



Research paper

Time lags between crown and basal sap flows in tropical lianas and co-occurring trees

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Water storage in the stems of woody plants contributes to their responses to short-term water shortages. To estimate the contribution of water storage to the daily water budget of trees, time lags of sap flow between different positions of trunk are used as a proxy of stem water storage. In lianas, another large group of woody species, it has rarely been studied whether stored water functions in their daily water use, despite their increasing roles in the carbon and water dynamics of tropical forests caused by their increasing abundance. We hypothesized that lianas would exhibit large time lags due to their extremely long stems, wide vessels and large volume of parenchyma in the stem. We examined time lags in sap flow, diel changes of stem volumetric water content (VWC) and biophysical properties of sapwood of 19 lianas and 26 co-occurring trees from 27 species in 4 forests (karst, tropical seasonal, flood plain and savanna) during a wet season. The plants varied in height/length from <5 to >60 m. The results showed that lianas had significantly higher saturated water content (SWC) and much lower wood density than trees. Seven of 19 liana individuals had no time lags; in contrast, only 3 of 26 tree individuals had no time lags. In general, lianas had shorter time lags than trees in our data set, but this difference was not significant for our most conservative analyses. Across trees and lianas, time lag duration increased with diurnal maximum changeable VWC but was independent of the body size, path length, wood density and SWC. The results suggest that in most lianas, internal stem water storage contributes little to daily water budget, while trees may rely more on stored water in the stem.

Keywords: frequency domain reflectometry, hydraulic capacitance, transpiration, volumetric water content, water relations, water storage.

Introduction

The function of water storage in the water budget of woody plants is increasingly being unraveled for trees in tropical (Goldstein et al. 1998, Meinzer et al. 2004, Scholz et al. 2007), subtropical (Carrasco et al. 2013, 2015) and temperate (Phillips et al. 2003, Čermák et al. 2007, Kumagai et al. 2009, Turcotte et al. 2011, Köcher et al. 2013) areas. Water storage is an important adaptation for plants to survive dry periods (Chapotin et al. 2006a, Scholz et al. 2007, 2008) and can

serve as a transient water source for daily transpiration, even in well-watered habitats (Goldstein et al. 1998). In woody plants, water released from all water reservoirs (roots, stems, branches and leaves, including different living tissues such as pith, parenchyma and ray cells) can replace the water that is lost by transpiration, thereby buffering the increasing xylem tension induced by transpiration (Zimmermann 1983, Holbrook 1995, Scholz et al. 2011). However, water storage capacity is variable across plants, and its relative contribution to total transpiration may vary

considerably among species and within species between seasons. The internal stored water can contribute to 10–50% of the daily water consumption among species from different ecosystems (Goldstein et al. 1998, Phillips et al. 2003, Meinzer et al. 2004, Čermák et al. 2007, Scholz et al. 2008, Köcher et al. 2013, Carrasco et al. 2015).

Tall trees often experience increased water stress in the canopy due to increased path length-dependent friction and gravity (Ryan and Yoder 1997, Koch et al. 2004, Ryan et al. 2006, Domec et al. 2008). For some tall trees, utilization of released water from stored compartments near the canopy may play an important role in mitigating the water stress of canopy leaves, thereby maintaining the stomata opening for photosynthesis (Scholz et al. 2011). Several studies showed that the utilization of stored water will cause significant time lags in flow between the basal stem and branches because of capacitance. Kumagai et al. (2009), for instance, reported apparent time lags among three height positions and that the higher positions initiated flow earlier than the lower positions. Therefore, sap flow measured in the basal stem may, therefore, represent water uptake rate from the soil rather than actual canopy transpiration. Furthermore, direct estimation of canopy transpiration based on basal stem sap flow measurement without correction may cause large errors if time lags are present between the basal and upper stem sap flows.

Comparison of the timing of sap flow in basal stem and branches of trees is widely used to estimate the contribution of internal water storage to daily water transpiration (Phillips et al. 1997, 2003, Goldstein et al. 1998, Meinzer et al. 2004, Chapotin et al. 2006a, Čermák et al. 2007, Scholz et al. 2007, Kumagai et al. 2009, Köcher et al. 2013, Carrasco et al. 2015). Time lag durations may be closely related to stem water storage (Köcher et al. 2013) and scale with the size or height of trees; larger trees are assumed to have higher water storage capacity than smaller ones (Goldstein et al. 1998, Phillips et al. 2003). Time lags of up to 90–120 min between canopy transpiration and basal sap flow showed an increase with height (Goldstein et al. 1998, Phillips et al. 1999, Scholz et al. 2008, 2011, Kumagai et al. 2009, Köcher et al. 2013). However, for some trees, such as 12-year-old *Pinus taeda* with an average height of 7 m, the time lag is only 30 min (Phillips et al. 1997). Contrary to these studies, no significant time lags were found in four 50-m-tall emergent trees in Bornean tropical rainforest (Kume et al. 2008) and two baobab trees (15–25 m in height and 1–2.3 m in diameter) in western Madagascar (Chapotin et al. 2006c).

Lianas comprise 25% of the woody species composition in tropical forests (Schnitzer and Bongers 2002) and are increasing in abundance (Schnitzer and Bongers 2011). They typically have long and slim stems and cannot support themselves (Schnitzer and Bongers 2002). Free from the mechanical demands of freestanding species (trees or shrubs), the stems of lianas can grow up to hundreds of meters in length before reaching the top of the canopy (Putz 1984). The relatively low

mechanical investments of lianas leads to the development of wide and long vessels and a high volume of parenchyma in mature lianas (Isnard and Silk 2009). Therefore, lianas are often considered to be extremely efficient in water transport (Ewers et al. 1989, Gartner 1991, Chiu and Ewers 1992, Isnard and Silk 2009, Zhu and Cao 2009, Angyalossy et al. 2012, van der Sande et al. 2013). However, this high transporting efficiency that results from wide and long vessels may trade off against hydraulic safety and may increase vulnerability to cavitation compared with co-occurring trees (Zhu and Cao 2009, Johnson et al. 2013, van der Sande et al. 2013). Because of their length, lianas may experience larger hydrostatic gradients and path lengths in their stems than co-occurring trees, imposed by the substantial distal resistance to water flow when xylem water ascends up to the canopy. It is likely that transpiration-induced water loss in lianas may exceed the water supply from the roots in the afternoon when all leaves are exposed under high vapor pressure deficit (VPD) and strong sunlight. Under such circumstances, lianas may face a great threat of cavitation caused by air seeding when the xylem tension reaches a critical threshold (Scholz et al. 2011). Despite such a disadvantage, lianas successfully occupy the upper canopy in many tropical forests. It remains unresolved how canopy lianas maintain continuity of the water flow in the xylem. In a recent study, we found that strong stomatal control played an important role in the daily water budget of lianas (Chen et al. 2015). Whether stored water in liana stems buffers the daily water use, as in trees, is not clear yet. Until now, few studies have investigated the role of water storage in the water relations of lianas and how these differ from trees (Phillips et al. 1999, Andrade et al. 2005).

