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Water-use advantage for lianas over trees in tropical seasonal forests

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Summary

- Lianas exhibit peak abundance in tropical forests with strong seasonal droughts, the eco-physiological mechanisms associated with lianas coping with water deficits are poorly understood.
- We examined soil water partitioning, sap flow, and canopy eco-physiological properties for 99 individuals of 15 liana and 34 co-occurring tree species in three tropical forests that differed in soil water availability.
- In the dry season, lianas used a higher proportion of deep soil water in the karst forest (KF; an area with severe seasonal soil water deficit (SSWD)) and in the tropical seasonal forest (TSF, moderate SSWD), permitting them to maintain a comparable leaf water status than trees in the TSF or a better status than trees in the KF. Lianas exhibited strong stomatal control to maximize carbon fixation while minimizing dry season water loss. During the dry period, lianas significantly decreased water consumption in the TSF and the KF. Additionally, lianas had a much higher maximum photosynthetic rates and sap flux density in the wet season and a lower proportional decline in photosynthesis in the dry season compared with those of trees.
- Our results indicated that access to deep soil water and strong physiological adjustments in the dry season together with active wet-season photosynthesis may explain the high abundance of lianas in seasonally dry forests.

Introduction

Lianas (woody climbers) are an abundant and diverse polyphyletic group of plants that contribute substantially to the floristic, structural, and functional diversity of tropical forests (Gentry, 1991; Gerwing & Farias, 2000; Chave *et al.*, 2001; Schnitzer & Bongers, 2002). Lianas compete intensely with trees and thereby contribute to a variety of tropical forest dynamics. Therefore, factors that are responsible for liana distribution in tropical forests are critical to our understanding of how tropical forest ecosystems function. Recent studies have reported that lianas peak in abundance in seasonal tropical forests that undergo extensive dry periods (Schnitzer, 2005; DeWalt *et al.*, 2010), and thus lianas appear to thrive in these highly seasonal tropical forests (reviewed by Schnitzer & Bongers, 2011; Schnitzer, 2014). Schnitzer (2005) suggested that lianas benefit from seasonal drought through a dry season growth advantage because they possess well developed roots that allow them to access deep soil water and maintain more growth than co-occurring tree species during the dry season. This hypothesis has been supported by studies in Southwest China (Cai *et al.*, 2009; Zhu & Cao, 2009), where photosynthesis of lianas decreased by only 12.8% during the dry season, whereas that of trees decreased by 30.1%. Nevertheless, there is still a lack of studies on water uptake and transport and leaf-level or whole-plant eco-physiology to support this hypothesis; therefore, it remains unclear how lianas respond physiologically to seasonal drought in tropical forests and whether lianas have a dry season advantage over co-occurring trees in terms of water use and whole-plant physiology.

Lianas do not invest a substantial proportion of biomass to build a rigid stem (cf trees); instead, they use the architecture of trees to ascend to the forest canopy and thus are able to invest much more biomass in stem elongation and leaf and root growth. Indeed, lianas are reputed to have up to five times more leaf area per stem diameter than trees (Gerwing & Farias, 2000). Because most lianas have narrow stems and a large leaf area, they have evolved wide and long vessels to supply water and nutrients to their leaves. In particular, some lianas have vessels with lengths of several meters and diameters > 100 μm, which afford them high specific hydraulic conductivity and a low Huber value (sapwood: leaf area), enabling them to compensate for their relatively small

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sapwood area (Ewers *et al.*, 1990; Ewers & Fisher, 1991; Gartner, 1991; Chiu & Ewers, 1992; Zhu & Cao, 2009; Jacobsen *et al.*, 2012). Fichtner & Schulze (1990) reported high sap flow and transpiration in lianas in a tropical deciduous forest, and Restom & Nepstad (2001) showed that three common liana species have higher transpiration rates than trees in an Amazonian secondary forest. However, maximum sap flux density between eight lianas and co-occurring trees of similar size did not differ in a Panamanian seasonally dry tropical forest (Andrade *et al.*, 2005). Thus, a direct comparision of water transport and utilization in multiple liana and tree species using consistent methodology is essential for determining differences in water-use characteristics between lianas and trees. Furthermore, studies in forests that vary in soil water availability are also necessary to understand how water-use strategies differ between lianas and trees and to explain how contrasting plant groups adjust their water use to deal with water deficits during the dry season.

Governing of stomata opening and closure is crucial for terrestial plants (particularly C_3 plants) to balance carbon acquisition and water loss by transpiration (Brodribb & Holbrook, 2003; Brodribb & McAdam, 2011). Under conditions of sufficient water availability, high stomatal conductance (high transpiration) promotes high carbon gain (Tyree, 2003). However, decreased transpiration caused by downregulation of stomatal conductance during high water deficits may be an adaptive behavior to protect the conducting system against hydraulic failure (Tyree & Sperry, 1988) while restricting the entry of CO_2 (McDowell *et al.*, 2008; McDowell, 2011). Lianas experience a particular challenge because most of their leaves are exposed at the top of the canopy (or in treefall gaps) (Ledo & Schnitzer, 2014), where sunlight and vapor pressure deficit (VPD) are high, even in the wet season. Rapid regulation of stomatal conductance accompanied by whole-plant conductance allowing lianas to maintain the balance between carbon gain and water loss, may potentially account for their prolification in the canopy (Cai *et al.*, 2009; Schnitzer & Bongers, 2011). However, few studies have compared the stomatal control of lianas and co-occuring trees (Cai *et al.*, 2009).

