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Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest

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Abstract Water uptake and transport were studied in eight liana species in a seasonally dry tropical forest on Barro Colorado Island, Panama. Stable hydrogen isotope composition (δD) of xylem and soil water, soil volumetric water content (θ_v), and basal sap flow were measured during the 1997 and 1998 dry seasons. Sap flow of several neighboring trees was measured to assess differences between lianas and trees in magnitudes and patterns of daily sap flow. Little seasonal change in θ_v was observed at 90–120 cm depth in both years. Mean soil water δD during the dry season was -19‰ at 0–30 cm, -34‰ at 30–60 cm, and -50‰ at 90–120 cm. Average values of xylem δD among the liana species ranged from -28‰ to -44‰ during the middle of the dry season, suggesting that water uptake was restricted to intermediate soil layers (30–60 cm). By the end of the dry season, all species exhibited more negative xylem δD values (-41‰ to -62‰), suggesting that they shifted to deeper water sources. Maximum sap flux density in co-occurring lianas and trees were comparable at similar stem diameter (DBH). Furthermore, lianas and trees conformed to the same linear relationship between daily sap flow and DBH. Our observations that lianas tap shallow sources of soil water at the beginning of the dry season and that sap flow is similar in lianas and trees of equivalent stem diameter do not support the common assumptions that lianas rely

primarily on deep soil water and that they have higher rates of sap flow than co-occurring trees of similar stem size.

Keywords Panama · Sap flow · Soil volumetric water content · Stable hydrogen isotope ratio · Tropical forest trees

Introduction

One important feature of tropical rain forests is the abundance of climbing plants, especially woody climbers such as lianas, which are present in both primary and secondary forests and are conspicuous in gaps and clearings (Richards 1996; Schnitzer and Bongers 2002). Lianas typically constitute about 25% of the woody stem abundance and species richness in many tropical forests (Gentry 1991), where they can utilize about 40% or more of the canopy tree species for support (Putz 1984). The slender stems of lianas can be more than 100 m long, potentially increasing the resistance to water transport from the soil to the leaves. Nevertheless, the water conducting capacity of lianas is generally thought to be greater than in trees of comparable stem diameter because of their longer and wider vessels (Zimmermann 1983; Carlquist 1985; Gartner et al. 1990; Ewers et al. 1991, 1997).

The presence of large diameter vessels and high leaf area: sapwood area ratios in lianas has led to the expectation that lianas have higher sap flow rates per stem cross-sectional area than co-occurring trees. However, this assumption is supported by limited evidence and may not be universally true. It has been reported that vines transpire more than trees with similar stem diameter in an Amazonian secondary forest, although trees show smaller reduction in transpiration from the wet to the dry season than do vines (Restom and Nepstad 2001). Fichtner and Schulze (1990) reported high sap flow and transpiration rates of three climbing plants in a tropical deciduous forest, but no comparative data on trees in the same site, measured with the same techniques, under the same environmental conditions, were obtained. However, despite the latest recognition that lianas play an

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integral role in several aspects of tropical forest dynamics (Schnitzer and Bongers 2002), studies on water transport and belowground acquisition of water by liana species are uncommon. Such studies are required to understand the interactions of lianas with other plant life forms and their contribution to whole-forest transpiration.

Stable isotope techniques have been used non-invasively to study spatial and temporal partitioning of soil water uptake in both temperate and tropical regions (Ehleringer and Dawson 1992; Flanagan et al. 1992; Jackson et al. 1995, 1999; Le Roux et al. 1995; Dawson 1996; Dawson and Pate 1996). Stable hydrogen (^1H , ^2H or D) isotope composition of the soil water usually varies with depth because of evaporative fractionation, which results in an enrichment of the heavier isotope in the upper soil layers. In tropical regions, evaporative fractionation is one of the major factors leading to variations in the isotope composition of soil water during prolonged dry periods. A number of studies have used xylem water isotope data to demonstrate partitioning of soil water resources among different species of tropical woody plants (Jackson et al. 1995, 1999; Meinzer et al. 1999), as well as among different sized individuals of the same species (Dawson 1996; Meinzer et al. 1999). In addition, seasonal differences in xylem water isotope ratios support the idea that exploitation of progressively deeper sources of water may permit some species to maintain relatively high rates of sap flow during a prolonged dry season (Dawson and Pate 1996; Meinzer et al. 1999).

Although lianas are widely believed to tap deep sources of soil water and have high rates of water use, there is a paucity of published studies in which water uptake and transport have been characterized simultaneously in lianas and co-occurring trees. In the present study, we investigated diurnal patterns of sap flow and its response to environmental variables in several liana and co-occurring tree species in a seasonally dry tropical forest on Barro Colorado Island, Panama. We also employed stable hydrogen isotope analyses to assess the degree of spatial and temporal partitioning of soil water among the liana species.