In the present study, we examined water use for transpiration of lianas and co-occurring trees in four forests during a wet season. Sap flow measurements were conducted in the basal and upper stem (near the crown) for both lianas and trees. The time lags between the two points were calculated using a cross-correlation analysis (Phillips et al. 1999). We assume time lags in sap flow indicate the use of water storage in the stem for transpiration; the longer the time lag, the more important the stem water storage. Additionally, we monitored the changes in stem volumetric water content (VWC) using a frequency domain reflectometry (FDR) that has proved to be an effective indicator with high precision and high time resolution to evaluate withdrawal and recharge of internal stem water (Carrasco et al. 2013, 2015, Hao et al. 2013). We related these measurements to stem anatomy and vessel characteristics. We specifically asked: (i) do lianas use stored water in daily transpiration? (ii) If so, what factors affect the duration of time lags? (iii) Does stored water use contribute equally to transpiration for lianas and trees? We hypothesized that lianas use more water from storage for transpiration than trees, because they possess stem biophysical properties that support greater water storage. Specifically, we predicted that time lags in morning sap flow between upper and

lower stems would be greater for lianas than trees because lianas support early morning sap flow in the upper canopy from stored reserves in stems. Further, we predicted that these greater time lags in lianas would be related to lower stem wood density and greater stem water content that together support greater stem water storage than found in co-occurring trees.

Materials and methods

Site description and plant species

We selected three tropical forest sites in Xishuangbanna and one savanna forest (SF) site in Yuanjiang, southwest China. The four sites differed in soil water availability during the dry season. Xishuangbanna has a typical tropical monsoon climate and a pronounced dry season from November to April. The mean annual precipitation is ~1560 mm, nearly 80% of which occurs during the wet season from May to October. The mean annual temperature is 21.7 °C with 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 established a 30 × 50 m study plot in each forest, namely, in a tropical seasonal forest (TSF), karst forest (KF), flood plain forest (FPF) and SF. The TSF plot was in a nature reserve [21°57'41"N, 101°12'0"E, 790 m above sea level (a.s.l.)] located ~8 km from the Xishuangbanna Tropical Botanical Garden (XTBG). This site had lateritic soil developed from siliceous rocks and was dominated by the trees *Pometia tomentosa* (Bl.) Teysm. et Binn. and *Terminalia myriocarpa* Van Heurck & Mull. Arg. (Zhang and Cao 1995). The KF plot was located in an old-growth tropical KF (21°54'39"N, 101°16'57"E, 720 m a.s.l.) at ~3 km from the XTBG. The KF plot has a brown calcareous soil with a coarse texture and a pH of ~7.3. Soil in the KF becomes extremely dry during the dry season (less than -3 MPa in the dry season above a depth of 100 cm, personal observation). The FPF plot was located in a primary flood plain seasonal forest at XTBG (21°55'52"N, 101°15'12"E, 580 m a.s.l.), which has fecund soils and a shallow water table. The SF site was in a valley of the Yuanjiang River, 10 km south of Yuanjiang City (23°27'56"N, 102°10'40" E, 481 m a.s.l.) and ~300 km north to the other three sites. According to a weather station near the plot (data from 2012 to 2013), the mean annual temperature at the site was 24.9 °C. April to June were the hottest months with a maximum air temperature of up to 42 °C. The average rainfall was ~666.4 mm. Most rainfall occurred between May and October. The soil is a typical US torrox, with a pH of 6.1 (Zhang et al. 2007). The vegetation was dominated by *Lannea coromandelica* (Houtt.) Merr., *Bauhinia brachycarpa* Wall., *Vitex negundo* Linn. and *Diospyros yunnanensis* Rehd. et Wils. (species information based on a census of a 1-ha permanent plot ~100 m from the study site).

A total of 45 individuals representing 27 species from 19 families were selected for study, of which 19 individuals were lianas and 26 individuals were trees. All targeted lianas were mature individuals with a diameter (1.3 m from the base) ranging

between 5.4 and 14.7 cm, all reaching the forest canopy. The height of the co-occurring trees varied greatly among the sites, from <5 m in the SF to nearly 40 m in the TSF (see detailed information in Table 1).

Meteorological measurements

We used meteorological data, including photosynthetic photon flux density (PPFD), air temperature, relative humidity and soil water moisture at a 10 cm depth from a weather station located in XTBG that was ~1 km from KF and FPF plots and from another weather station on a 70-m-tall tower located 100 m away from the TSF plot. In the SF plot, a meteorological tower was located at ~100 m from the study plot. All climatic variables were recorded at 30-min intervals.

Sap flow and stem VWC measurement

Sap flow was measured using self-made Granier (1987) type thermal dissipation probe (TDP) sensors (20 mm in length and 2 mm in diameter with two probes). The TDP sensors contained a 0.2-W heater and a reference probe 15 cm apart. The temperature difference between the heater and reference probes was recorded and converted to sap flux density (J_s , g m⁻² s⁻¹) according to the formula described by Granier (1987). For each individual, we monitored J_s in the wet season (from August to October 2013) and selected clear days for time lag estimation.

In the Xishuangbanna sites, two pairs of sensors were installed at the top of the main stem (~10 cm below the first main canopy branch) at a 90° angle for each individual. The upper stem sensors were installed with the aid of mechanical rope ascender systems. The basal sensors were installed at breast height (~1.3 m). The distance between the basal and upper stem sensors ranged from <10 m to almost 30 m for both lianas and trees. At the SF site, the heights of selected trees were 6–8 m and the lengths of lianas were 10–12 m. All basal sensors in this site were installed at a height of 20 cm from the base. The distance between the basal and upper sensors ranged from 2 to 5 m.