Access to deep soil water via deep roots is another important adaptation facilitating the survival of plants growing in water-stressed environments and conferring such plants with a competitive advantage against shallow-rooted neighbors (Wright *et al.*, 1992; Canadell *et al.*, 1996; Cao, 2000; Oliveira *et al.*, 2005). Oliveira *et al.* (2005) revealed that 83% of water use of trees during the dry season can be attributed to the uptake of deep soil water in a savanna community in central Brazil. Deep roots may occur in vegetation that experiences strong seasonal drought periods, for example tropical savannas or seasonally dry forests (Canadell *et al.*, 1996; Schenk & Jackson, 2005). Lianas are generally thought to have deep root systems that would enable them to access deep water sources and thus explain their peak abundance in seasonally dry tropical forests (Schnitzer, 2005; Schnitzer & Bongers, 2011). However, due to the difficulties of root excavation, few studies have investigated liana rooting depth; indeed, only one study has reported the rooting depth of a single liana species (*Davilla kunthii*) in eastern Amazonia, in which the roots of small individuals (< 2 m tall) reached a depth of over 10 m (Restom & Nepstad, 2004). The recent development of isotopic ratio techniques has made it possible to determine the relative contribution of different water sources (e.g. fog, rainfall, or underground water of different depths) to xylem sap (Jackson *et al.*, 1995; Meinzer *et al.*, 1999; Phillips & Gregg, 2003; Liu *et al.*, 2007, 2010; Querejeta *et al.*, 2007; Stahl *et al.*, 2013). Using this technique, Andrade *et al.* (2005) showed that all eight lianas examined used shallow water at the beginning of the dry season and shifted to deeper water sources at the end of dry season. However, no studies have tested the water-use depth in lianas and trees across forests that differ in water availability. Therefore, it is still not known whether the use of deep soil water by lianas is a general phenomenon.

In this study, we selected three forest sites that varied substantially in soil water availability in the same area. We measured the depth of water acquisition from the soil, as well as the sap flow and leaf eco-physiological traits for 99 individuals of 15 lianas and 34 co-occurring tree species from three forests during the dry and wet seasons. The specific goals of the study were to qualify the spatial partitioning of soil water use for lianas and co-occurring trees in the dry and wet seasons among sites, determine the seasonal changes in leaf physiological performance for lianas and trees, and characterize the regulation of whole-plant water use. We hypothesized that lianas would use more water from the deep soil layer and thus maintain better water status and eco-physiological performance than trees during the dry season. Moreover, we expected that lianas had strong stomatal control to avoid excessive water loss during conditions of water deficits.

Materials and Methods

Field sites

This study was conducted in Xishuangbanna in southern Yunnan Province, Southwest China, a global biodiversity hotspot (Myers *et al.*, 2000). Liana abundance is high in Xishuangbanna (Zhu *et al.*, 2006), but similar to other liana-rich areas (e.g. Schnitzer, 2005; DeWalt *et al.*, 2010). The region has a typical tropical monsoon climate and a pronounced dry season from November to April. The mean annual precipitation is *c.* 1560 mm, nearly 80% of which occurs during the wet season (May to October). The mean annual temperature is 21.7°C with a monthly mean temperatures of 15.9°C in the coldest month (December) and 25.7°C in the hottest month (June) (Cao *et al.*, 2006).

We selected three primary tropical forests that differed in their dry season soil water status and established a 20 m × 30 m study plot in each forest. The karst forest (KF; 21°54′N, 101°46′E, 580 m above sea level (asl)) is *c.* 3 km from the Xishuangbanna Tropical Botanical Garden (XTBG) and has a brown calcareous soil with a coarse texture and a pH of *c.* 7.3. Because the water leakage of the substrate, the soil in the KF becomes extremely dry during the dry season (Fu *et al.*, 2012). The tropical seasonal forest (TSF) is in a nature reserve (21°55′N, 101°15′E, 750 m asl) located *c.* 8 km away from XTBG and is dominated by the trees *Pometia tomentosa* and *Terminalia myriocarpa* (Zhang & Cao, 1995). This site has lateritic soil developed from siliceous

rocks. The flood plain forest (FPF) is located in XTBG and has deep, rich soil and a shallow water table. We used this site to represent ever-wet soils as a control for testing the water-use advantage of lianas in the dry season.

We used meteorological data (photosynthetic photon flux density (PPFD), air temperature, relative humidity, and air pressure) from a weather station located 1 km between KF and FPF and from another weather station on a 70 m tall tower located 100 m away from the TSF plot. Both weather stations are managed by Xishuangbanna Tropical Rainforest Ecosystem Station of the Chinese Academy of Sciences, and climatic variables were recorded at 30 min intervals.

