AND STEM WATER POTENTIALS

We selected nine species (three individuals per species) in total, consisting of four liana species (*Celastrus paniculatus*, *Mucuna interrupta*, *Marsdenia sinensis* and *Ventilago calyculata*) and five tree species (*Celtis tetrandra*, *Ficus concinna*, *Harpullia cupanioides*, *Michelia hypolampra* and *Strobilus asper*) for quantification of the gas exchange parameters: photosynthetic rate (P_n) and stomatal conductance (g_s). Measurements were conducted at 2-h intervals between 08:00 and 18:00 over five clear days between 8 and 21 October 2012. Access to the forest canopy was attained through the use of a truck crane. Six sun-exposed leaves from three individuals per species were marked prior to the gas exchange measurements to ensure that all diurnal course measurements were made on the same leaves. Gas exchange was measured using an open-flow gas exchange system (LI-6400; LI-COR, Lincoln, NE, USA) with a 2 × 3 cm leaf chamber. Temperature, CO₂ concentrations, light and humidity in the leaf chamber were the same ambient environmental conditions. The rate of air flow rate through the leaf chamber was set to 500 μmol s⁻¹. Measurements were logged once the rate of gas exchange stabilized. Finally, leaf stomatal conductance was plotted against the chamber VPD.

For each species, six fully expanded new leaves from neighbouring sun-exposed terminal branches were selected for measurement

of leaf water potential (Ψ_{leaf}) concurrently with the gas exchange measurements. Leaf samples were cut with a razorblade and sealed in plastic bags containing moistened paper towels, then kept in a cold box for 20 min to attain a balancing pressure. Water potential of the samples was obtained using a pressure chamber (PMS1000; PMS Instrument Company, Corvallis, OR, USA). Stem water potential (Ψ_{stem}) was estimated by measuring the water potential of a non-transpiring leaf. Six sun-exposed leaves were sealed in plastic bags and covered with aluminium foil the previous evening for the Ψ_{stem} measurements. All measurements were completed *in situ* within 1 h following leaf excision.

MAXIMUM VESSEL LENGTH AND STEM HYDRAULIC MEASUREMENTS

The maximum vessel length (MVL) was measured using the air-injection method (Ewers & Fisher 1989) before performing stem hydraulic property measurements. Ten branches from four individuals per species were cut for use in the MVL quantification. The apex end (≈ 5 mm in diameter) of each stem was cut and connected to a tube connected to 100-kPa compressed nitrogen gas, with the distal end immersed in water. The stem was shortened at 1 cm intervals successively until the first bubble emerged, with MVL defined as the amount to the remaining stem length plus 0.5 cm.

Maximum stem sapwood-specific conductivity ($K_{s\text{-max}}$, $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) was determined using a hydraulic conductivity measurement system, as described by Sperry, Donnelly & Tyree (1988), during July and October 2014. Briefly, a total of 10–12 segments (ca. 1.5 times the length of MVL) per species were cut before sunrise, placed in black plastic bags and then transported to the laboratory within 1 h. Stem segments were then trimmed to lengths ca. 10% longer than MVL underwater. Each stem segment was flushed with degassed ultrafiltered 10 mM KCl solution at pressures of 100 kPa for about 30 min to remove emboli. Flushed segments were subsequently connected to a pressure head (~ 5 kPa) containing the same filtered KCl solution as above. The distal end of each segment was connected with a pipette to obtain a flushed flow rate, and the maximum stem sapwood-specific conductivity was calculated as follows:

$$K_{s\text{-max}} = FL/(\Delta P A_{sw}), \quad \text{eqn 1}$$

where F is the flow rate (kg s^{-1}), L is the stem length (m), ΔP is the driving force (MPa) and A_{sw} (m^2) is the cross-sectional area of the active xylem.

We measured vulnerability curves (VCs) using the bench dehydration method (Sperry, Donnelly & Tyree 1988) for six of the bine species. An air-injection method (Cochard, Cruziat & Tyree 1992) was used to determine the VCs of two latex-containing tree species (*S. asper* and *F. concinna*). We did not measure the hydraulic properties (VCs and native percentage loss of conductivity) for the liana *M. interrupta* because the terminal branches of this species were too thin (commonly < 3 mm in diameter) to conduct measurement (Appendix S1, Supporting Information).

NATIVE STEM SAPWOOD-SPECIFIC CONDUCTIVITY AND DIURNAL PERCENTAGE LOSS OF CONDUCTIVITY

Several recent studies have shown that the diurnal percentage loss of conductivity (PLC) and recovery cycles previously reported in the literature could be artefacts of sample preparation or measurement methodologies (Cochard & Delzon 2013; Torres-Ruiz *et al.* 2014; Wang *et al.* 2014; Zhang & Holbrook 2014). Wheeler *et al.* (2013) reported that the high PLC values and subsequent repairing observed in red maple and white ash trees were actually simple due to sampling under tension and that there was no significant

difference in PLC between pre-dawn and midday if tension was relaxed prior to hydraulic measurements. Direct X-ray microtomography (Torres-Ruiz *et al.* 2015) also confirmed that high PLC values are artefacts of stems cut while under tension. In contrast, tension-cutting effects are not found in other studies (Trifilò *et al.* 2014; Venturas, MacKinnon & Jacobsen 2014; Scoffoni & Sack 2015). Trifilò *et al.* (2014) and Venturas, MacKinnon & Jacobsen (2014) suggest that relaxation procedures favour embolism repairs and thus lead to underestimations of PLC values.