Materials and methods

Field site and species

Field measurements were conducted from January through April in 2 consecutive years (1997 and 1998) on Barro Colorado Island (BCI), Panama ($9^\circ 09'\text{N}$, $79^\circ 51'\text{W}$). The island is covered by semi-evergreen moist tropical forest with a canopy height of 35–40 m and has a mean annual rainfall of 2,600 mm, with a marked dry season from mid-December through April (Leigh and Wright 1990). The study site was located on a plateau near a permanent 50-ha plot, established in 1980 (Hubbell and Foster 1983). Fifteen circular plots (30 m in diameter) were established during 1996 in which trees greater than 20 cm DBH and lianas greater than 5 cm DBH were marked and identified. Liana species represented by at least three different individuals with their crowns in the canopy were chosen for measure-

ments of xylem sap δD and sap flow. A subset of trees was also selected in the same plots and used to measure sap flow at the same time as in the neighboring lianas. A list of the eight liana species studied, their size, and their relative abundances are presented in Table 1.

Soil volumetric water content (θ_v) was monitored at 0–15 cm, 15–30 cm, 30–60 cm, 60–90 cm, and 90–120 cm with 1.2-m multi-segment profiling TDR probes (type A, Environmental Sensors, Victoria, BC, Canada) installed permanently in four randomly chosen study plots during the dry seasons of 1997 and 1998. The probes were read with an MP-917 TDR unit (Environmental Sensors).

Xylem and soil water hydrogen isotope composition

Xylem tissue samples from three to four individuals of six liana species were obtained by extracting small cylinders of wood with an increment borer at a height of about 0.1 m above the ground. The outer bark and other non-xylem tissue were removed and the active xylem tissue was immediately placed in glass containers, sealed with a rubber stopper and Parafilm, and kept frozen until vacuum distillation in the laboratory. Each individual was sampled twice (21 March and 18 April 1997). Soil samples were collected with an auger at 10-cm intervals down to 100 cm in two to three sites with the highest density of the liana species on the same dates that xylem tissue samples were collected.

Soil and xylem samples were sent to Mountain Mass Spectrometry Laboratory (Evergreen, Colo., USA) for preparation and analysis. Water was extracted by cryogenic vacuum distillation and the stable hydrogen isotope composition was analyzed using mass spectroscopy. The stable hydrogen isotope composition was expressed in conventional delta (δ) notation as the D/H ratio relative to the V-SMOW standard (Ehleringer and Osmond 1989; Smith and Ziegler 1990):

$$\delta\text{D}\text{‰} = [(D/H_{\text{sample}} - D/H_{\text{standard}}) - 1] \times 100$$

data for soil δD were grouped into three intervals: 0–30 cm, 30–60 cm, and 90–120 cm, which showed the highest δD differences and also correlated with θ_v values.

Sap flow measurements

Sap flow was measured using the constant heat dissipation method described by Granier (1985, 1987). Pairs of 20-mm-long, 2-mm-diameter temperature probes (UP, Munich, Germany) were installed in the sapwood near the base of the liana and tree stems, approximately at 1.5 m from the ground. The upper (downstream) probe was continuously heated with a constant current power supply (UP, Munich) while the lower unheated probe measured the reference temperature of the sapwood. The protruding portions of both probes were insulated with a layer of foam rubber surrounded by an outer shield of reflective material and transparent plastic. Probe temperatures were recorded continuously with a datalogger (CR21X, Campbell

Scientific, Logan, Utah, USA) equipped with a 32-channel multiplexer (AM416, Campbell Scientific) and 10-min averages were stored in a solid-state storage module (SM192, Campbell Scientific). Concurrent measurements were made in a total of 12–18 individuals of lianas and trees distributed between two different plots. Sap flow was measured continuously during a 5–7 day period in each individual on five occasions between January and April 1998.

Sap flux density was calculated from the temperature difference between the probes using an empirical relationship developed by Granier (1985) and revalidated by Clearwater et al. (1999). Mass flow of sap was obtained by multiplying sap flux density by the sapwood cross-sectional area. Sapwood cross-sectional area was determined by dye injections (0.1% indigo carmine) in the main stem. Upstream cores were extracted after injection and the width of colored sapwood measured to calculate the cross-sectional area of active xylem.

Environmental variables were recorded as 10-min averages with an automated weather station installed on a 40-m canopy tower on BCI. Photosynthetic photon flux density (PPFD) was measured with a quantum sensor LI190SB (Li-Cor, Lincoln, Neb., USA) and atmospheric saturation deficit (ASD) was calculated from measurements of air temperature and relative humidity made with shielded sensors (HMP35C, Campbell Scientific).