During the same period, we monitored the stem VWC (m³ m⁻³; see Figure 4) of nine individuals at the height where the sap flow sensors were installed using the FDR method (model GS3, Decagon Devices, Pullman, WA, USA). Each FDR sensor consisted of three 3.2-mm-diameter stainless steel probes that were 55 mm in length. Three parallel holes (5.5 mm in depth, 3.2 mm in diameter and 25 mm apart) were drilled in selected individuals. The FDR sensors were inserted completely into the drilled holes and covered with reflective aluminum plastic to prevent rainfall infiltration and heating by direct sunlight.

Data from sap flow and FDR sensors were scanned every 10 s and recorded every 10 min using a CR1000 data logger connected via an AM16/32 type multiplexer (Campbell Scientific, Logan, UT, USA). Stem maximum Δ VWC was defined as the difference between the maximum and minimum VWC value during a day.

Table 1. Information on the species used in this study. A total of 45 individuals (19 lianas and 26 trees) of 27 species from 19 families and 10 orders were studied. TSF: four lianas and eight trees; KF: six lianas and nine trees; FPF: six lianas and five trees; SF: three lianas and four trees. Time lags were calculated using a cross-correlation analysis (Phillips et al. 1999) between basal and upper stem sap flux density. ΔH , the distance between basal and upper sensors; R_{\max} , maximum correlation coefficient; SWC, sapwood saturated water content; ρ , sapwood density; ΔVWC , maximum changeable volumetric water content; –, no data.

Site	Order	Family	Species	Growth type	No.	Height/length (m) ¹	DBH (cm)	ΔH (m)	Ave. time lag (min)	Number of days measured	R_{\max}	SWC	ρ (g cm ⁻³)	ΔVWC (m ³ m ⁻³)
TSF	Fagales	Fagaceae	<i>Castanopsis indica</i>	Tree	1	22.5	36.3	8.4	12.0	20	0.99	46.22	0.71	–
	Ericales	Lecythidaceae	<i>Barringtonia fuscarpa</i>	Tree	1	19.5	35.7	10.9	9.5	20	0.98	53.34	0.59	0.017
				Tree	2	17.5	31.3	10.5	2.0	20	0.98	53.57	0.59	–
				Tree	3	21.5	36.1	10.5	0.5	20	0.99	50.99	0.62	–
	Sapindales	Sapindaceae	<i>P. tomentosa</i>	Tree	1	31.6	39.3	17.5	6.0	20	0.96	45.41	0.72	–
				Tree	2	39.5	74.8	18.5	7.5	4	0.97	44.04	0.74	–
				Tree	3	38.2	83.1	15.4	13.5	17	0.97	47.64	0.68	–
	Rosales	Ulmaceae	<i>Aphananthe cuspidata</i>	Tree	1	18.2	34.9	10.9	11.5	20	0.99	43.34	0.72	–
	Gentianales	Loganiaceae	<i>Strychnos wallichiana</i>	Liana	1	62.5	10.2	24.2	8.4	19	0.98	65.00	0.41	0.034
	Celastrales	Hippocrateaceae	<i>P. arborea</i>	Liana	1	33.4	7.7	28.5	38.0	20	0.97	71.36	0.33	–
<i>Combretum latifolium</i>			Liana	1	46.5	5.4	19.8	4.0	20	0.99	64.59	0.38	–	
Magnoliales	Annonaceae	<i>Artabotrys hongkongensis</i>	Liana	1	54.8	7.6	28.4	0.0	20	0.99	68.18	0.33	0.008	
Sapindales	Burseraceae	<i>Garuga floribunda</i>	Tree	1	28.5	45.2	13.5	33.3	18	0.94	53.15	0.58	0.02	
			Tree	2	22.5	53.8	8.7	23.9	18	0.99	59.90	0.49	0.03	
			Tree	1	39.8	60.8	23.5	0.0	18	0.93	43.42	0.75	0.006	
Magnoliales	Annonaceae	<i>Pseuduvaria indoehinensis</i>	Tree	1	29.5	38.7	13.1	1.1	18	0.99	39.57	0.80	–	
Myrtales	Lythraceae	<i>Lagerstroemia tomentosa</i>	Tree	1	23.6	30.6	9.5	14.6	13	0.96	48.87	0.66	–	
			Tree	2	34.8	66.9	9.8	21.1	18	0.97	47.45	0.68	0.05	
			Tree	3	36.5	63.1	13.6	11.7	18	0.98	49.50	0.64	–	
			Tree	4	26.3	72.0	11.8	6.2	16	0.99	49.66	0.65	–	
Rosales	Ulmaceae	<i>Celtis wightii</i>	Tree	1	17.8	22.3	5.3	7.2	18	0.99	39.72	0.81	–	
Fabales	Leguminosae	<i>Acacia pennata</i>	Liana	1	54.8	8.6	15.6	2.9	14	0.99	62.24	0.45	–	
			Liana	2	46.4	13.5	6.7	0.0	18	0.90	61.08	0.44	–	
			Liana	3	43.6	8.6	13.5	0.0	18	0.97	58.87	0.49	–	
			Liana	4	56.5	5.7	22.5	1.4	14	0.99	69.91	0.44	–	
			Liana	5	52.5	6.7	17.8	0.8	13	0.99	61.06	0.38	–	
Myrtales	Combretaceae	<i>Combretum latifolium</i>	Liana	1	35.6	10.5	6.5	0.0	18	0.99	48.02	0.66	–	