We conducted tension-relaxation procedures (1–2 h) similar to those described by Wheeler *et al.* (2013) 1–2 h prior to all native PLC measurement because we believed that cavitation refilling could not occur in detached branches in such a relatively short time. We avoided long time relaxation (> 2 h) to prevent embolism refilling by capillary pressure (Torres-Ruiz *et al.* 2015). We measured the native PLC on sunny days during May and June 2014. Pre-dawn samples were collected between 05:30 and 06:30 before sunrise, whereas midday samples were collected between 13:00 and 15:00. To avoid cutting effects like those mentioned above, we collected branches of lengths that would ensure that segments were at least double the length of the MVL for each species. All branches were cut from the canopy, with the cut ends wrapped in parafilm (Parafilm M; Bemis Inc., Oshkosh, WI, USA) to reduce water loss. Each branch was sprayed with water to maintain wetness and then enclosed in a black plastic bag (1.5 m \times 1.5 m). For liana species, nearly all leaves were located on the top of the branches, so only top stem segments with leaves were bagged. Samples were brought to the laboratory within 30 min of excision, and water was sprayed on the branches every 3–5 min to minimize desiccation. All samples were recut underwater in the laboratory (to remove ca. 40 cm in length), then kept in darkness for 1–2 h to release tension in the xylem conduits (Wheeler *et al.* 2013). *Celastrus paniculatus* and *V. calyculata* were selected for determination of xylem tension based on preliminary research, which revealed that the two species exhibit high midday PLC. Changes in leaf water potential were recorded at 30-min intervals over the first 2-h rehydration; leaf water potentials after 1 h of rehydration ranged from -0.3 MPa to -0.5 MPa (see Fig. S1). The remaining stem was recut (to remove 1.5 times MVL in length, which was used to determine $K_{s\text{-max}}$ following Eqn 1) underwater. The targeted stem segment (ca. 20-cm length) was cut for the determination of PLC as follows:

$$\text{PLC} = 100 \times (K_{\text{max}} - K_0)/K_{\text{max}}, \quad \text{eqn 2}$$

where K_0 and K_{max} were the actual and maximum hydraulic conductance, respectively.

The native stem sapwood-specific conductivity (K_s , $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) was calculated as follows:

$$\text{Native } K_s = K_{s\text{-max}} \times (1 - \text{PLC}). \quad \text{eqn 3}$$

Seven of the eight liana and tree species exhibited significant midday increases in PLC compared to pre-dawn, indicating that rehydrating the samples for 1–2 h to ca. -0.4 MPa probably does not refill xylem embolisms, as was suggested by Trifilò *et al.* (2014) and Venturas, MacKinnon & Jacobsen (2014). It is possible that species with large vessels are prone to cutting artefacts even when xylem tensions are as low as ca. -0.4 MPa. It is unknown whether the cutting under tension artefact is xylem tension-dependent, but the magnitude of the artefact is species-dependent (Wheeler *et al.* 2013). Therefore, the given species may have some structural properties (e.g. vessels) that require full relaxation (i.e. 0 MPa) to avoid cutting artefacts. However, relaxation to 0 MPa may cause embolism refilling by capillary pressure, which would confound the results and complicate PLC analyses (Torres-Ruiz *et al.* 2015). Many uncertainties in explaining observed diurnal PLC patterns remain, and further research involving more direct measurements, such as X-ray microtomography, are needed to resolve the current controversies.

LEAF PRESSURE–VOLUME CURVES

Pressure–volume (P–V) curves were determined for 10–12 mature leaves from three individuals using the bench dehydration technique described by Lenz, Wright & Westoby (2006). Terminal branches were cut under water and then rehydrated overnight to ensure that $\Psi_{\text{leaf}} > -0.1$ MPa. Leaf fresh mass and Ψ_{leaf} were measured repeatedly during slow desiccation until Ψ_{leaf} stabilized or began to rise. The osmotic potential at full turgor (π_o , MPa), the turgor loss point (π_{tlp} , MPa), the bulk modulus of elasticity (ϵ , MPa) and absolute capacitance (C_{leaf} , mol m⁻² MPa⁻¹) were calculated following procedures described by Sack, Pasquet-Kok & contributors, P. (2011). A few oversaturated samples, detected by a plateau in the initial P–V curves, were discarded.

SAP FLOW

Sap flow was monitored during the end of the wet season (8–21 October 2012). We measured sap flow for all nine species (three to five individuals per species) mentioned above (data for the tree *Ficus concinna* were excluded because the sap-flow sensors were broken down during measurement). The diameter at breast height was greater than 5 cm for lianas and 10–60 cm for trees. Sap flow was measured using 20-mm-length thermal dissipation sensors with two probes, as described by Granier (1987). Sensors were inserted into the stems 1.3 m above the ground for trees and 1.3 m from the last rooting points for lianas and covered with reflective material to avoid temperature effects from direct radiation. We measured light intensity using a light meter (QRT1; Hansatech Instruments, Norfolk, UK) and determined that the light intensity at heights of 1.3 m above the ground average about 1–2% that of full light. We ignored temperature gradients over the course of the day. The differences in temperature between two probe needles of a sensor (ΔT) were monitored every 30 s, with 10-min averages recorded with a datalogger (CR1000; Campbell Scientific, Logan, UT, USA) connected to a 32-channel multiplexer (AM16/32). The ΔT between the heated and reference probes were converted to sap flux density (g m⁻² s⁻¹) based on the following equation:

$$J_s = 119 \times ((\Delta T_{\text{max}} - \Delta T) / \Delta T)^{1.231}, \quad \text{eqn 4}$$

where ΔT_{max} represents the temperature difference between the heated and reference probes when sap flux is zero. We assume that zero sap flow could be achieved during the night because of low nocturnal air VPD in the wet season. In a preliminary study of 29 individuals, we found time lags between base and canopy sap flow for only two trees (<30 min) and one liana individual (<10 min) during the wet season, so we used base sap flow to represent canopy transpiration. The daily hourly averages of J_s were plotted against concurrent ambient VPD to show how J_s responds to increasing VPD in lianas and trees. Concurrent VPD values were calculated using air temperature and humidity.

We recorded the maximum sap flow on a given day, J_{max} . We defined start time of sap flow as the time when J_s rises to 10% of J_{max} in the morning, start time of peak sap flow as the time when J_s rises to 80% of J_{max} , and daily peak sap-flow interval as the time during which J_s is above 80% of J_{max} . We defined sap-flow response time as the time interval when J_s rises from 10% to 80% of J_{max} .