To compare sap flow in tree stems with dimensions similar to those of lianas, upper canopy branches of *Ficus insipida* and *Luehea seemannii* trees were accessed with the Smithsonian Tropical Research Institute canopy crane in the Parque Natural Metropolitano near Panama City during the dry season of 1997 (for details on the site and methodology see Andrade et al. 1998). Sap flow in trees and lianas was assumed to be constant across the entire sapwood depth. However, for some Panamanian tree species, sap flux density is maximal in the outermost 4 cm of sapwood (where we actually measured it) and declined with increasing distance into the sapwood (James et al. 2002).

Statistical analysis

For both liana and tree species, linear correlations were obtained to describe the relationships of maximum sap flux density and both daily duration of maximum sap flux den-

sity and the initial slope of the sap flux velocity versus air saturation deficit (ASD) relationship, and also between these two last variables. Maximum sap flow density was determined as the maximum constant value that lasted for more than 30 min with a 5% variation during clear days. Additionally, differences between the liana and tree species were tested for the variables: duration of maximum sap flow and the slope of the sap flux density versus ASD relationship, using a Student *t*-test.

Results

The eight liana species were relatively abundant in the study site. Three species, *Combretum decandrum*, *Maripa panamensis*, and *Prionostemma aspera*, had seven or more individuals per hectare that had already reached the canopy (DBH > 5 cm; Table 1). On the other hand, *Hiraea reclinata*, *M. panamensis*, and *P. aspera* had the greatest densities of small individuals (>200 per ha). The species *E. monostachya* and *H. volubilis* had the largest individuals in our sample (average DBH 11.9 cm and 7.5 cm, respectively) but the lowest densities (Table 1).

Total rainfall on BCI from January through late April 1997 was 99.6 mm, about 46% of the 68-year average value for the period (Windsor 1990). Two significant precipitation events occurred during the 1997 dry season; 41.2 mm of rainfall on 5 and 6 February, and 31.2 mm on 22 April (Fig. 1). Soil volumetric water content (θ_v) in the upper 30 cm was about 15% prior to the February rainfall, then increased to 32%, after which it declined steadily to a minimum value of 11% before the rain on 22 April (Fig. 1). Between 30 and 60 cm depth, θ_v did not increase significantly following the rains in early February and late April, and remained at about 30% during the entire dry season. At 90–120 cm depth, θ_v remained at about 50% during much of the dry season, then declined slowly to 40% over a 40-day period, but the rains of late April and early May increased it again to 50% (Fig. 1).

During March and April 1997, soil water δD values decreased from -19.2‰ in the upper 30 cm to -34.2‰ at 30–60 cm depth, and to -49.9‰ at 90–120 cm depth (Fig. 1). Water samples from springs on BCI during this

Table 1 Abundance of liana species used for xylem water samples and sap flow measurements. The size-class density distribution data are from 16 (24 × 36 m) plots (13,824 m² total area) located in intact old-growth forest stands on BCI. All individuals >50 cm height and >0.3 cm DBH were included. Data are reported on number of individuals per ha (Schnitzer and Carson, unpublished information)

Species	Family	Density (per ha)		
		<5 cm dbh	5 to 10 cm dbh	Total
<i>Abuta racemosa</i> (Thunb) Tr. & Planch	Menispermaceae	33	0	33
<i>Clitoria javitensis</i> H.B.K	Fabaceae	36	1	37
<i>Combretum decandrum</i> Jacq	Combretaceae	38	7	45
<i>Entada monostachya</i> DC	Fabaceae	0	0	0
<i>Hippocratea volubilis</i> L.	Hippocrateaceae	9	0	9
<i>Hiraea reclinata</i> Jacq	Malpighiaceae	337	1	338
<i>Maripa panamensis</i> Hemsl	Convolvulaceae	364	9	373
<i>Prionostemma aspera</i> (Lam.) Miers	Hippocrateaceae	214	23	237

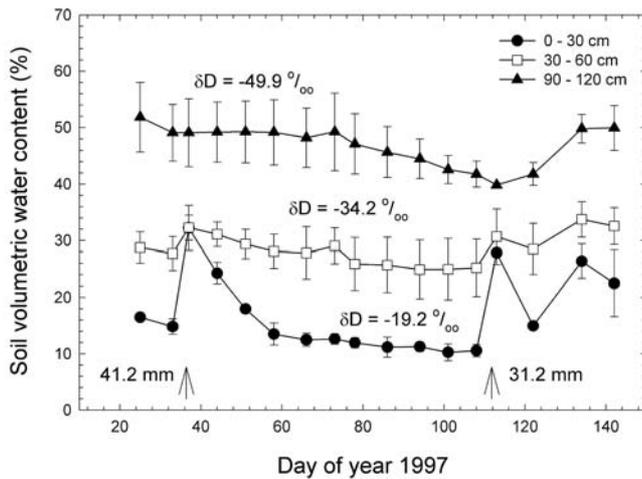


Fig. 1 Soil volumetric water content at different depths during the 1997 dry season on Barro Colorado Island, Panama ($n = 2-4$ soil probes). Arrows show rainfall events greater than 10 mm. Average delta deuterium (δD) is shown for each soil depth in March and April