Sap flow measurement

We measured sap flow in all lianas with a diameter at breast height (DBH) ≥ 5 cm at the height of 1.3 m and in all trees with DBH ≥ 15 cm located in each of the three plots. We studied a total of 99 individuals of 49 species (15 liana species and 34 tree species; KF, 17 liana individuals and 16 trees; TSF, 18 liana individuals and 19 trees; and PFP, 13 liana individuals and 16 trees; see Supporting Information Table S1). Sap flow was measured using self-made 20 mm long thermal dissipation sensors (with two probes for one sensor) following Granier (1987). To minimize the injury to trees and lianas, we installed only one pair of probes for each individual. We placed the sensors 1.3 m from the base of each of tree and liana and covered the sensors and stem with aluminum foil to prevent sunlight heating on the stem. The difference in temperature ($\triangle T$) between the two probes was scanned every 30 s, and average values were recorded every 10 min using a data logger (CR1000; Campbell Scientific, Logan, UT, USA) connected via a 32-channel multiplexer (AM16/32).

Sapwood depth at breast height was estimated using a dye method (Goldstein *et al.*, 1998; Meinzer *et al.*, 2001). Between 08:00–11:00 h in July 2012, we collected one 5-mm diameter core with an increment borer (drilled at 90° angles) to the center of the trunk at a height of 1.3 m. We then injected a methyl blue solution into the hole, which was refilled when necessary, and collected a second core 10 cm above the injection point the following day to determine the sapwood width. The active sapwood area of the stem was then calculated as the area of the stem ring with the sapwood width. Nearly all the cross-sections of lianas are conductive (Angyalossy *et al.*, 2012); therefore, for liana species, we defined the sapwood area as the cross-sectional area of the stem excluding the pith and bark. For tree species, we calculated the percentage of cross-sectional sapwood area by collecting 4–6 stem cores from individuals of each of our study species of similar diameter that were growing outside the plot.

The temperature difference ($\triangle T$) between the heated and reference probes was converted to sap flux density ($g\,m^{-2}\,s^{-1}$) according to the formula described by Granier (1987):

$$J_s = 119 \times ([\Delta T_{max} - \Delta T]/\Delta T)^{1.231} \quad \text{Eqn 1}$$

where ΔT_{max} is the temperature difference between the two probes when sap flux is assumed to be zero. Daily water use ($kg\,d^{-1}$) was calculated by multiplying the sap flux density by the sapwood area and time course.

Xylem tissue samples and soil hydrogen isotope composition

We collected soil samples and xylem tissue samples for two seasons in each of the plots on 19 April 2012 and 20 September 2012, which represented the dry and wet season, respectively. To avoid influencing the sap flow measurement, we selected nearby conspecific individuals outside the plot with a similar size to extract xylem tissue samples, except in the flood plain forest plot (FPF), where it was impossible to find enough individuals. We sampled the xylem tissue from two individuals for each species using an increment borer to collect two small cylinders of wood at DBH. The outer bark and other nonxylem tissues were removed, and the outer living xylem tissues were immediately placed in glass containers, sealed with parafilm, and stored at 4°C.

Soil samples were collected using an auger at depths of 30, 60, 100, 150, 200, and 250 cm in the KF and TSF. The TSF and especially the KF sites had shallow soils. By contrast, the soil in the FPF site was deep; no stones were found, even at depths of up to 5 m. We simultaneously collected soil samples for water potential measurements. Soil water potential was measured using a dewpoint potentiometer (WP4-T; Decagon, Pullman, WA, USA).

All of the xylem and soil samples were analyzed using an elemental analyzer (Flash EA 1112, Thermo Electron Corporation, Beverly, MA, USA) interfaced to an isotope ratio mass spectrometer (Thermo Finnigan MAT DELTA plus XP; Thermo Electron Corporation).

$$\Delta D‰ = ([D/H_{sample} - D/H_{standard}]) - 1 \times 1000‰ \quad \text{Eqn 2}$$

The contribution of water from different soil depths was calculated for each tree and liana using the Iso-Source mixing model (http://www.epa.gov/wed/pages/models.htm) (Phillips & Gregg, 2003). This model gives the distribution of the proportions of feasible sources when a high number of potential sources is present and is based solely on isotopic mass balance constraints. We considered three depths of water sources (0–60, 61–150 and 151–250 cm) and used deuterium (D) data for the model calculations.

Leaf gas exchange and water potential

We examined leaf gas exchange and water potential in 56 species (six branches from three individuals for each species). We selected the dominant or common tree and liana species in each site (TSF, 10 liana and 18 tree species; KF, 12 liana and 13 tree species; and FPF, four liana and six tree species; Table S2). Measurements were conducted during October 2011 (wet season) and March 2012 (dry season). We also assessed leaf water potential using a pressure chamber (PMS, Albany, OR, USA). Predawn samples

($\Psi_{predawn}$) were collected from 06:00 to 07:00 h and midday samples (Ψ_{midday}) were collected from 13:00 to 15:00 h. All measurements were completed in the field.