FPF	Magnoliales	Annonaceae	<i>Polyalthia cheliensis</i>	Tree	1	22.6	49.0	13.2	23.9	18	0.96	49.57	0.63	–
	Malpighiales	Euphorbiaceae	<i>Bischofia polycarpa</i>	Tree	1	21.4	38.1	9.5	31.1	18	0.97	49.62	0.66	–
	Fabales	Leguminosae	<i>Albizia lucidior</i>	Tree	1	32.5	49.5	14.4	1.8	17	0.97	52.30	0.60	–
	Sapindales	Meliaceae	<i>Melia toosendan</i>	Tree	1	28.6	43.8	12.6	0.6	18	0.97	56.53	0.50	–
	Rosales	Moraceae	<i>Streblus asper</i>	Tree	1	14.8	37.0	8.8	0.7	14	0.99	53.58	0.59	–
	Gentianales	Apocynaceae	<i>M. sinensis</i>	Liana	1	34.7	5.8	8.5	10.0	5	0.99	69.18	0.35	–
	Celastrales	Celastraceae	<i>Celastrus paniculatus</i>	Liana	1	40.2	13.8	12.4	1.1	18	0.99	55.50	0.54	–
	Fabales	Leguminosae	<i>Mucuna interrupta</i>	Liana	1	33.8	9.5	14.5	4.4	18	0.99	69.18	0.35	–
	Rosales	Rhamnaceae	<i>Ventilago calyculata</i>	Liana	1	38.5	8.1	18.5	0.0	18	0.96	53.24	0.60	–
					2	38.8	14.7	20.2	1.1	18	0.98	53.66	0.50	–
					3	36.8	12.2	17.6	0.0	18	0.96	48.15	0.59	–
SF	Sapindales	Anacardiaceae	<i>L. coromandelica</i>	Tree	1	4.3	22.6	2.9	11.0	10	0.96	50.55	0.56	0.017
					2	7.8	31.7	5.3	0.0	10	0.98	53.28	0.52	–
					3	8.1	38.6	4.9	0.0	10	0.99	51.52	0.57	–
	Gentianales	Rubiaceae	<i>Haldina cordifolia</i>	Tree	1	7.2	24.8	4.9	14.0	10	0.95	46.28	0.61	–
	Vitales	Vitaceae	<i>Vitis species</i>	Liana	1	10.8	6.5	5.5	0.0	10	0.96	76.48	0.27	0.01
					2	8.55	6.9	3.1	1.0	10	0.97	75.17	0.26	–
					3	8.5	8.9	4.2	2.0	10	0.98	73.81	0.28	–

¹For authorities consult the tropicos data base (<http://www.tropicos.org>).

For liana individuals, the value represents the length of each individual and for trees, the total height of the trees.

Sapwood biophysical properties

Stem sapwood cylinders of each individual were obtained with a 5-mm-diameter increment borer at a similar height as the basal sap flow sensors and kept in sealed bags for transport to the laboratory. The volume of each sample (V , cm^3) was determined using the water displacement method (Scholz et al. 2007). Then, all samples were rehydrated in distilled water for ~24 h to reach saturation, and saturated weight (SW) was determined. All samples were then oven-dried to constant weight (48 h at 80 °C), and dry weight (DW) was determined. The wood density (ρ , g cm^{-3}) and saturated water storage [saturated water content (SWC), g g^{-1}] were calculated as follows:

$$\text{SWC (\%)} = \frac{\text{SW} - \text{DW}}{\text{SW}} \times 100,$$

$$\rho = \frac{\text{DW}}{V}$$

Data analysis

We assessed the time lags and the maximum correlation coefficient (R_{max}) between basal and upper stem sap flows using a cross-correlation analysis (Phillips et al. 1999), which is useful for determining the time delay between two signals, e.g., the initiation of sap flux in plants on different positions. By calculating the cross-correlation of the two sap flow data sets between basal and upper positions, the maximum correlation coefficient indicates the point in time at which the two data sets are best aligned. Clear days (from August to October 2013) were selected from the measurement periods, and the time lags of sap flow between upper and basal locations for each individual were calculated for each day. Our cross-correlation estimates of time lag were only approximate because the raw data had only been recorded every 10 min. Therefore, to improve this estimation, we measured the cross-correlations for multiple days for each individual and then averaged the calculated time lag values across the days. Between 4 and 20 clear days were available for each individual plant (Table 1).

To formally test whether sap flow time lags differ between lianas and trees, we log-transformed the sap flow time lag data using the transform $\ln(x + 0.2)$, which accommodated the zero time lags and normalized the data. We modeled the transformed time lag data using a linear mixed model, using the lmer() function of lme4 in R (Bates et al. 2015). As we were specifically interested in whether time lags differed between trees and lianas, we included Growth Type (tree or liana) as our fixed effect. We included sampling site (Site) as a random effect in our model.

The individual species were sampled with different replication within the plots, and replication for all species was very low. So, we did not have sufficient replication to estimate variances for individual species or even for families. However, we were concerned that the uneven replication between species might be biasing the result. Therefore, we ran two separate regression analyses, one with all 45 individual records (hereafter 'full data set') and one with a data subset of 27 sampling units consisting

of one individual per species per site (there were 26 species but one liana species was sampled at two sites, and so was included twice) selected at random from the 45 records (hereafter 'species-only data set'). We present the results of a single sampling run below. (In fact, we checked that the sample was representative of all the individuals measured by sampling the data set and deriving the regression coefficient 1000 times to ensure that our initial sample was not an outlier value located in the top or bottom 5% of possible resamplings.)

In a separate analysis, we tested whether individual stem traits explained time lag responses. We used the same linear mixed effects modeling framework with the response, sap flow time lag, modeled as a function of the fixed effects: ΔH (the distance between basal and upper sensors), diameter at breast height (DBH), SWC and ρ , with Site included as a random effect in each analysis. Once again, as the number of replicates measured per species differed, we ran the analyses using the full data set and the reduced species-only data set. Finally, we also modeled sap flow time lag as a function of ΔVWC , which had been measured on nine different species and, therefore, did not need to be subsampled.

Results

The daily patterns of PPFD and VPD were similar in the three sites in Xishuangbanna (Figure 1). Although SF had the highest PAR and VPD among the four sites on clear days, the wet season in SF tended to be cloudy and windy. Therefore, the daily PAR and VPD fluctuated, but night-time VPD was higher in SF than in the other three sites. There were several rainfall incidents during the measurement periods (TSF: 18.4 mm; KF and FPF: 30.6 mm; and SF: 49.3 mm in total; Figure 1). The soil relative humidity at a depth of 10 cm was comparable in TSF, KF and SF, but it was slightly lower in the FPF (Figure 1).