period yielded an average δD value of about -60‰ . In all six liana species from which xylem sap was obtained, δD values were more negative at the end of the dry season (day 108) than near the middle (day 80) of the dry season (Fig. 2). For example, *Entada monostachya* had the least negative xylem sap δD value (-27‰) at day 80, implying that soil water uptake was largely restricted to the soil layer between 0 and 60 m (Figs. 1, 2). At day 108, the xylem sap δD value for this species was -52‰ , suggesting that most of the water was obtained from depths greater than 100 cm. In *Hippocratea volubilis*, on the other hand, the average xylem sap δD value was -43‰ at the middle of the dry season, suggesting that soil water uptake may have been restricted to soil layers deeper than 60 cm. By day 108, its xylem sap δD value had decreased to -62‰ , a value close to that of ground water.

Typical daily courses of sap flow for co-occurring liana and tree species on clear days with comparable PPFD and air saturation deficit regimes are shown in Figs. 3, 4, 5. Lianas and trees appeared to differ with respect to two notable features of their daily courses of sap flow. The initial rate of increase in sap flow in the morning was usually greater in lianas than in trees, and maximal or near-maximal rates of sap flow were maintained for a longer period of time in lianas than in trees. Comparisons of the mean duration of maximum sap flux density and the mean initial slope of the relationship between sap flux density and air saturation deficit for all liana and tree species in which sap flow was measured (Table 2), confirmed the apparent trends seen in Figs. 3, 4, 5. The mean duration of maximum sap flux density for lianas (3.4 h) was twice that of trees (1.7 h; $P < 0.001$), and the mean slope of the morning increase in sap flow with increasing air saturation deficit was more than twice as great in lianas than in trees ($P < 0.001$).

Maximum sap flux density decreased sharply and then more gradually with increasing DBH for both lianas and tree branches and stems (Fig. 6a,b). For a stem size of about

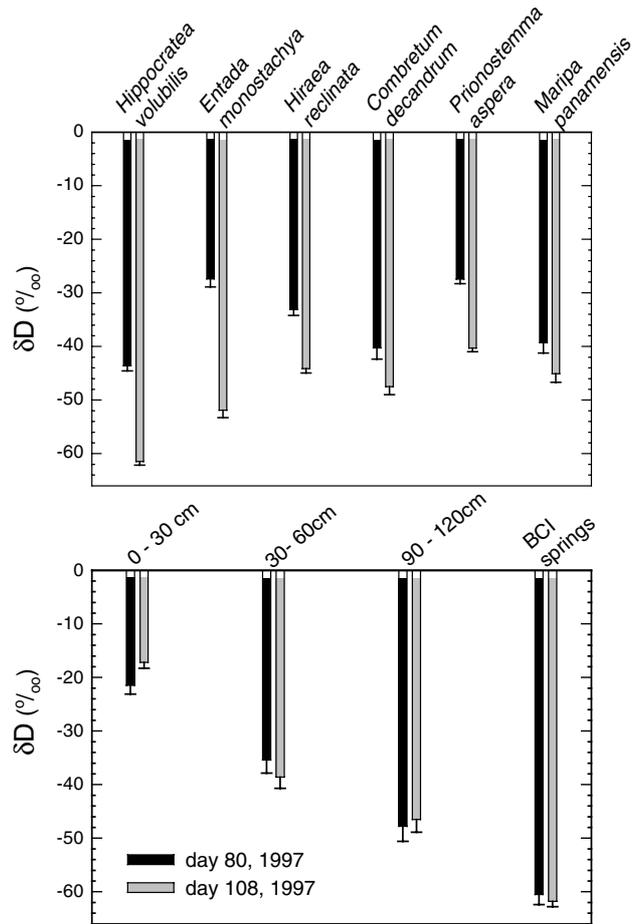


Fig. 2 Average xylem sap delta deuterium (δD) sampled on 21 March (day 80) and 18 April (day 108), 1997 for six liana species ($n=4$ plants; upper panel) and soil and springs δD sampled on the same dates ($n=6$ samples; lower panel) on Barro Colorado Island, Panama

5 cm DBH the maximum sap flow was about 0.4 m h^{-1} and decreased exponentially to about 0.15 m h^{-1} for a stem size of about 20 cm DBH. All lianas and trees conformed to the same linear relationship between daily sap flow and DBH (Fig. 6c).