DATA ANALYSIS

We calculated species mean values for MVL, $K_{\text{s-max}}$, water potential at 50% loss of conductivity (P_{50} , MPa), midday PLC and K_s , P–V parameters, J_{max} , duration of daily peak sap flow and sap-

flow response time. All response variables were tested for normality and natural log or square-root transformed when necessary. We compared the differences in the means between lianas and trees using Student's *t*-tests. We also extended these analyses to consider the differences among three groups (lianas, deciduous trees and evergreen trees) using one-way ANOVA and *post hoc* tests with Bonferroni corrections. All group comparisons were conducted using SPSS version 16.0 software (SPSS, Chicago, IL, USA).

We tested whether the relationships between g_s and each of three predictors – leaf water potential, xylem water potential and VPD – differed between lianas and trees using a mixed model, with species treated as the random effect. Both random slopes and random intercepts were included in the initial model, but random slopes were excluded from the final model because likelihood ratio tests determined that they did not explain significant variation in the data. Significance of the fixed effects was also examined using likelihood ratio tests, and non-significant effects were removed using backward selection with likelihood ratio tests. These analyses were conducted using the lmer() function of lme4 in R (Bates *et al.* 2015).

Results

STEM AND LEAF HYDRAULIC PROPERTIES

Maximum vessel length varied greatly among the species, ranging from 110 to 301 cm in lianas and from 61 to 192 cm in trees (Table 1). Mean MVL of lianas was more than twice that of trees; however, the difference in MVL was not statistically significant between the two groups due to the high interspecific variance within growth forms. Similarly, liana and tree species differed in $K_{\text{s-max}}$ but not in P_{50} ; lianas had higher $K_{\text{s-max}}$ and P_{50} than the three evergreen tree species ($K_{\text{s-max}}$: 8.0 vs. 1.9 kg m⁻¹ s⁻¹ MPa⁻¹, $P < 0.05$; P_{50} : -1.34 MPa vs. -2.56 MPa, $P = 0.055$; Fig. 1 and Table S1), but these values did not differ from those of the two deciduous trees ($K_{\text{s-max}}$: 8.0 vs. 5.1 kg m⁻¹ s⁻¹ MPa⁻¹; P_{50} : -1.48 MPa vs. -1.34 MPa; see Table S1). Leaf drought tolerance was comparable in lianas and trees, or among three growth forms (see Table S1) based on π_o , π_{tlp} , ϵ and C_{leaf} .

DAILY WATER RELATIONS AND NATIVE PERCENTAGE LOSS OF CONDUCTIVITY

The water potentials of sun-exposed leaves and stems declined in both liana and tree species during the daytime, with seven of the eight species losing their leaf turgor (Fig. 2); all species recovered overnight, however. At midday, lianas maintained higher daily minimal stem water potentials than trees (minimal Ψ_{stem} in lianas: -1.11 ± 0.1 MPa, $n = 4$ vs. in trees: -1.62 ± 0.2 MPa, $n = 5$; $t = 2.45$, $P < 0.05$), but midday leaf water potentials were comparable in lianas and trees (minimal Ψ_{leaf} in lianas: -2.48 ± 0.6 MPa, $n = 4$ vs. in trees: -2.37 ± 0.5 MPa, $n = 5$; $t = -0.33$, $P = 0.75$). Differences between minimal leaf and stem water potentials ($\Delta \Psi_{\text{stem-leaf}}$) during the day were higher in lianas than tree species (lianas: 1.37 ± 0.2 MPa, $n = 4$; trees: 0.75 ± 0.2 MPa,

Table 1. Stem and leaf hydraulic properties of four liana and five tree species in the present study. Values are means \pm S.E. $n = 10-12$. MVL, maximum vessel length; $K_{s,max}$, maximum stem sapwood-specific conductivity ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$); P_{50} , xylem water potential at 50% loss of hydraulic conductivity (MPa); PLC, percentage loss of conductivity (%); midday K_s , midday stem sapwood-specific conductivity ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$); π_o , osmotic potential at full turgor (MPa); π_{lp} , leaf water potential at turgor loss point (MPa); ϵ , bulk modulus of elasticity (MPa); C_{leaf} , absolute capacitance ($\text{mol m}^{-2} \text{MPa}^{-1}$). Different superscript letters represent significant difference at $P = 0.05$. ND means no data available

Species form	Growth	Leaf phenology	MVL	$K_{s,max}$	P_{50}	Midday PLC	Midday K_s	π_o	π_{lp}	ϵ	C_{leaf}
<i>Celastrus paniculatus</i>	Liana	D	301	8.62 \pm 1.6	-1.42	40.91	7.97 \pm 1.8	-1.28 \pm 0.2	-1.57 \pm 0.2	14.48 \pm 2.4	0.85 \pm 0.1
<i>Marsdenia sinensis</i>	Liana	E	235	10.57 \pm 1.3	-1.04	38.27	3.27 \pm 1.2	-0.97 \pm 0.1	-1.49 \pm 0.1	10.91 \pm 1.4	1.70 \pm 0.6
<i>Ventilago calyculata</i>	Liana	E	110	4.8 \pm 0.6	1.57	28.53	7.28 \pm 1.0	-2.02 \pm 0.1	-2.34 \pm 0.1	21.61 \pm 2.4	0.30 \pm 0.1
<i>Mucuna interrupta</i>	Liana	E	ND	ND	ND	ND	ND	-0.99 \pm 0.1	-1.17 \pm 0.1	7.42 \pm 0.5	0.12 \pm 0.0
<i>Celtis tetrandra</i>	Tree	D	120	6.21 \pm 0.6	-1.53	34.67	4.61 \pm 0.7	-1.96 \pm 0.1	-2.23 \pm 0.0	16.53 \pm 1.9	0.40 \pm 0.0
<i>Ficus concinna</i>	Tree	D	61	3.95 \pm 0.7	-1.43	29.55	2.21 \pm 0.8	-1.63 \pm 0.1	-2.06 \pm 0.1	25.81 \pm 2.0	0.26 \pm 0.0
<i>Harpullia cupanioides</i>	Tree	E	192	2.2 \pm 0.2	-2.51	15.45	1.96 \pm 0.2	-2.04 \pm 0.1	-2.37 \pm 0.1	16.67 \pm 1.7	0.49 \pm 0.0
<i>Michelia hypolampra</i>	Tree	E	74	1.69 \pm 0.2	-2.25	24.85	1.13 \pm 0.1	-1.06 \pm 0.1	-1.40 \pm 0.1	11.0 \pm 1.5	0.43 \pm 0.0
<i>Streblus asper</i>	Tree	E	72	1.86 \pm 0.4	-2.93	14.07	1.22 \pm 0.5	-1.78 \pm 0.0	-2.26 \pm 0.0	15.11 \pm 0.8	0.55 \pm 0.0
Liana mean			215.33 \pm 56 ^a	8.00 \pm 1.7 ^a	-1.34 \pm 0.2 ^a	35.90 \pm 3.8 ^a	6.17 \pm 1.5 ^a	-1.32 \pm 0.3 ^a	-1.64 \pm 0.2 ^a	13.61 \pm 3.0 ^a	0.74 \pm 0.4 ^a
Tree mean			103.80 \pm 24.3 ^a	3.18 \pm 0.9 ^b	-2.13 \pm 0.3 ^a	23.72 \pm 4.0 ^a	2.23 \pm 0.6 ^b	-1.69 \pm 0.2 ^b	-2.06 \pm 0.2 ^b	17.02 \pm 2.4 ^a	0.43 \pm 0.0 ^a