The diurnal course of basal and upper J_s showed a similar pattern for both lianas and trees. In lianas, sap flow tended to start earlier in the morning, and maximal sap flux density was maintained for a longer period than in co-occurring trees (Figure 2 and Figure S1 available as Supplementary Data at *Tree Physiology* Online). Among the four sites, 12 of 19 liana individuals showed time lags between basal and upper stem flow. These ranged from 0.8 min for *Marsdenia sinensis* #1 in FPF to 38 min for *Pristimera arborea* #1 in TSF. In contrast,

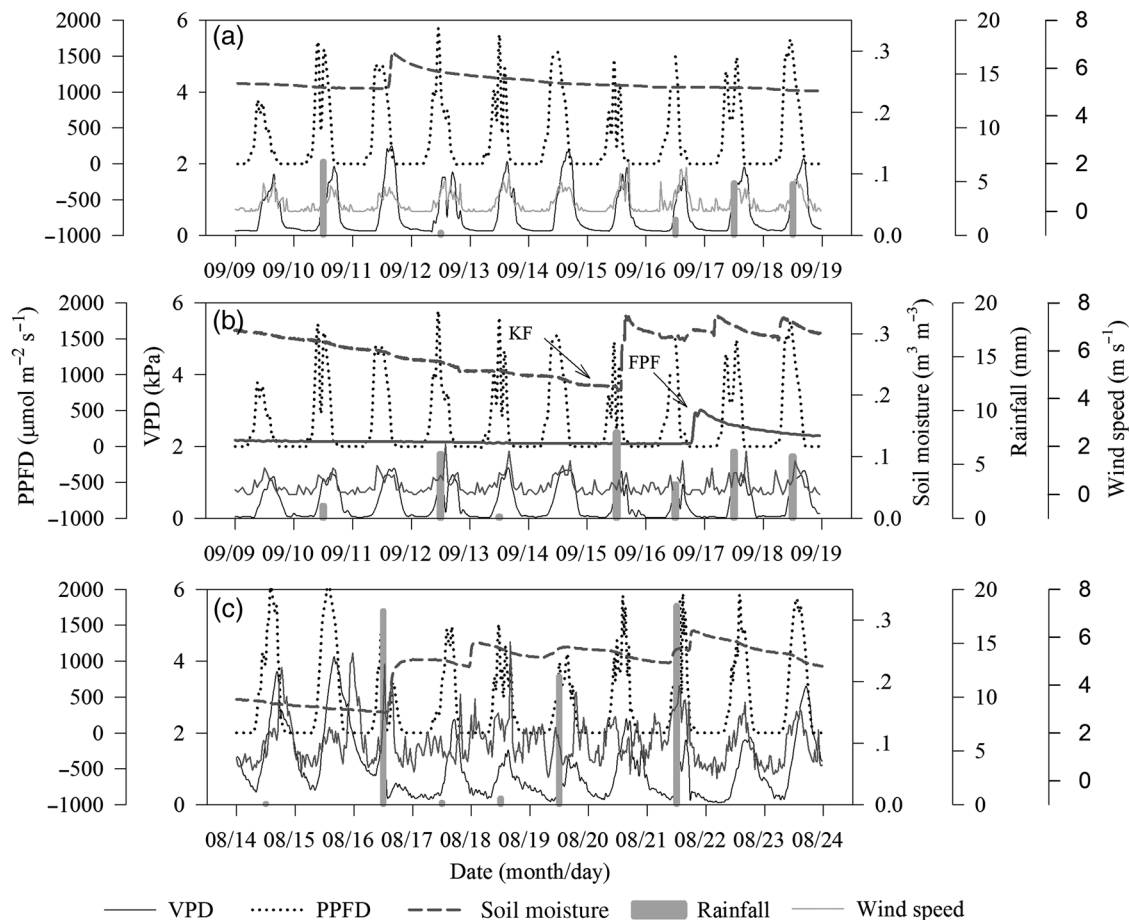


Figure 1. Diurnal PPFD, vapor pressure deficit (VPD), daily rainfall, soil moisture at a depth of 10 cm and canopy wind speed during the measuring periods in a TSF (a), KF and FPF (b), and SF (c). Note: the KF and FPF share climatic data from the same weather station.