Discussion

We found that six liana species utilized water from soil layers deeper than 30 cm during the middle of the dry season (average xylem $\delta D = -35\text{‰}$) and all species switched to deeper water sources (more than 60 cm deep) by the end of the dry season (average xylem $\delta D = -48\text{‰}$). The largest seasonal changes in xylem water δD occurred in relatively large individuals of *E. monostachya* and *H. volubilis*. This pattern was not observed in larger trees, which tend to extract water from shallower sources than do smaller trees as the dry season progresses (Meinzer et al. 1999).

The results in Fig. 1 suggest that soil water at depth remains readily available during the dry season on Barro Colorado Island. There was little change in soil volumetric water content (θ_v) at 90–120 cm depths during the dry

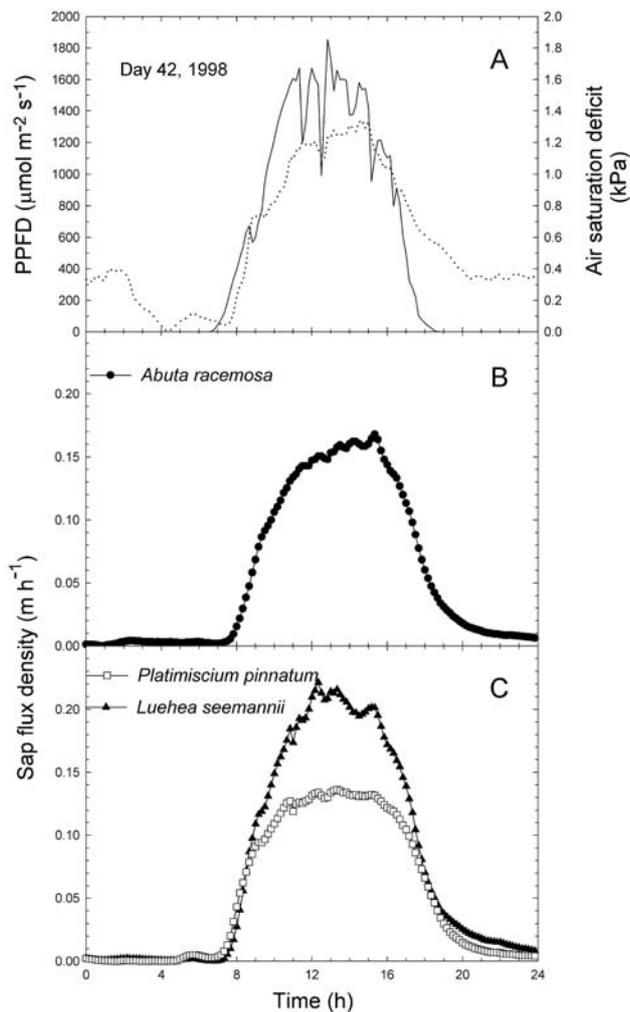


Fig. 3 Diurnal courses of **a** photosynthetic photon flux density (PPFD, solid line) and air saturation deficit (dotted line), **b** basal sap flux density for the liana *Abuta racemosa*, and **c** basal sap flow for the tree species *Luehea seemannii* and *Platimiscium pinnatum*, on 11 February 1998 (day 42)