The maximum leaf area-based photosynthetic rate (P_{max}) and maximum stomatal conductance (g_s) were measured between 09:00–12:00 h in the wet season in 2011 and in the dry season 2012. Gas exchange was measured on six sunlit leaves from two or three individuals per species using a LI-6400 portable photosynthesis system (Li-Cor, Lincoln, NE, USA). The air CO_2 concentration in the leaf chamber was maintained at 400 μmol mol^{-1}, and the PPFD was 1500 μmol m^{-2} s^{-1}.

Statistical analysis

The daily mean sap flux density (J_s) in each season was calculated by the mean of values from 5 to 10 clear days for each individual. We calculated the ratio of changes in sap flux density (ΔJ_s), water use (ΔWU), and gas exchange (ΔP_{max} and Δg_s) in the dry season relative to the wet season. We used a two-way analysis of variance (ANOVA) to compare the differences between growth form (liana and tree), season (wet and dry), and their interactions for variables P_{max}, g_s, $\Psi_{predawn}$, Ψ_{midday} and mean J_s. Data were tested for normality and homogeneity of variance and log_{10}-transformed when necessary. We used a two-parameter exponential function to fit the relationship between diurnal sap flux density (J_s) to VPDs for all lianas and trees. All statistical analyses were conducted using SPSS version 13.0 (SPSS, Chicago, IL, USA).

Results

Soil water availability and partitioning of soil water use

During the wet season, the soil water potential was high, ranging from −0.58 to −0.24 MPa and was similar among the three sites (Fig. 1a). During the dry season, the soil water potential remained high (> −1.0 MPa) in the flood plain forest (FPF), but decreased to < −1.5 MPa in the deeper soils (> 200 cm) of the tropical seasonal forest (TSF) and was consistently below −3.0 MPa at all soil depths in the karst forest (KF, Fig. 1b).

The main source of water taken up by both lianas and trees in the FPF was from the depth of 151–250 cm, regardless of season. In the wet season, however, the main source of water was from the upper 60 cm soil layers for both trees and lianas in the KF and TSF (Figs 2, S1). In these two sites, the pattern of seasonal water use differed between the two growth forms. In the driest site (KF), lianas used a higher proportion of deep soil water (151–250 cm) than trees (lianas, 40.6%; trees, 28.4%). In the dry season, nearly 50% of the water use by trees in KF was still taken up from the shallow soil layer (0–60 cm; Fig. 2). In the TSF, lianas also shifted their water use to the deep layer (151–250 cm) during the dry season when the water potential of shallow soils decreased. In this site in the dry season, *c.* 38% of water in lianas were from the deep soil layers (151–250 cm) while trees used less deep soil water (27.6%) and more water (54%) from medium-depth soils (61–150 cm) (Fig. 2).

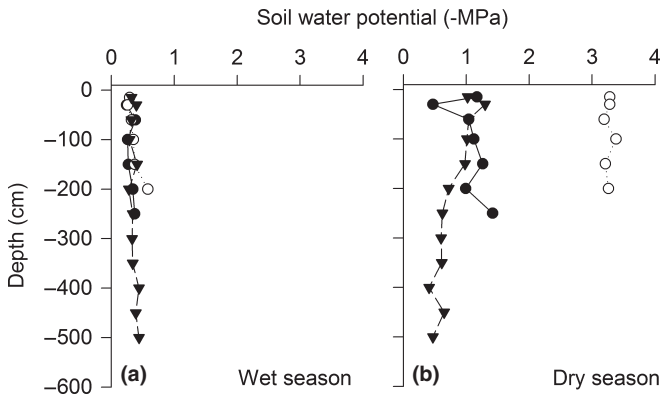

Fig. 1 Soil water potential of the karst forest (KF, open circles), tropical seasonal forest (TSF, closed circles), and the flood plain forest (FPF, triangles) during the dry and wet seasons in Xishuangbanna, Southwest China.

Water status of lianas and trees in the wet and dry seasons

Predawn ($\Psi_{predawn}$) and midday (Ψ_{midday}) leaf water potentials were significantly more negative in the dry season than in the wet season for both liana and tree species in the KF and TSF (Fig. 3a,b; Tables 1, S2). In the KF, where the soil water deficit in the dry season was most severe among all of the study sites, lianas had a much higher $\Psi_{predawn}$ than trees during the dry season (-1.4 ± 0.2 MPa for 10 common liana species and -2.4 ± 0.5 MPa for 11 common trees; Fig. 3a; Table S2), indicating that lianas were able to access more soil water. By contrast, in forest with moderate dry season soil water conditions (TSF and FPF), lianas and trees had comparable $\Psi_{predawn}$ and Ψ_{midday}. During the wet season, however, lianas and trees in the KF did not differ in $\Psi_{predawn}$ and Ψ_{midday}. Additionally, lianas and trees also did not differ in their $\Psi_{predawn}$ and Ψ_{midday} during either the dry or wet season in both TSF and FPF sites (Fig. 3b,c; Table 1).