Nomenclature follows Flora of China (<http://foc.eflora.cn/>).

$n = 5$; $t = 2.5$, $P < 0.05$). Evergreen trees had lowest $\Delta\Psi_{\text{stem-leaf}}$ value among the three growth forms (see Table S1).

Seven of the eight species had higher PLC at midday than at pre-dawn (Fig. 3). Although the mean value of midday PLC for lianas was much greater than trees (Table 1), these were only marginally significant ($P = 0.087$). Specifically, the three liana species (ranging from 28.5% for *V. calyculata* to 40.9% in *C. paniculatus*) and two deciduous trees (ranging from 29.6% for *F. concinna* to 34.7% for *C. tetrandra*) had relatively greater PLC at midday than did the three evergreen tree species (ranging from 14.1% for *S. asper* to 24.9% for *M. hypolampra*; see Table S1). However, lianas still exhibited significantly greater conductivity than trees at midday (midday K_s : in lianas: $6.17 \pm 1.5 \text{ kg m}^{-1} \text{ s}^{-1} \text{MPa}^{-1}$, $n = 3$; in trees: $2.23 \pm 0.6 \text{ kg m}^{-1} \text{ s}^{-1} \text{MPa}^{-1}$, $n = 5$; $t = 2.9$, $P = 0.027$).

DIURNAL VARIANCES IN LEAF PHOTOSYNTHESIS AND STOMATAL CONDUCTANCE

Both lianas and trees reached maximal photosynthesis at 10:00–11:00 (with the exception of *V. calyculata* and *M. hypolampra*, both of which peaked between 12:00 and 13:00; Fig. 4). With increasing VPD, photosynthetic rates of both lianas and trees decreased rapidly in late morning or early afternoon. However, all liana species exhibited a sustained decline in photosynthesis until dark, whereas a slow decrease (Fig. 4g, i) or even a slight increase in the early afternoon (Fig. 4e, h) was observed in four of five tree species. Leaf stomatal conductance of lianas was high before 10:00, then decreased and remained low in the afternoon (Fig. 4a–d); the stomata of one liana species, *M. interrupta*, were almost entirely closed during the afternoon (Fig. 4b). In contrast, three of five trees species exhibited a slight increase in g_s during the period 14:00–16:00 (Fig. 4f–h). Surprisingly, no differences in leaf-level water-use efficiency were observed between lianas and trees over the course of the day, with the exception of the 10:00 period (see Fig. S2).

DYNAMICS OF SAP FLOW

Mean maximal PPFD and VPD were approximately $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ and 3 kPa, respectively, during the sap-flow measurement period (Fig. 5a), with a 3-h time lag between maximum PPFD and VPD (PPFD peaked at 12:00, VPD peaked at 15:00). Liana species reached maximum sap flow faster than trees (Fig. 5b; Table S2); sap flow was initiated at around 9:00 and reached peak sap flow (80% J_{max}) at around 10:50 in lianas, whereas trees initiated sap flow at around 9:50 and reached peak sap flow at around 12:20 (see Table S2). Thus, liana species quickly reached peak sap flow earlier (when VPD was close to 1 kPa) and sustained it for a longer period of time than tree species; in trees, sap flow tended to begin to