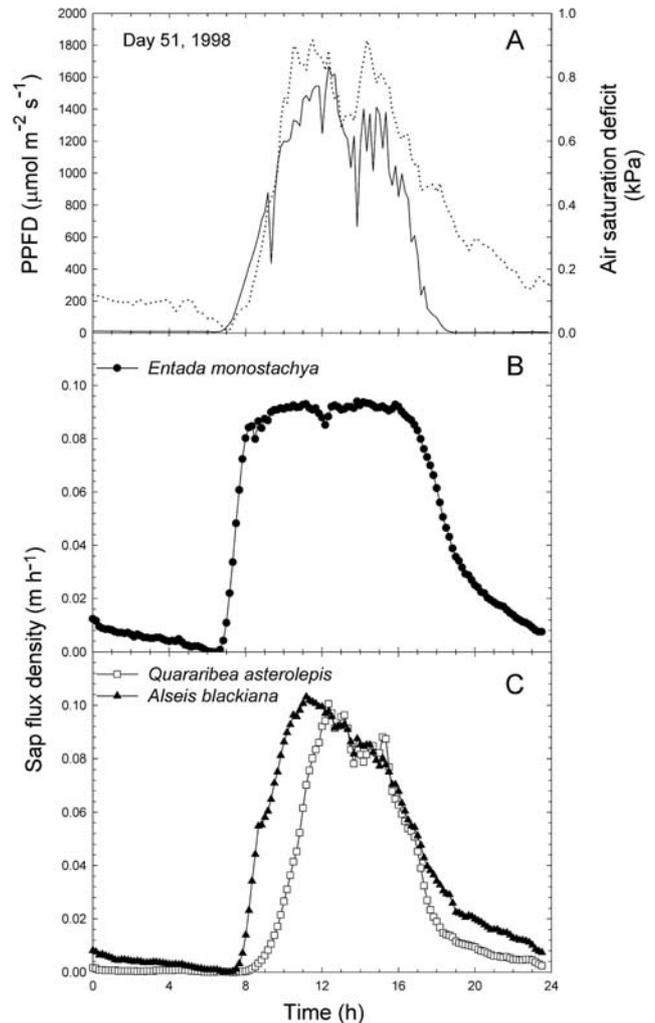


Fig. 4 Diurnal courses of **a** photosynthetic photon flux density (PPFD, solid line) and air saturation deficit (dotted line), **b** basal sap flux density for the liana *Entada monostachya*, and **c** basal sap flow for the tree species *Alseis blackiana* and *Quararibea asterolepis*, on 20 February 1998 (day 51)

season of both 1997 and 1998. Shallower water content differed between the 2 years, however. During the 1998 dry season (El Niño year), three main precipitation events did not permit θ_v at 0–30 cm depth to drop below 15% (data not shown), although the total amount of rainfall for that period was similar to the 1997 dry season. During the dry season of 1997, however, there was a significant decrease in θ_v at 0–30 cm depth due to evapotranspiration (Fig. 1). The duration and severity of the dry season in lowland seasonal Panamanian forests can vary considerably (Windsor 1990). Though El Niño lowers total annual precipitation, it does not necessarily affect the length of the dry season.

Pronounced droughts may affect shallow-rooted understory plants and even some trees in tropical forests (Becker et al. 1988; Chiarello et al. 1987; Oberbauer et al. 1987). Soil water potentials measured at 20 cm depth during a dry season on the plateau of Barro Colorado Island dropped to -2.3 MPa, which affected the predawn water potentials of the shallow-rooted *Psychotria horizontalis* but not those of

the deep-rooted *Trichilia tuberculata* (Becker et al. 1988). Although it has been suggested that shrubs and tree saplings may have roots at depths between 30 to 120 cm on Barro Colorado Island, an irrigation experiment did not show any change in tree phenology of the Barro Colorado Island forests (Wright 1996), suggesting that most species have access to the water table during the dry season. Indeed, some canopy trees in this forest have been shown to extract water from deeper and more reliable sources to maintain similar sap flow rates during the dry season (Meinzer et al. 1999).

Lianas are considered among the most deep-rooted species in tropical forests and there is evidence that their roots can grow belowground to a depth of several meters (Holbrook and Putz 1996; Tyree and Ewers 1996). Using stable hydrogen composition of xylem water, Jackson et al. (1995) found that the liana *Bauhinia* sp. had access to water from much deeper portions of the soil profile compared to sympatric tree species.

Table 2 Sap flow characteristics for seven liana species and eight tree species from Barro Colorado Island. Values are means \pm SE (n = sample size)

	Duration of maximum sap flux density (h)	Slope of sap flux density versus ASD ($\text{m h}^{-1} \text{ kPa}^{-1}$)	n
Liana species			
<i>Abuta racemosa</i>	2.38 \pm 0.26	0.13 \pm 0.02	8
<i>Clitoria javitensis</i>	6.83 \pm 0.44	0.52 \pm 0.04	3
<i>Combretum decandrum</i>	1.83 \pm 0.46	0.22 \pm 0.02	6
<i>Entada monostachya</i>	4.80 \pm 0.50	0.39 \pm 0.06	8
<i>Hippocratea volubilis</i>	4.60 \pm 0.76	0.40 \pm 0.06	7
<i>Hiraea reclinata</i>	1.25 \pm 0.25	0.03 \pm 0.01	4
<i>Prionostemma aspera</i>	2.14 \pm 0.57	0.15 \pm 0.05	7
Mean \pm SE	3.40 \pm 0.31	0.26 \pm 0.03	43
Tree species			
<i>Alseis blackiana</i>	1.35 \pm 0.51	0.10 \pm 0.02	7
<i>Guatteria dumetorum</i>	0.56 \pm 0.03	0.11 \pm 0.00	3
<i>Hura crepitans</i>	2.93 \pm 0.43	0.10 \pm 0.02	3
<i>Luehea seemannii</i>	1.46 \pm 0.25	0.19 \pm 0.02	5
<i>Platimiscium pinnatum</i>	2.57 \pm 0.41	0.13 \pm 0.02	8
<i>Quararibea asterolepis</i>	0.98 \pm 0.20	0.09 \pm 0.02	6
<i>Trichilia tuberculata</i>	1.73 \pm 0.33	0.11 \pm 0.01	9
<i>Virola surinamensis</i>	1.86 \pm 0.33	0.06 \pm 0.02	4
Mean \pm SE	1.68 \pm 0.12	0.11 \pm 0.01	45