Comparison of sap flow between the wet and dry seasons

Liana and co-occurring tree species in the three sites differed in their daily course of sap flow on clear days with comparable climatic conditions. In the dry season, trees had a slight decrease (1.7% in the KF and 12.7% in the FPF) or increase (28.5% in the TSF) in daily mean sap flux density (J_s, Figs 4, 5a, S2a). By contrast, most liana species in the three sites experienced great decline in J_s in the dry season, with mean reduction up to 55.8% in the KF, 33.8% in TSF, and 22.8% in the FPF (Figs 4, 5a, S2a).

Consequently, compared with the wet season, the daily water consumption decreased consistently in the three sites for lianas in the dry season (decreased by 40.1% in the KF, 32.8% in the TSF, and 23.5% in the FPF; Figs 5b, S2b; Table S1). By contrast, trees consumed comparable water in the dry season and in the wet season in the KF and TSF sites (Figs 5b, S2b).

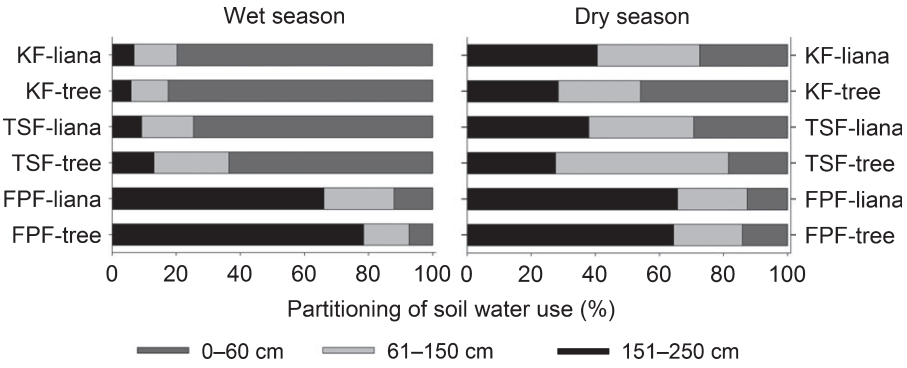

Fig. 2 Partitioning of soil water use for liana and tree species in the karst forest (KF), tropical seasonal forest (TSF), and flood plain forest (FPF) during the dry and wet seasons. Values are averages of lianas and trees in each of the three sites and seasons.

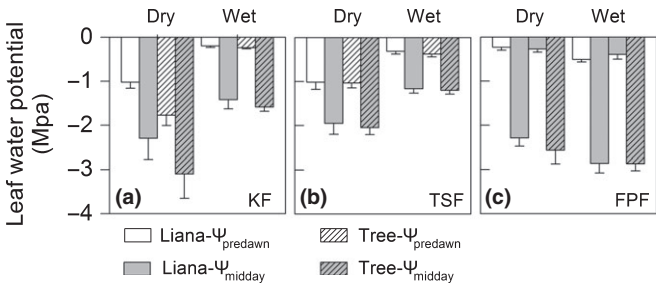

Fig. 3 Seasonal change in predawn ($\Psi_{predawn}$) and midday (Ψ_{midday}) leaf water potentials for liana and tree species in the karst forest (KF, a), tropical seasonal forest (TSF, b), and the flood plain forest (FPF, c). Values are means ± standard error (SE).

Table 1 Two-way ANOVA showing the effects of growth form (liana vs tree), season (wet vs dry), and the growth form × season interaction on photosynthesis, water status, and daily mean sap flux density in the karst forest (KF), tropical seasonal forest (TSF), and flood plain forest (FPF) in Xishuangbanna, southern China

Site	Variable	P_{max}	g_s	$\Psi_{predawn}$	Ψ_{midday}	Mean J_s
KF	Growth form	**0.000**	**0.000**	**0.005**	0.164	**0.009**
	Season	**0.000**	**0.000**	**0.000**	**0.001**	**0.001**
	Growth form × season	0.689	**0.026**	**0.011**	0.347	**0.002**
TSF	Growth form	**0.000**	0.398	0.338	0.269	**0.000**
	Season	**0.000**	**0.000**	**0.000**	**0.000**	0.147
	Growth form × season	0.183	0.203	0.721	0.38	**0.007**
FPF	Growth form	0.958	0.712	0.617	0.52	**0.000**
	Season	0.107	0.127	**0.018**	0.065	0.117
	Growth form × season	0.586	0.479	0.316	0.543	0.362

P_{max}, maximum photosynthetic rate; g_s, leaf stomatal conductance; $\Psi_{predawn}$, predawn leaf water potential; Ψ_{midday}, midday leaf water potential; Mean J_s, daily mean sap flux density. Bold values indicate significant differences, $P < 0.05$.

Seasonal changes in physiological parameters

In general, liana and tree species had higher P_{max} and g_s values in the wet season for all of the sites (Fig. 5c,d; Tables 1, S2). In addition, lianas had a smaller proportional decline in P_{max} and g_s than trees from the wet to the dry season (Fig. S2c,d). Lianas also had significantly higher mean P_{max} and g_s values than tree species in the KF and TSF sites in both seasons, while this difference was not significant for the FPF site (Fig. 5c,d; Tables 1, S2).