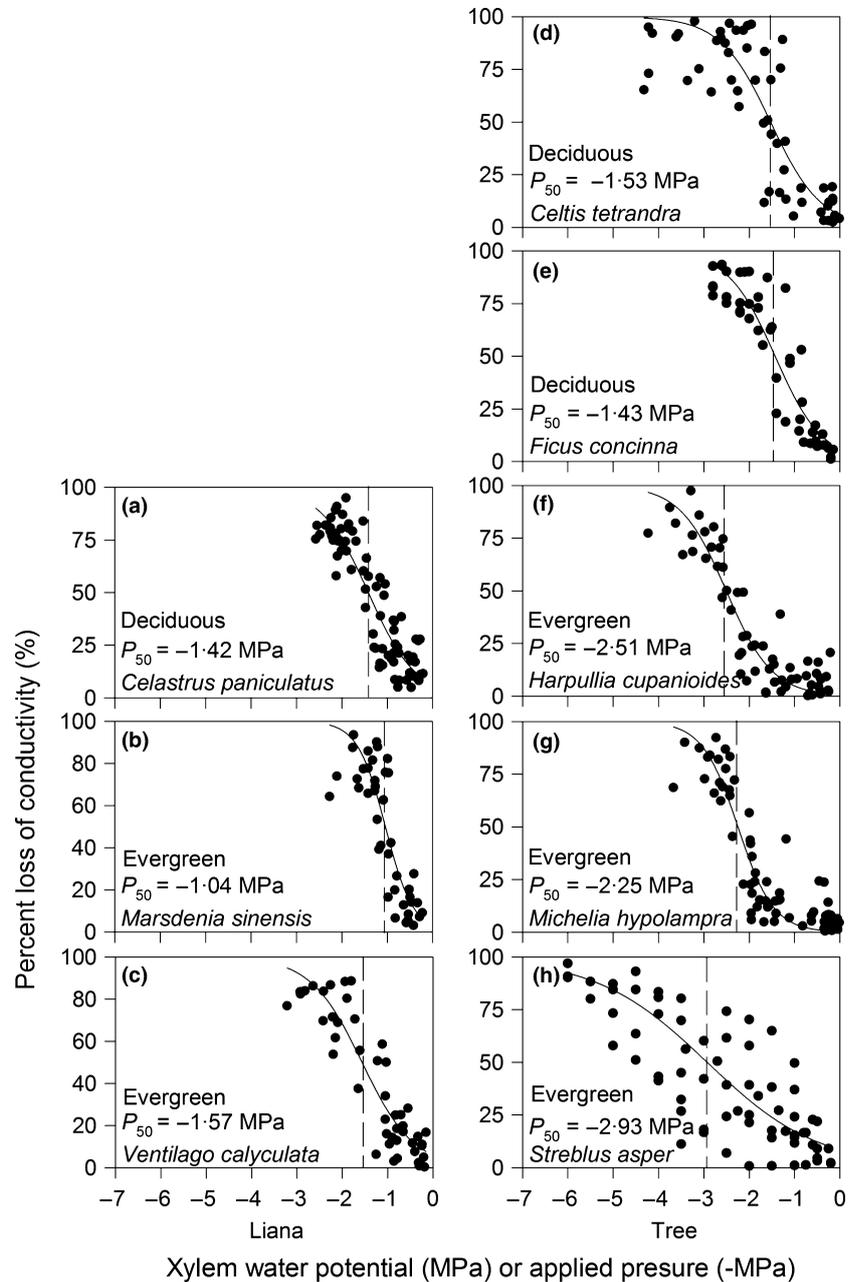


Fig. 1. Stem vulnerability curves for three liana (a–c) and five tree (d–h) species. PLC = the percentage loss of conductivity. $P < 0.001$ for all regression lines. The vertical dashed lines indicate the xylem water potential at 50% loss of stem hydraulic conductivity (P_{50}).

decline immediately following peak flow (Fig. 5b). Liana species had 1.7 times greater mean J_{\max} than trees ($P < 0.01$, Fig. 5b; Table S2).

STOMATAL CONDUCTANCE AND SAP FLOW IN RELATION TO WATER STATUS AND VPD

Our mixed-model analysis comparing stomatal conductance in trees and lianas against leaf water potential, xylem water potential and VPD indicated that g_s in both liana and tree species decreased with decreasing Ψ_{leaf} and Ψ_{stem} and decreased with increasing VPD (Fig. 6), but that there were no significant differences between lianas and trees in the responsiveness of stomatal conductance for these parameters based on gas exchange data (Fig. 6; Table S3).

However, we observed that the J_s of lianas increased at a quicker rate with increasing VPD than that of trees when VPD < 1 kPa (Fig. 7).

Discussion

Lianas seem to deploy a more 'risky' hydraulic strategy in terms of their high stem sapwood-specific conductivity and corresponding susceptibility to embolism, which is consistent with previous research on juveniles (van der Sande *et al.* 2013) and mature (Zhu & Cao 2009; Johnson *et al.* 2013) individuals. Evergreen trees had a particularly conservative hydraulic strategy compared to both lianas and deciduous trees, whereas liana and the deciduous tree species were more susceptible to drought-induced cavitation

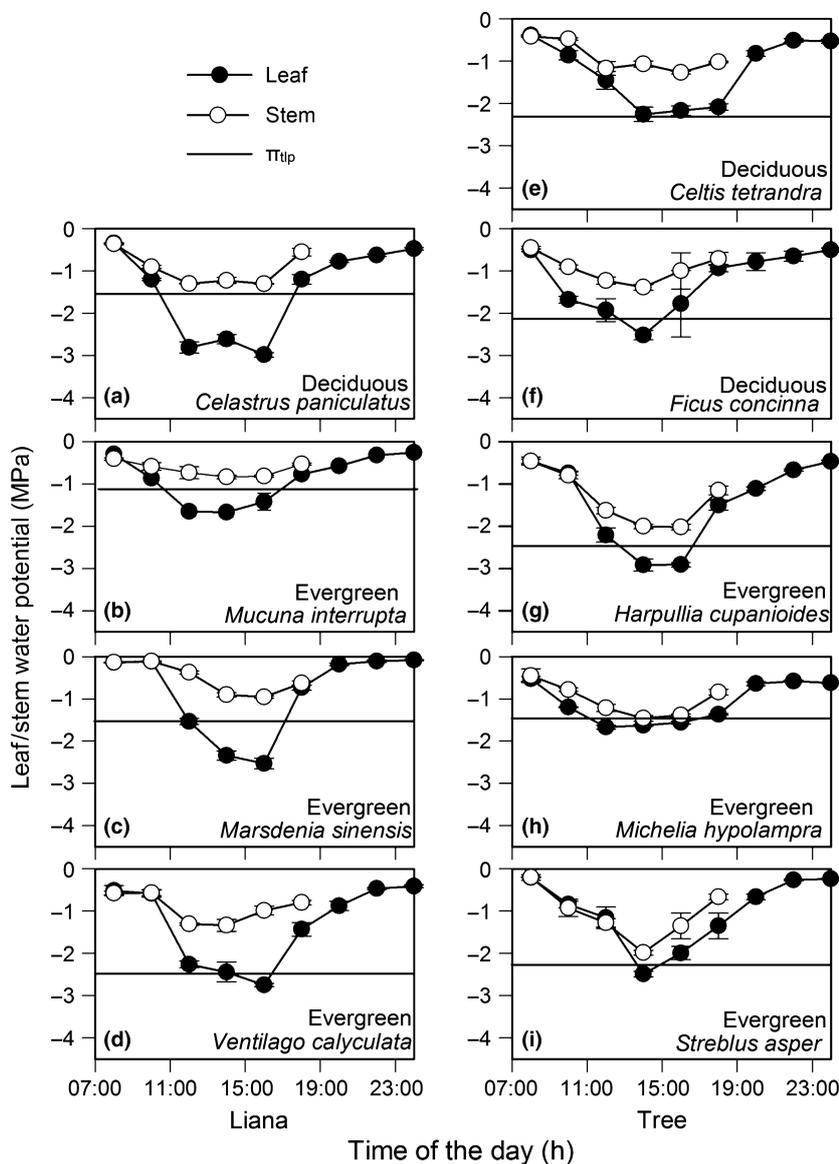


Fig. 2. Diurnal variation in sun-exposed leaf and stem water potentials for four liana (a–d) and five tree (e–i) species. Values are means \pm SE, $n = 6$. The solid lines represent leaf turgor loss point (π_{tip}).