A notable feature of daily courses of sap flow in some of the liana studied was a rapid early morning increase to a plateau of several hours duration (e.g. Figs. 4b, 5b). Strong stomatal limitation of water loss apparently allowed sap flow to remain nearly constant despite increasing air saturation deficit. The daily courses of basal sap flow for lianas showed two distinct patterns (Figs. 3, 4, 5 panel b). Similar patterns were observed in the daily courses of sap flow for two liana species in a dry tropical forest in Mexico (Fitchner and Schulze 1990). Sensitivity of stomata to humidity has been documented for some temperate and tropical liana species (Castellanos 1991; Teramura et al. 1991), where stomatal closure with increasing ASD resulted in a little or no increase in the rate of water loss. Sustained maximum transpiration rates can also be maintained by a large water storage capacity, as observed in some large tropical trees (Goldstein et al. 1998). Teramura et al. (1991) suggested that the ability of temperate lianas to maintain relatively high leaf water potentials despite high transpiration rates may be associated with considerable amounts of stored water, possibly located in large tuberous roots (Forseth and Teramura 1987). Large tubers have been observed in some tropical lianas (Tyree and Ewers 1996). However, there was no evidence that the liana species in this study possess this type of underground organ, and we therefore suspect that the flat profile of sap flow time courses results from stomatal control. Because maximum stem diameter and sap wood volume are typically smaller in lianas than in trees, maximum stem water storage capacities in lianas are expected to be smaller than in trees. However, the architecture of many lianas, consisting of leafy stems in the canopy supported by long sections of thick, leafless stem, may enhance their stem water storage capacity relative to transpiring leaf

area. Our results raise a number of questions regarding the water storage capacity, stomatal behavior, and regulation of water balance among different liana species. For example, relatively high transpiration rates are maintained over an extensive portion of the day in *C. javitensis*, which has very slender stems and therefore potentially low stem water storage capacity. This species is among the 20 most abundant liana species in the BCI forest (Table 1; Putz 1984), and would be a good candidate for future ecophysiological studies.

The xylem sap flux density (sap flow rate per cross-sectional area of sapwood) in vines of a Mexican dry forest was several times greater than rates reported for temperate trees (Fichtner and Schulze 1990). Nevertheless, maximum sap flux densities in lianas on Barro Colorado Island were similar to those in tree branches with comparable cross-sectional area (Fig. 6), consistent with recent universal allometric scaling models for plant vascular systems (Meinzer et al. 2001). According to the Hagan–Poiseuille equation describing water transport in conduits, larger vessels should result in higher sapflow velocities at a given pressure gradient (Nobel 1991). However, high specific hydraulic conductivity associated with larger vessels in lianas could result in smaller water potential gradients in lianas than in trees, and therefore similar sap velocities in trees and lianas (Ewers et al. 1991; Tyree and Ewers 1996). It is important to note that because sap velocity cannot be measured directly with techniques commonly used to measure sap flux density, sap flux density is an unreliable indicator of true sap velocity as shown by tracer studies (James et al. 2003).

In summary, our observations that lianas tap shallow sources of soil water at the beginning of the dry season