The regulation of whole-plant water use in response to VPDs

The relationship between J_s and VPDs was similar among the three sites both in the wet (Fig. 6a–c) and dry seasons (Fig. 6a′–c′). Both lianas and trees showed faster increase in J_s with VPDs in the wet season than in the dry season. The J_s of lianas increased more rapidly than that of tree species at a lower VPD (< 1 kPa) and maintained a constant high level at a higher VPD. By contrast, the J_s of tree species continuously increased with increasing VPDs but remained at much lower rates than that in lianas.

Discussion

Lianas used a higher ratio of deep layer soil water and maintained better water status and photosynthesis activity than trees in forests with seasonal soil water deficit

Higher predawn leaf water potential in the dry season (particularly in the karst forest, Fig. 1b) supported the hypothesis that lianas were able to access deep sources of soil moisture, presumably because they have a particularly deep root system (Schnitzer, 2005). Cao (2000) also observed that deep-rooting *Dipterocarpus* saplings in a Bornean tropical heath forest well maintained leaf water status, high photosynthesis, and stomatal conductance during severe drought. In the present study, both lianas and trees in the dry season switched to uptake water from deep soil layers in forests with SSWDs. However, lianas were able to utilize a higher proportion of deep soil water than co-occurring trees (Fig. 2). More access to deep soil water may explain why lianas presented lesser declines in P_{max} and g_s.

Better water status and higher photosynthesis activity may potentially favor the persistence of lianas during the dry season. Using data from 69 tropical forests worldwide, as well as sites across the Isthmus of Panama, Schnitzer (2005) first proposed the dry season growth advantage hypothesis based on the observation that lianas grew nearly seven times as much as trees during the dry season but only twice as much during the wet season. Cai