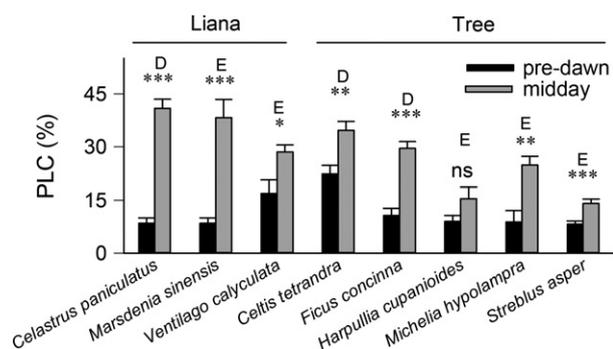


Fig. 3. The native percentage loss of conductivity (PLC) in three liana and four tree species. Values are mean \pm SE. $n = 10$. ns $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; D, deciduous; E, evergreen.

than the evergreen trees, as indicated by their lower negative P_{50} and higher midday PLC values. However, lianas also tended to have higher stem sapwood-specific

conductivity than did the co-occurring trees, conferring lianas with greater water transport efficiency. Thus, despite losing up to nearly half of their conductivity at midday (i.e. midday PLC ranging from 28.5% in *V. calyculata* to 40.9% in *C. paniculatus*), lianas were able to continue to transport water efficiently to the canopy during the afternoon. The larger degree of interspecific variance and limited number of species included in this study resulted in non-significant differences between the lianas and trees in regard to many parameters (e.g. MVL, P_{50} , midday PLC and P-V curve), and therefore, such findings must be validated by future research using a far larger range of species.

Deciduous tree species had similar hydraulic properties as lianas, suggesting that lianas and deciduous trees may share similar water-use strategies for dealing with water deficits. Root pressure may be a driving force for refilling diurnally dysfunctional vessels, especially in monocots (Cao et al. 2012; Yang et al. 2012). Until now, there has

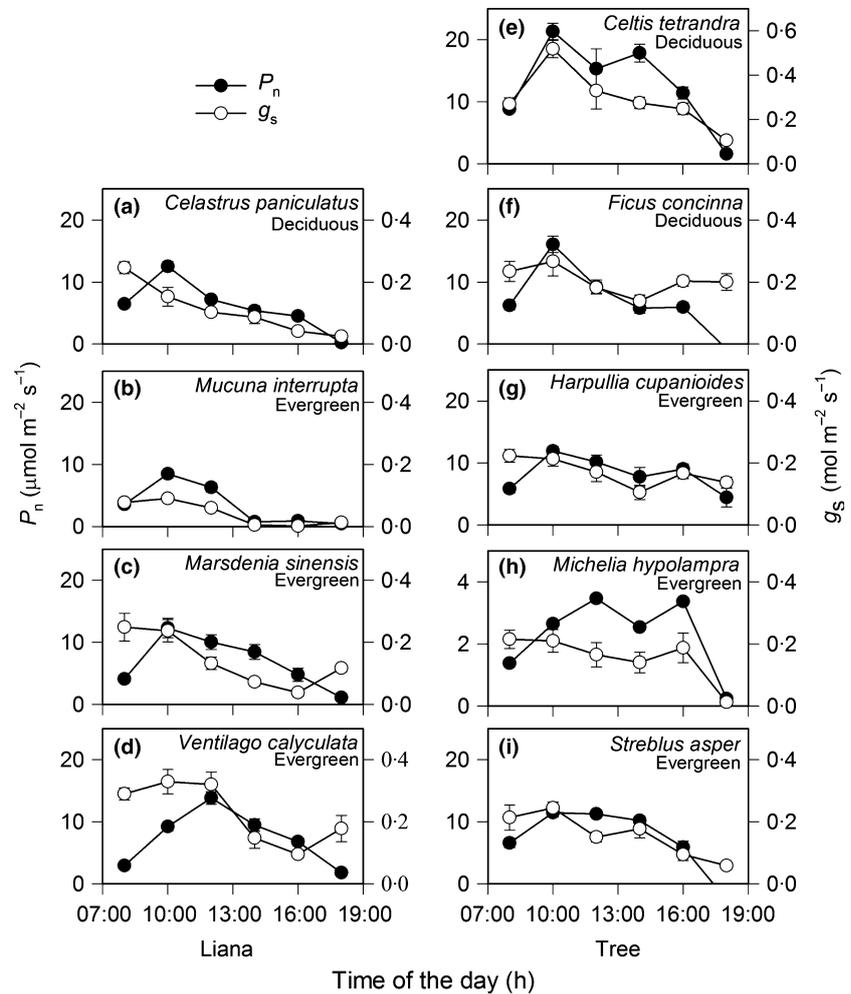


Fig. 4. Diurnal variation in photosynthetic rate (P_n) and stomatal conductance (g_s) for four liana (a–d) and five tree (e–i) species. Values are means \pm SE, $n = 6$. Note the different axial scales in (e) and (h).

been no convincing empirical evidence that lianas can refill emboli in conduits solely using root pressure, given that in most lianas, species root pressure alone is insufficient for refilling gas-filled vessels in the upper stems (Ewers, Cochard & Tyree 1997; Tibbetts & Ewers 2000). Further studies are needed to test whether cavitation occurs during the day and how the refilled conduits are able to reconnect to functional conduits (Rockwell *et al.* 2014).