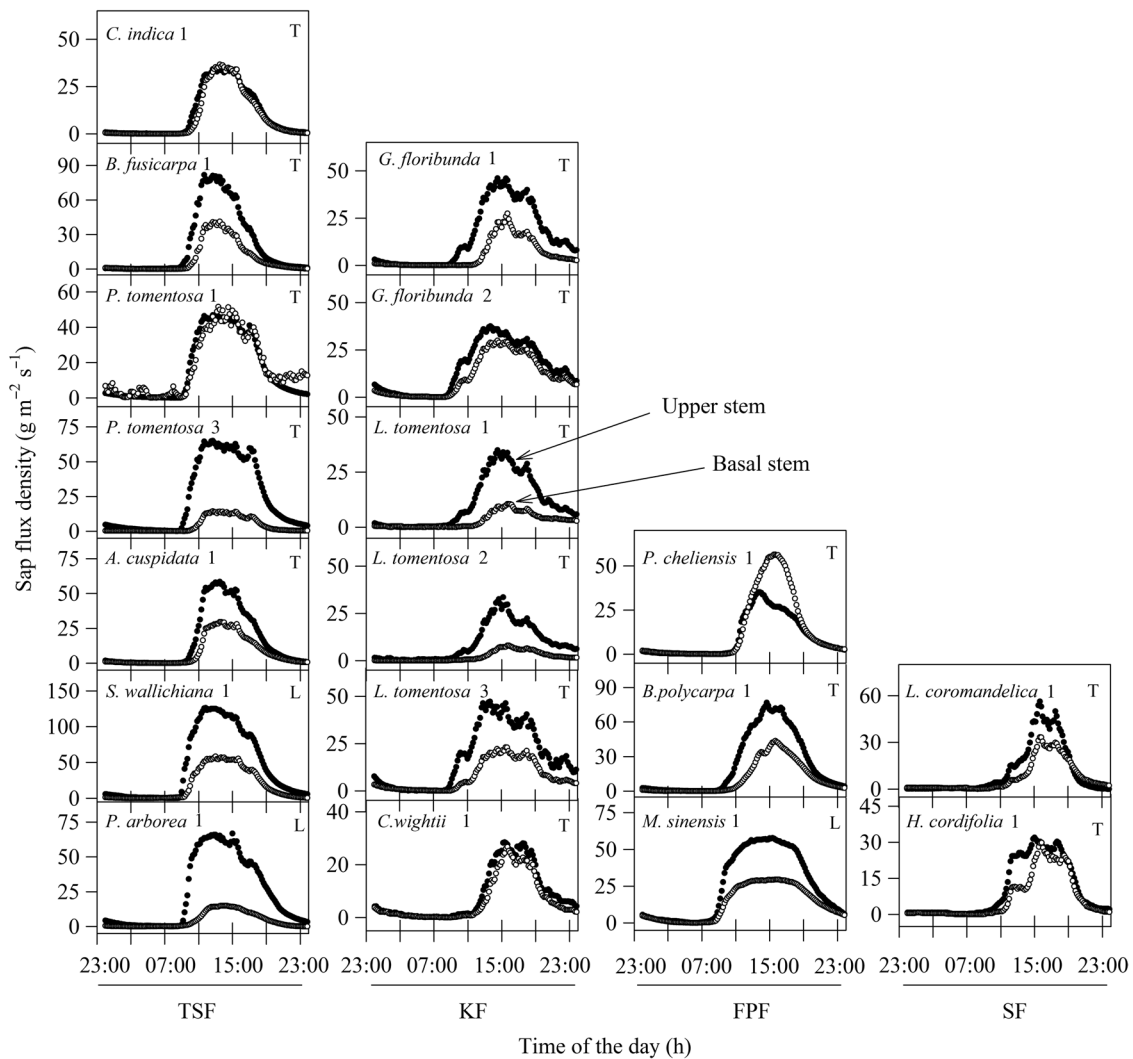


Figure 2. Diurnal course of upper (closed symbols) and basal (open symbols) stem sap flux density for liana (L) and tree (T) individuals in four sites: TSF, KF, FPF and SF. Data represent one clear day in each site, i.e., 13 September 2013 for TSF, KF and FPF, and 9 August 2013 for SF, respectively. Only those individuals with time lags in sap flow between the upper and basal stem are presented here.

23 of 26 tree individuals showed time lags, ranging from 0.5 to 33.3 min (Figures 2 and 3; Table 1). The high R_{\max} values indicate that the time lags reported are well defined. Although stem VWC varied widely among individuals, diel VWC followed the same patterns in all individuals (Figure 4). Beginning in the late afternoon, stem VWC increased and reached a peak in the next early morning (from 7:00 to 10:00) in all plants, with the exception of *A. hongkongensis* #1 in the TSF, which peaked near noon. When sap flow initiated, stem VWC decreased rapidly (Figure 4).

When we modeled sap flow time lag as a function of growth type, we obtained different results depending on the data set used. For the full data set, time lag was significantly shorter for lianas than for trees ($t = 2.855$, $df = 42$, $P < 0.01$). For the reduced species-only data set, we found no significant differences in time lag between trees and lianas ($t = 1.072$, $df = 24$).

Lianas had significantly higher SWC than trees (means \pm SE; liana: $63.7 \pm 2.6\%$, tree: $48.5 \pm 1.3\%$; $t = 5.7$, $df = 26$, $P < 0.001$) and much lower wood density (liana: $0.42 \pm 0.04 \text{ g cm}^{-3}$, tree: $0.65 \pm 0.02 \text{ g cm}^{-3}$; $t = -5.7$, $df = 26$, $P < 0.001$). However, when sap flow time lag was regressed against SWC, wood density, DBH and ΔH , only DBH has a significant positive effect on sap flow time lag, and only for the full data set ($t = 2.472$, $df = 42$, $P < 0.05$) (Figure 5) and not for the reduced species-only data set (Tables S1 and S2 available as Supplementary Data at *Tree Physiology* Online). In contrast, stem ΔVWC , which was measured only on nine individuals, had a significant positive effect on sap flow time lag ($t = 2.648$, $df = 6$, $P < 0.05$) (Figure 5e). The random effect, Site, did not explain variation in any analysis. Thus, our estimated coefficients were equivalent to those estimated using ordinary linear models on the same data.

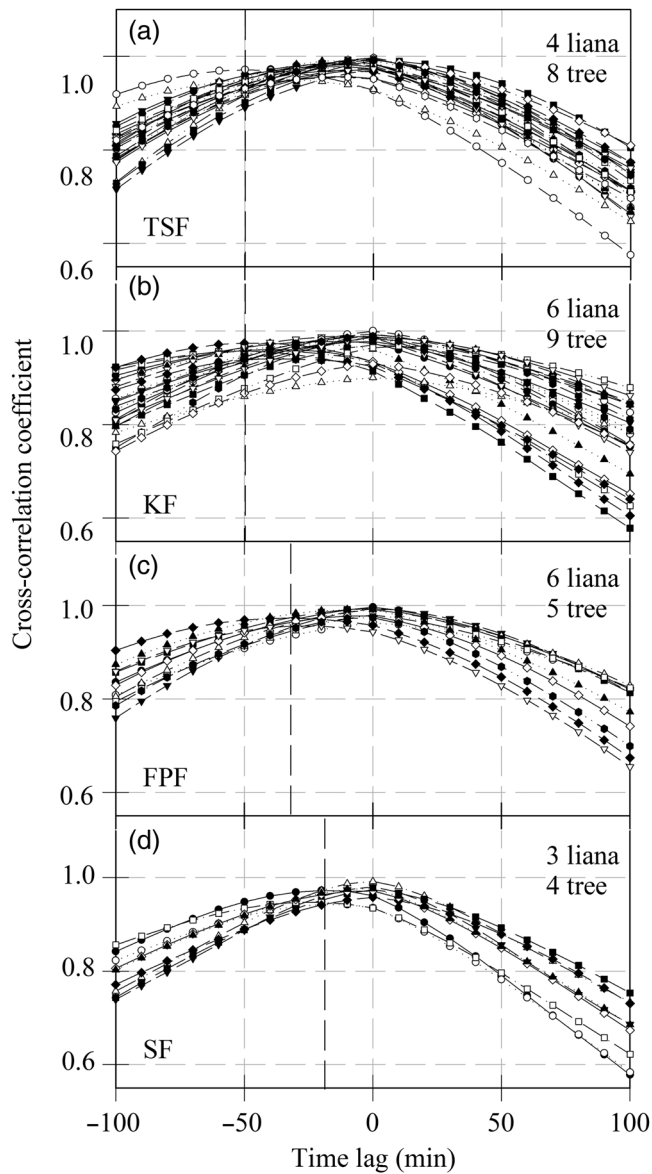


Figure 3. Cross-correlation coefficient between sap flux density in basal and upper stem positions. Data presented were selected from the same day as that presented in Figure 2. Different symbols in each panel represent an individual. The maximum correlation coefficient for each individual directly indicates the time lag for that individual. Vertical dashed lines show the largest time lag at each site. TSF, tropical seasonal forest; KF, karst forest; FPF, flood plain forest; SF, savanna forest.