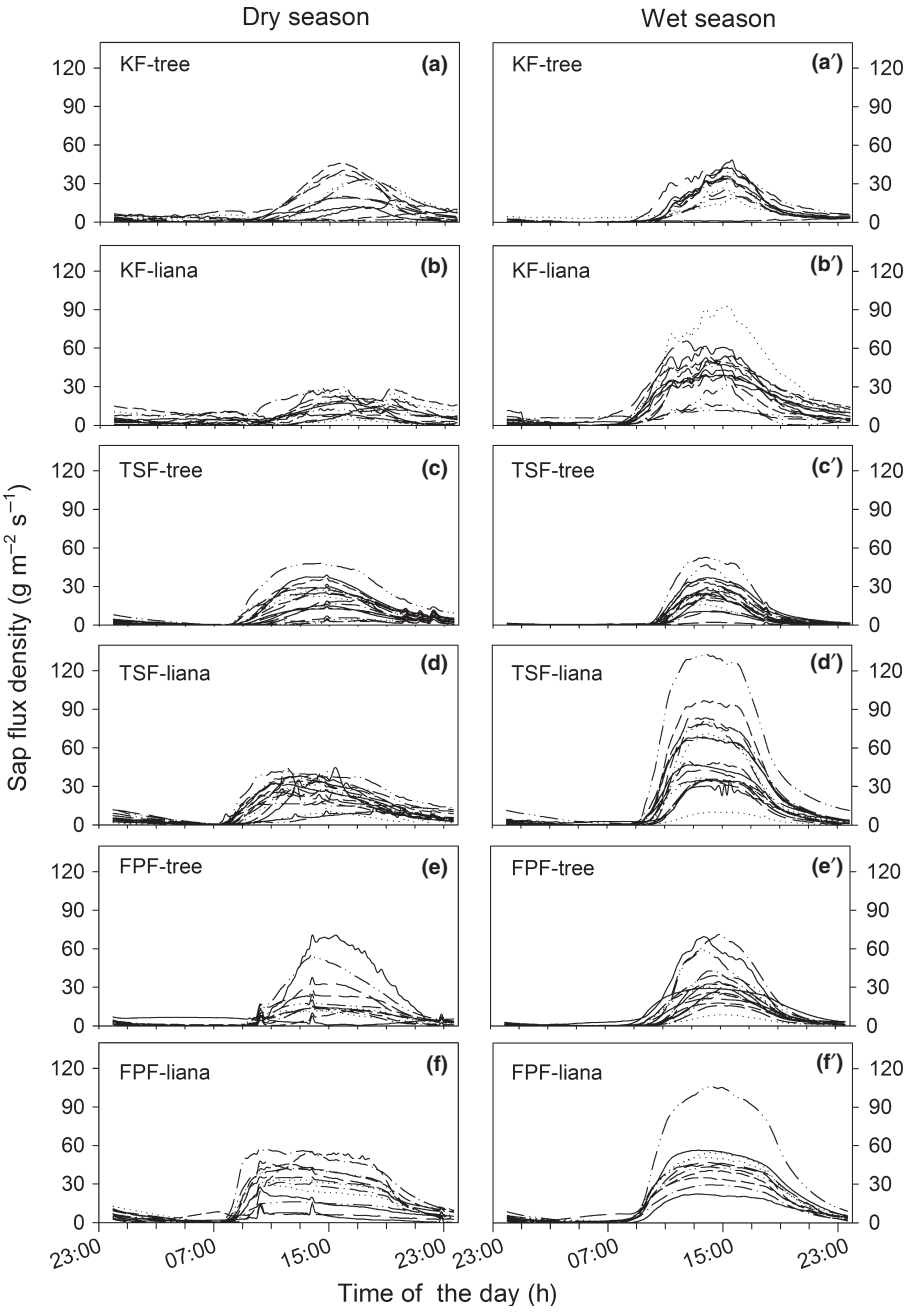

Fig. 4 Diurnal courses of sap flux density for liana and tree species in the karst forest (KF), tropical seasonal forest (TSF), and flood plain forest (FPF) in the dry (a–f) and wet (a′–f′) seasons. Values are averages of 5–10 representative clear days for each individual.

et al. (2009) further supported the dry season growth advantage hypothesis by reporting that lianas had a significantly smaller seasonal variation in leaf-level photosynthesis than trees in a tropical seasonal forest. Our findings, which are based on a large sample size from three forests, confirmed that lianas experienced a lower decline in P_{max} and g_s in the dry season (Figs 5, S2). The higher dry season photosynthetic capacity may potentially allow lianas to fix more carbon during the dry season. According to Schnitzer (2005), the additional 3–4 months of relatively better growth could give lianas an advantage in tropical forests with seasonal drought and may explain why liana abundance tends to peak in forests with relatively low average rainfall and high seasonality (DeWalt *et al.*, 2010).

Strong stomatal control may prevent lianas from excessive dehydration

Our sap flow measurements showed that lianas had a stronger stomatal control than trees, which could reduce water loss and maintain better leaf water status under extreme water deficit (in karst forest). The nonlinear increase in J_s with increasing VPDs was attributed to the closure of stomata (Meinzer, 1993; Monteith, 1995; Oren *et al.*, 1999; Pataki *et al.*, 2000), which appears to be an adaptation to avoid excessive dehydration. Lianas could access light and start carbon fixation earlier in the morning, when the VPD was low, and then rapidly close their stomata later in the day, when the VPD was high. Lianas were able to reach

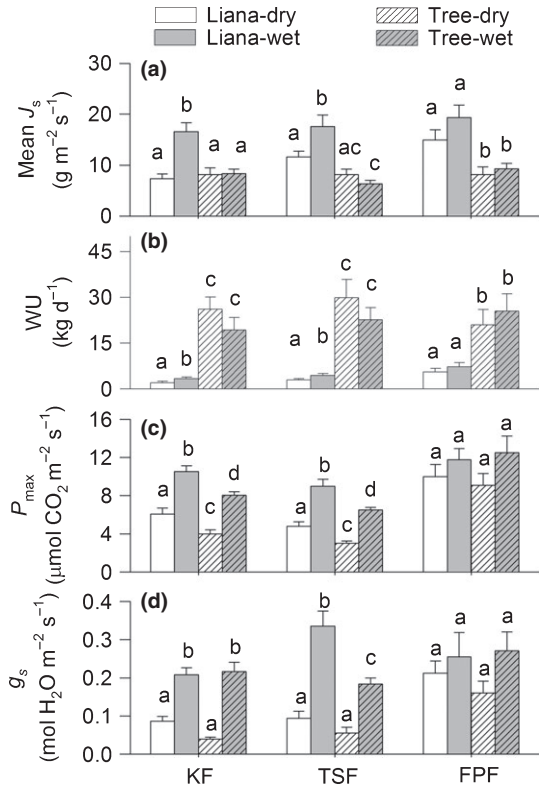

Fig. 5 Mean sap flux density (J_s, a), water use per day (WU, b), maximum photosynthetic rate (P_{max}, c) and stomatal conductance (g_s, d) for liana and tree species in the karst forest (KF), tropical seasonal forest (TSF) and flood plain forest (FPF) during the dry and wet seasons. Values are means ± standard error (SE). Different letters represent significant differences at $P < 0.05$.