In this study, sun-exposed leaf water potentials of all species reached or were close to their turgor loss points, implying possible leaf wilting and stomatal closure, which slowing further water loss. However, lianas lost leaf turgor earlier (about 2 h) than trees, which may be attributed to their earlier exposure to light than trees, as the majority of liana leaves are at the top of the canopy. The ability of lianas to close their stomata rapidly in response to declining leaf or stem water potential allows them to reduce water consumption under conditions of high VPD, giving them an advantage in terms of maintaining stem water potential. Moreover, the higher stem water potential despite comparable leaf water potential in lianas at midday compared to trees probably benefit from their efficient water transport. Lianas tend to have higher stem sapwood-specific conductivity and trunk (main stem) maximum sap flux density

than do co-occurring trees owing to a comparatively well-developed vessel system (e.g. wide and long vessels); lianas are thus able to supply far more water to their leaves per active xylem area than trees are. Furthermore, the ability to efficiently transport water from the soil to the stems via their deep roots (Restom & Nepstad 2004) may help lianas buffer daytime water loss by transpiration because they are considered to have deep roots (Chen *et al.* 2015).

Liana species initiated and reached peak sap flow faster and earlier than trees, suggesting that lianas may be more reliant to on water transported from the soil rather than water stored in stems. Therefore, there are short time lags between basal sap flow and canopy transpiration in lianas, whereas in trees, in contrast, the gradual and slow increase in sap flow despite high canopy transpiration (high g_s) in the morning ($\sim 10:00$) suggests substantial buffering from the internal water-storage pool. This contrasting sap-flow pattern between lianas and trees has been demonstrated in previous studies (Phillips *et al.* 1999; Chen *et al.* 2015, 2016a). Tropical trees differ in the size of their internal water storage, with some large trees providing substantial amounts of water to the transpiration stream; for example, a study of canopy trees in Panama found that the amount of water withdrawn from stem water storage and used to

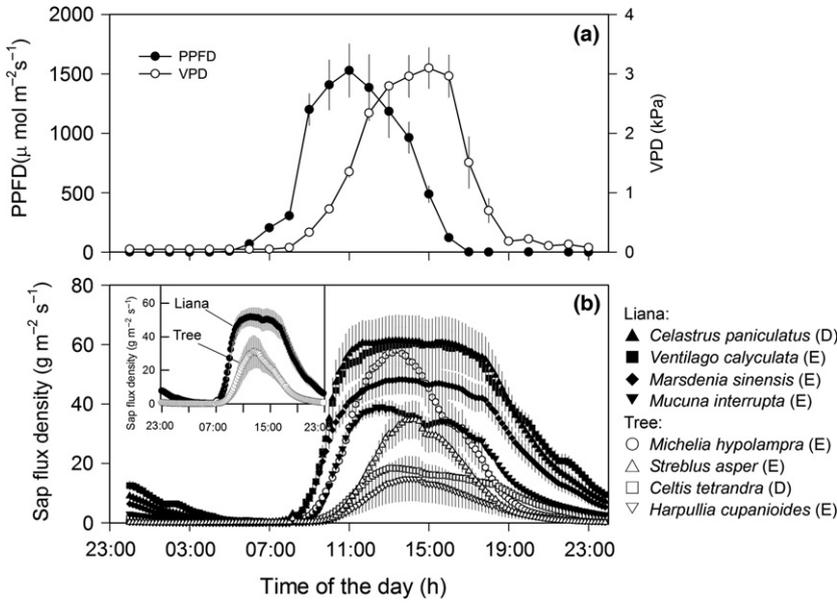


Fig. 5. Diurnal variation in photosynthetic photon flux density (PPFD), vapour pressure deficit (VPD) (a), and in sap flux density (b) of four liana and four tree species. Values are means \pm SE for each species over four clear days during the period 8–21 October 2012. Inset figure shows mean $J_s \pm$ SE of lianas and trees. D, deciduous; E, evergreen.

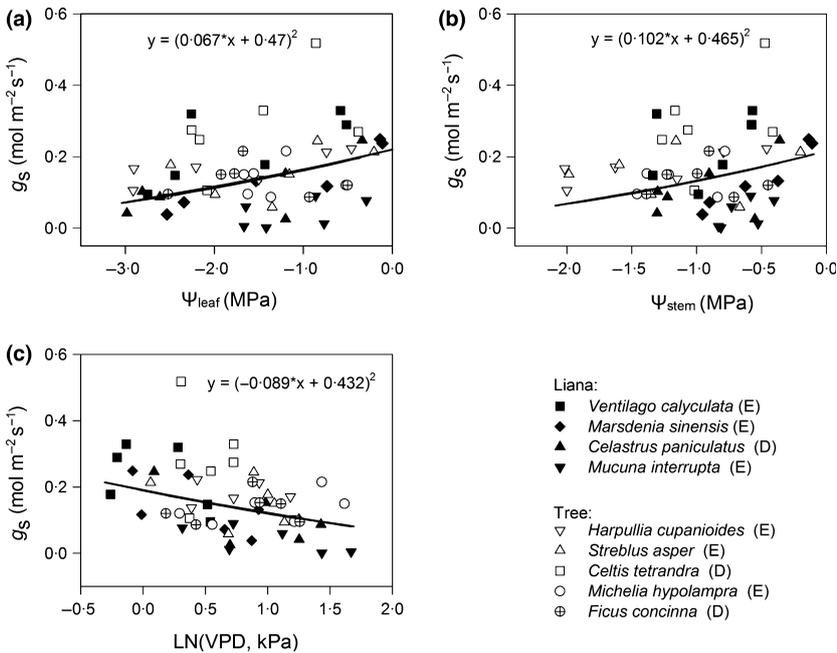


Fig. 6. The relationships of leaf stomatal conductance (g_s) with leaf (Ψ_{leaf} , a) and xylem (Ψ_{stem} , b) water potential and vapour pressure deficits (VPDs, c) in four liana and five tree species. Values are means for each species over four clear days during the period 8–21 October 2012. D, deciduous; E, evergreen. Results of mixed model (see Table S3) showed that there were no significant differences in slopes and intercepts in the responsiveness of g_s to Ψ_{leaf} , Ψ_{stem} and VPD between lianas and trees.

replace transpirational water losses range from 4 kg day⁻¹ to 54 kg day⁻¹ daily, depending on the main stem size, representing 9–15% of a tree’s total daily water loss (Goldstein *et al.* 1998).