Discussion

In the present study, we assumed that the duration of time lags between the basal and upper stem sap flow was a proxy for the capacity of water storage to supply water to transpiration. The time lags were calculated using cross-correlation analysis instead of the simple lag between the sap flow onsets at different positions (Burgess and Dawson 2008, Phillips et al. 2009), and the daily sap flow at each point was thus treated as a whole. We observed that a far greater proportion of trees had time lags than lianas. We also found that lianas had a shorter time lag than

trees when we analyzed the data using all 45 individuals. However, this signal disappeared when we used the reduced data set to account for the uneven sampling replication. This suggests either that we had insufficient data to detect a signal given the coarse sampling frequency (measurements taken every 10 min) or that differences between species and families may be more important than differences between growth types. Thus, we tentatively suggest that trees use more water storage to buffer water loss by transpiration and that lianas have better access to ground water and thus faster replenishment of such water loss (Chen et al. 2015).

Some previous studies have shown that increased withdrawal of internal stored water occurs during water deficits (Cruziat et al. 2002, Čermák et al. 2007, Scholz et al. 2007); others have shown that stem-stored water may be used for buffering the daily water deficit even when soil water is abundant (Holbrook 1995, Goldstein et al. 1998). We confirmed that stored water can be used to buffer daily water deficits by some species, but that it may be a trait infrequently associated with lianas. Almost all the studied trees had time lags between the two positions in the stem, whereas only two-thirds of liana individuals had time lags. This confirms that these trees release stored water for transpiration even during the wet season when soil water is highly available. The duration of time lags in our study are within the range of those found in previous studies (Goldstein et al. 1998, Phillips et al. 1999, 2003, Čermák et al. 2007, Köcher et al. 2013). However, the path lengths between the upper and basal sap flow sensors for the targeted trees ranged from only several meters to almost 30 m: much shorter than those in previous studies (Goldstein et al. 1998, Phillips et al. 2003, Burgess and Dawson 2008, Kume et al. 2008). Leaves and branches can contribute substantially to whole-plant water storage (Schulze et al. 1985, Zweifel et al. 2000, Ishii et al. 2014). Thus, the uppermost (branches and leaves) that were above the upper stem sensors may also serve as water storage compartments. Therefore, the contribution of total stored water (released from all storage compartments) to diel transpiration in our studied trees is presumably larger than we showed (Meinzer et al. 2004).

Our results are in accordance with Phillips et al. (1999), the only other report available in which no time lags between basal stem and branch sap flow were observed in two liana species (but only four individuals included). The lack of time lags between basal and upper stem sap flows in many lianas during the wet season in our study suggests that lianas are able to replenish transpired water directly by extracting water from soil. We propose two putative mechanisms to account for the insignificant contribution of stem-stored water to daily transpiration of lianas. The first mechanism is that lianas are able to replace transpired water rapidly from deeper, high potential water sources. Lianas are considered to have a deep root system that taps deep underground water, enabling them to maintain active

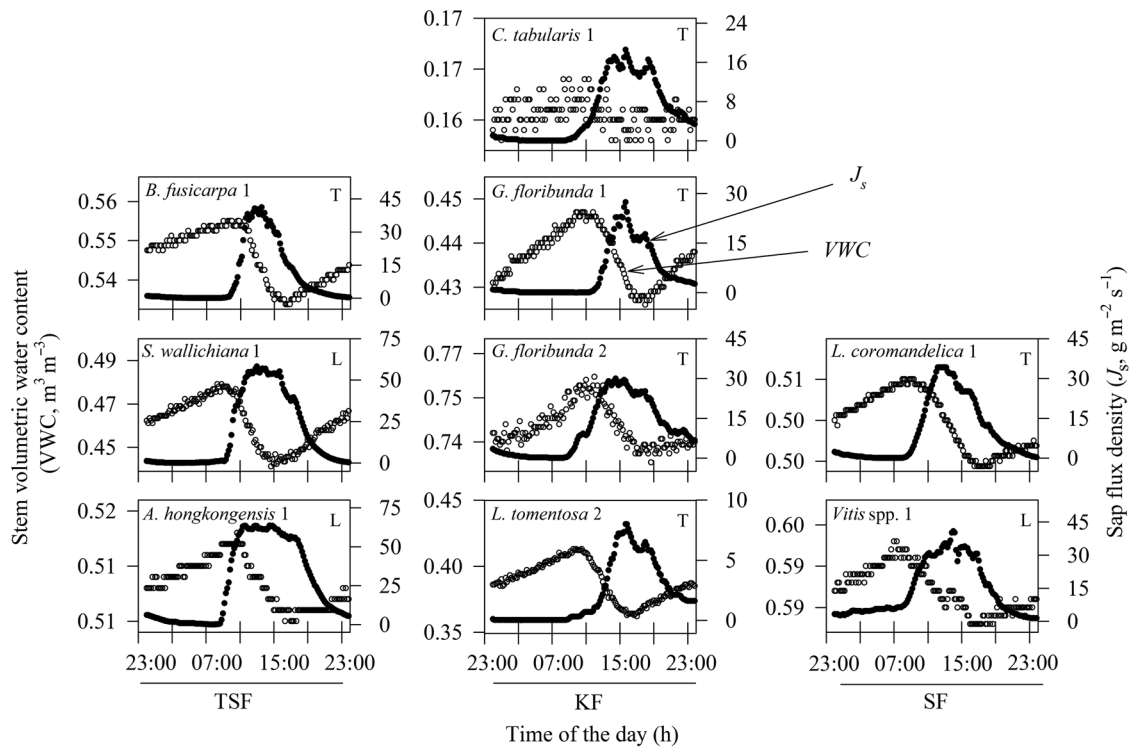


Figure 4. Diurnal course of stem sap flux density (J_s) and VWC of three liana individuals (L) and seven tree (T) individuals in TSF, KF and SF. Data were selected from the same day as that presented in Figure 2.

photosynthesis even in the dry season when shallow soil water is scarce (Schnitzer and Bongers 2011). Restom and Nepstad (2004) reported roots of small liana saplings in eastern Amazonia that were >10 m in depth. In a recent study, we found that liana species tended to use more deep soil water than their co-occurring trees in the dry season and thus maintained better leaf water status (Chen et al. 2015). The second mechanism is that lianas are able to replace transpired water rapidly because of their highly efficient water transport systems: water flux loss by transpiration can be replaced in a timely manner via the wide, highly conductive vessel elements of lianas because they typically have greater transporting efficiency (i.e., higher maximal J_s ; Figure 2 and Figure S1 available as Supplementary Data at *Tree Physiology* Online) (Zhu and Cao 2009) and a larger fraction of conductive area in cross section than trees (Angyalossy et al. 2012).