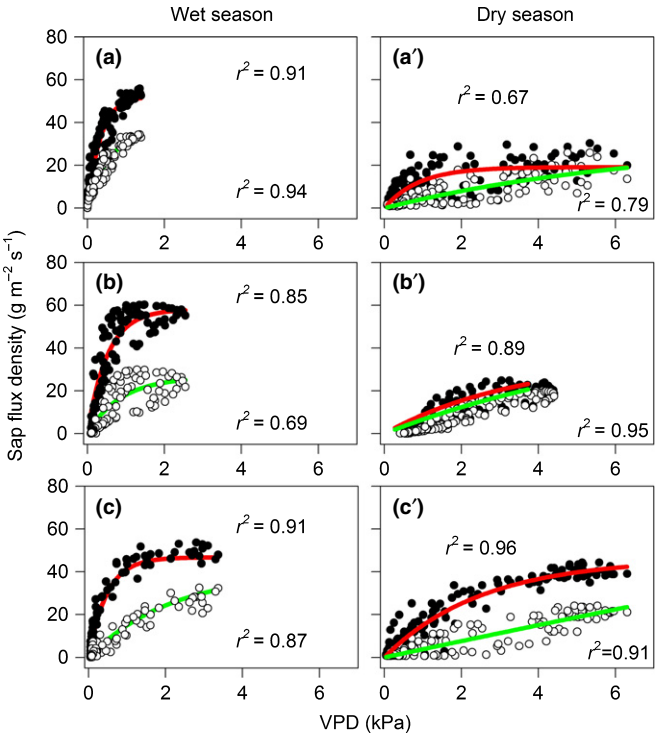

Fig. 6 The relationship between sap flux density (J_s) and vapor pressure deficit (VPD) for lianas (closed circles) and trees (open circles) in the karst forest (KF, a, a′), tropical seasonal forest (TSF, b, b′), and flood plain forest (FPF, c, c′). $P < 0.0001$ for all the regression lines.

maximum sap flux density earlier and had a shorter reaction time during the day than trees (Fig. 6), which allowed the lianas to photosynthesize earlier and avoid the high midday VPDs that are common above the canopies of tropical forests. The effect on daytime whole-plant water loss governed by leaf stomatal conductance was also confirmed by the observed plateau of daytime sap flow (Fig. 4), which revealed that lianas maintained steady water loss despite increases in VPD. This phenomenon has also been reported in previous studies (Fichtner & Schulze, 1990; Andrade *et al.*, 2005). The strong stomatal control of lianas is crucial for the maintenance of hydraulic function during the dry season, when soil water is relatively scarce, as it allows lianas to respond quickly to changes in ambient VPD to prevent excessive dehydration. Consequently, lianas presented a greater decline in both J_s value and daily water use to enhance their water conservation in the dry season and to reduce the risk of vessel embolism, as lianas have been reported to be more vulnerable to embolism than trees (Zhu & Cao, 2009; Sande *et al.*, 2013).

Our finding also suggested that whole-plant carbon fixation for lianas may be greatly depressed in the dry season, but maximized in the wet season, as indicated by sap flow data, representing a trade-off between active carbon assimilation and the maintenance of hydraulic safety by reducing water loss. Additionally, lianas had much higher J_s than trees in the wet season, particularly in the karst forest and tropical seasonal forest (203% and 217%, respectively, those of co-occurring trees), suggesting potentially higher carbon fixation compared with trees. Therefore, the lianas in these two forests appeared to benefit from high photosynthesis and high stomatal conductance during the wet season.

Our findings may provide an explanation for why lianas are increasing in abundance in neotropical forests. To date, 12 studies have found a pattern of increasing liana abundance or productivity relative to trees in neotropical forests (Wright *et al.*, 2004; Chave *et al.*, 2008; Ingwell *et al.*, 2010; Schnitzer & Bongers, 2011; Schnitzer *et al.*, 2012; Yorke *et al.*, 2013; Schnitzer, 2014). One of the mechanisms to explain increasing liana abundance is increasing drought and thus evapotranspirative demand in tropical areas (Schnitzer & Bongers, 2011; Schnitzer, 2014). Our data suggested that lianas are adapted to seasonal water deficit and thus the increase in drought conditions may explain increasing liana abundance in tropical forests.

Conclusion

We demonstrated that lianas utilized a higher percentage of deep soil water (151–250 cm) than trees during the dry season, which enabled the lianas to maintain a better water status during water deficits and subsequently show proportionally less decline in maximum photosynthesis during the dry season compared with trees. Moreover, in forests with deep soils and

abundant soil moisture, liana and tree species exhibited comparable P_{max}, g_s, and J_s values, with nonsignificant seasonal changes. However, in soils with seasonal water deficits, lianas were able to outperform trees in terms of physiological changes during the dry season. Strong stomatal control appeared to allow lianas to quickly respond to changing VPDs, permitting lianas to maximize their carbon fixation with less water loss than trees. Additionally, rapid downregulation of stomatal conductance may allow lianas to reduce their water consumption and avoid excessive water loss when the soil water level is low. Our findings supported the dry season growth advantage hypothesis proposed by Schnitzer (2005) which asserts that access to deep soil water and strong physiological adjustments may explain the higher abundance of lianas in seasonally dry forests. However, we also provide evidence that lianas in forests with seasonal water deficits appear to gain advantages over trees due to high rates of photosynthesis and high stomatal conductance during the wet season.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Partitioning of soil water use for liana and tree species during the wet and dry seasons in the karst forest (KF), tropical seasonal forest (TSF), and flood plain forest (FPF).

Fig. S2 Ratio of seasonal changes in daily water use (J_s and WU) and photosynthetic parameters (P_{max} and g_s) for liana and tree species in the three sites.

Table S1 Species, family, leaf habit, DBH, sapwood area, and daily water consumption for the 99 individuals in this study

Table S2 Maximum photosynthetic rate (P_{max}), leaf stomatal conductance (g_s), and predawn ($\Psi_{predawn}$) and midday (Ψ_{midday}) leaf water potentials in the wet and dry seasons in the karst forest (KF), tropical seasonal forest (TSF), and flood plain forest (FPF)

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