At the leaf level, lianas and co-occurring trees exhibited similar responsiveness of stomatal conductance to increasing VPD and coupled decreasing leaf or stem water potential during the day; these findings were not aligned with those for the whole-plant sap-flow data. Obviously, lianas reached maximum transpiration at a relative low VPD (<1 kPa) than did trees; in contrast, trees conformed to a near-linear increase of transpiration against increasing VPD. This inconsistency between leaf and whole-plant performance may be partly attributed to the fact that only a

few sun-exposed leaves were included in the canopy gas exchange analyses; on the other hand, it is possible that the gas exchange system could not fully match the ambient and within-cuvette VPDs, specifically when under high transpirational demand in the canopy.

The earlier, high level of transpiration in lianas potentially indicates their vigorous carbon fixation during the morning hours. Lianas are believed to be capable of ramping up photosynthesis more rapidly than trees due to their larger investment in photosynthetic chemistry (e.g. higher mass-based photosynthetic pigments, N and P; Asner & Martin 2012). This physiological adaptation may be an essential feature of lianas given the unequal distribution of their leaves, with most occurring at the top of the canopy

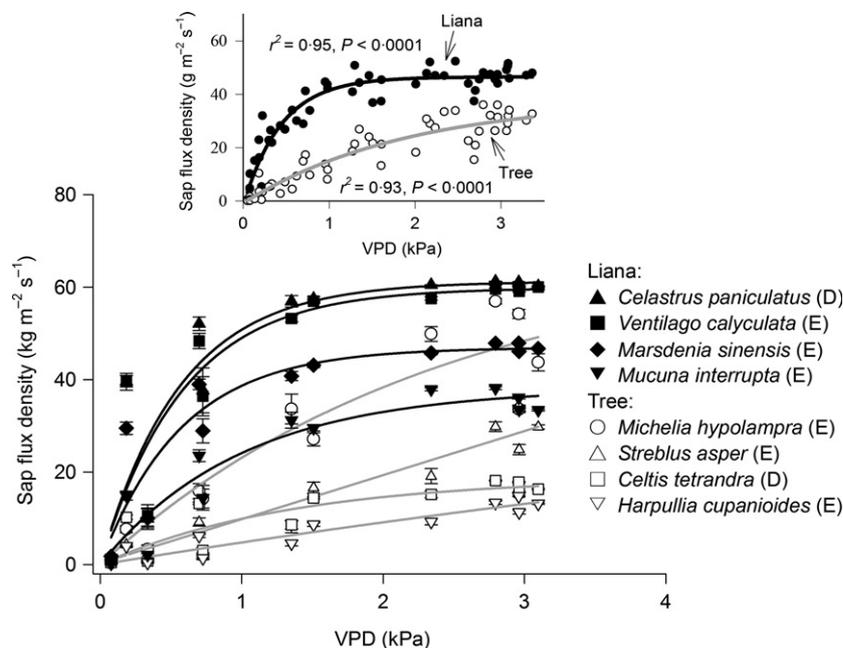


Fig. 7. The response of sap flux density (J_s) to increasing vapour pressure deficits (VPDs, kPa) during the daytime (8:00–19:00) over four clear days during the period 8–21 October 2012. Values are means \pm SE of hourly averages of each species. Inset figure shows the relationship between mean $J_s \pm$ SE and VPDs in lianas ($n = 4$) and trees ($n = 4$). Data were fitted using a two-parameter exponential function as: $y = a \times (1 - \exp(-b \times x))$. $P < 0.001$ for all regression lines. D, deciduous; E, evergreen.

where they are exposed to sunlight, wind and high temperatures throughout the day; in contrast, only the top leaves of the co-occurring trees are sunlit, and much of the rest of the canopy is sheltered by the upper leaves of the trees and their liana competitors. The vertical distribution of tree leaves may allow them to utilize a spatial segmentation strategy, wherein the top exposed leaves fix carbon in the morning when VPD is low, and the shaded leaves can fix carbon later in the day, when most sun-exposed canopy leaves are downregulated under direct light and high VPD.

The constantly high transpiration in lianas as a result of higher transpirational demand (>1 kPa) may be attributed to the sharp decline in stomatal conductance in the afternoon due to stomata closure. The whole-plant transpiration may remain high even as g_s decreases as a consequence of rising VPD. Thus, stomatal closure may permit lianas to maintain high and steady transpiration rates with increasing VPD, especially early in the day, which may also help lianas reduce water loss during the dry season when soil water is limited (Chen *et al.* 2015).

Conclusions

Lianas appear to have low water-storage capacity and are vulnerable to drought-induced cavitation due to their wide vessels and slim stems. However, physiological regulation (stomatal closure) and efficient water transport from the soil to terminal branches (high stem sapwood-specific conductivity and sap flux density) may help lianas maintain stem water potential within the safe range to avoid xylem dysfunction. Physiological regulation may be particularly important for lianas, which tend to deploy the majority of their leaves at the top of the forest canopy, where they flourish despite the trifecta of high light intensity, temperatures and windiness – all of which increase VPD and thus

water stress. Our results therefore provide a potential physiological explanation of how lianas can have large vascular systems, which permit them to transport copious amounts of water and yet still avoid catastrophic hydraulic failure and thrive in tropical forest canopies. However, further research involving more species is needed to determine whether these physiological adaptations are common among lianas.

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Data accessibility

Data are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.bm2c2g> (Chen *et al.* 2016b).

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1. Vulnerability curve measurements.

Fig. S1. The change of xylem water potential at 30-min intervals during the first 2 h rehydration in *Celastrus paniculatus* and *Ventilago calyculata*.

Fig. S2. Diurnal variation in leaf water-use efficiency (WUE) for four liana and five tree species.

Table S1. Mean stem and leaf hydraulic properties of the three growth forms (lianas, deciduous trees and evergreen trees) and results of ANOVA testing for differences between the growth forms.

Table S2. Sap-flow characteristics of four liana and four tree species.

Table S3. Results of mixed-models examining the relationships between stomatal conductance (g_s) and leaf water potential (Ψ_{leaf}), xylem water potential (Ψ_{stem}) and VPD in trees and lianas.