Čermák et al. (2007) suggested that the path length between measuring points might affect the time lags, whereas Phillips et al. (1999) and Köcher et al. (2013) found that time lag was independent of distance between sensors. Our results support the findings of Phillips et al. and Köcher et al. (Figure 5a). We did not find a consistent relationship between time lags and DBH, as we detected a positive effect for the full data set (Figure 5) but not for the species-only data set. Thus, our findings do not fully support the findings of Goldstein et al. (1998), Meinzer et al. (2004) and Verbeeck et al. (2007) (Figure 5b). The positive relationships between the duration of time lag and

diel maximum Δ VWC may be explained by the fact that Δ VWC directly represents the water status of stem resulting in the shrinkage and swelling of stems. However, stem SWC reflects the theoretical maximum water content rather than the usable water content, commonly negatively correlated with sapwood density (Stratton et al. 2000, Bucci et al. 2004). Wood density is inversely correlated with sapwood water storage (Meinzer et al. 2003, 2006, Scholz et al. 2007, Carrasco et al. 2013, Köcher et al. 2013). However, in the present study, time lags appeared to be independent of sapwood density and SWC. A consistent result has been shown for Madagascar baobab trees (*Adansonia* spp.) that have up to 79% sapwood water content, low wood density (0.09–0.17 g cm⁻³) and high volume of parenchyma tissues (69–88%) (Chapotin et al. 2006b), and do not utilize stored water to buffer daily water deficits (Chapotin et al. 2006a, 2006c).

In the wet season, most lianas relied little on stored water to buffer daily water loss due to transpiration. In contrast, stem storage played an important role in the daily water use of their co-occurring trees. We suggest that basal stem sap flow measurement can directly represent the canopy transpiration for lianas, but that time lags need to be taken into account for trees. Furthermore, we found that the duration of time lags (assumed as a proxy for capacity of water storage in this study) tended to be higher in plants with greater diurnal maximum Δ VWC, but was independent of body size, path length, wood density and SWC.

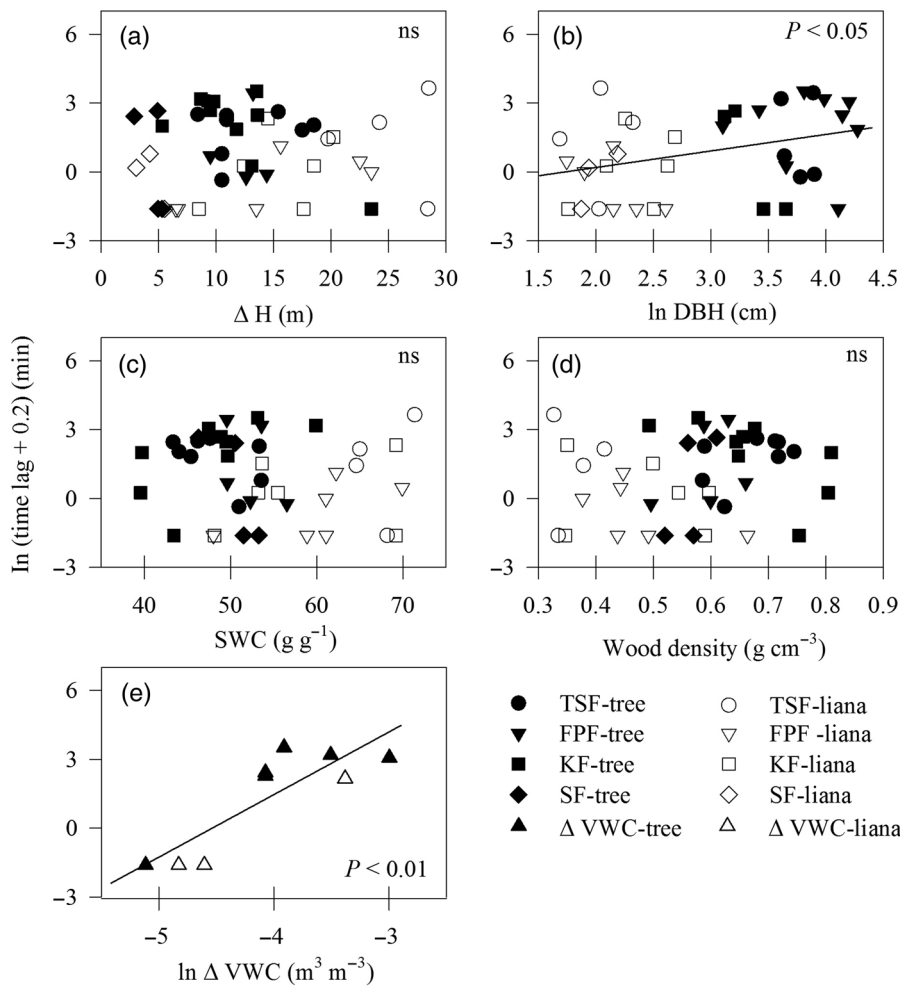


Figure 5. Relationships between duration of time lag and path length (ΔH , a), \ln DBH (b), SWC (c), wood density (ρ , d) and \ln stem maximum Δ VWC (e) for lianas (open symbols) and trees (closed symbols). Time lag was $\ln(x + 0.2)$ transformed to normalize the variable.

In this study, all measurements were conducted only in the wet season under high soil water content because some species in our study are deciduous and dropped leaves during the dry season. It is plausible that the relative contribution of stored water to the daily water budget may increase under water deficit conditions during the dry season (Scholz et al. 2007). Verbeeck et al. (2007) reported a substantial variance of stored water relative to daily transpiration (1–44%) over time in Scots pine. Similarly, old-growth Douglas-fir trees also showed seasonal changes in the contribution of water storage to daily water use (Čermák et al. 2007). Further study should include long-term monitoring to determine whether time lags occur for lianas or time lags increase for trees in the dry season when soil water is scarce and transpiration demand is high.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

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Conflict of interest

None declared.

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