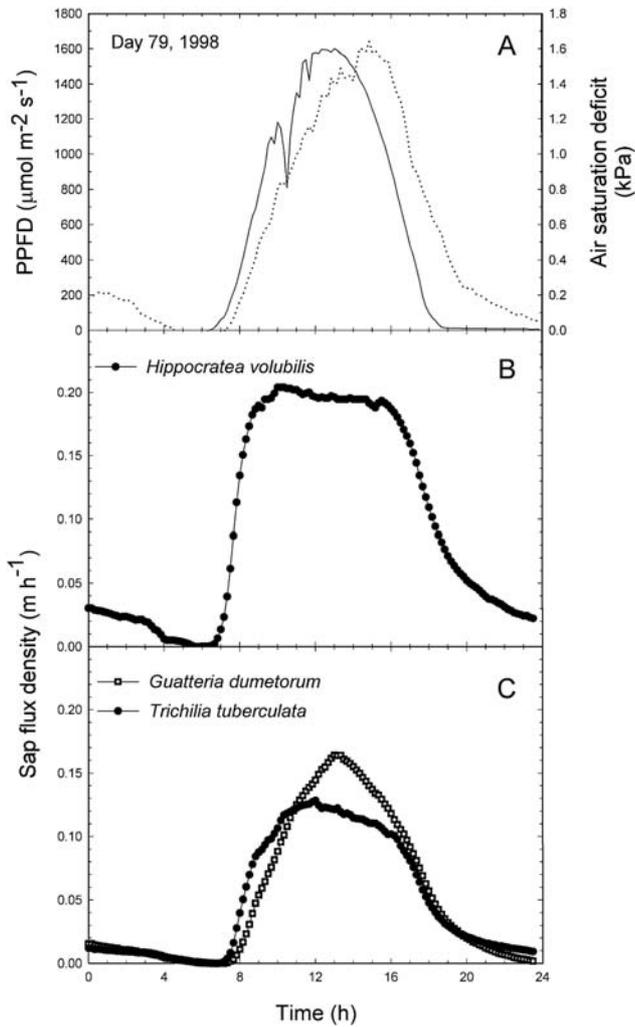


Fig. 5 Diurnal courses of **a** photosynthetic photon flux density (PPFD, solid line) and air saturation deficit (ASD, dotted line), **b** basal sap flux density for the liana *Hippocratea volubilis*, and **c** basal sap flow for the tree species *Guatteria dumetorum* and *Trichilia tuberculata*, on 20 March 1998 (day 79)

and that sap flux density is similar in lianas and trees of equivalent stem diameter do not support the common assumptions that lianas rely primarily on deep soil water and that they have higher rates of sap flux density than co-occurring trees of similar stem size. Maximum sap flow rates with deuterated tracers should be measured in lianas and co-occurring trees to assess if predictions made based on xylem anatomy are correct.

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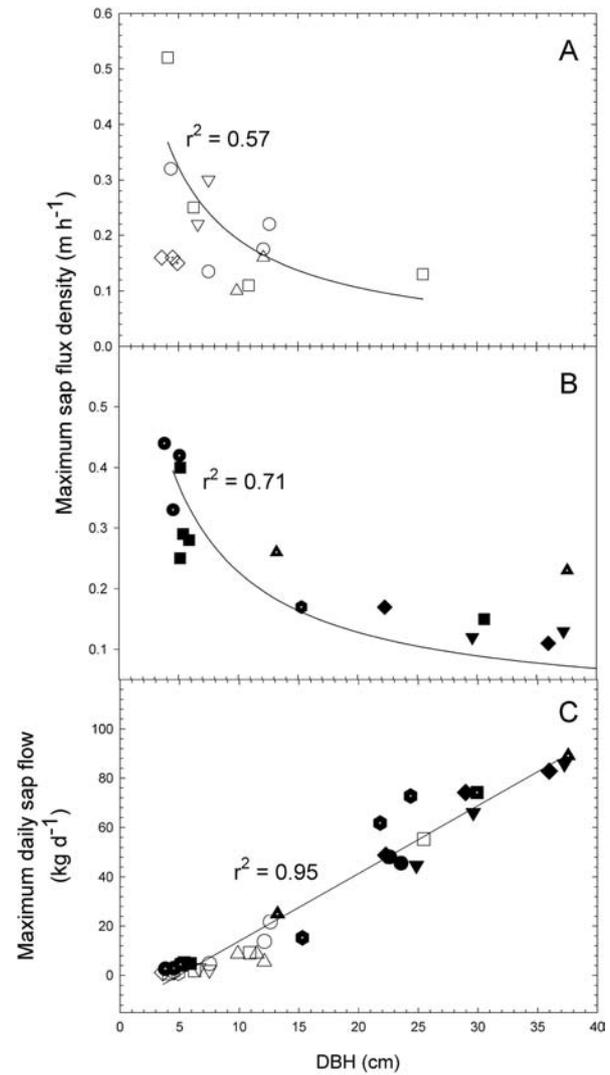


Fig. 6 **a**, **b** Maximum sap flux density and **c** maximum daily sap flow for lianas (open symbols) and branches and trees (closed symbols) as a function to diameter at breast height. Open circle *Hippocratea volubilis*, open square *Entada monostachya*, open diamond *Clitoria javitensis*, open inverted triangle *Abuta racemosa*, diamond with a dot within *Combretum decandrum*, open inverted triangle *Prionostemma aspera*, black circle *Trichilia tuberculata*, black square *Luehea seemanii*, black triangle *Platimiscium pinnatum*, black inverted triangle *Quararibea asterolepis*, black diamond *Alseis blackiana*, dark bordered circle *Ficus insipida*, dark bordered square *Guatteria dumetorum*, hexagon *Ochroma pyramidale*, circle with a dot within *Cecropia obtusifolia*. Values for tree branches from 4 to 6 cm diameter were measured in 1997 and other values were measured in 1998

References

- Andrade JL, Meinzer FC, Goldstein G, Holbrook NM, Cavelier J, Jackson P, Silveira K (1998) Regulation of water flux through trunks, branches, and leaves in trees of a lowland tropical forest. *Oecologia* 115:463–471
- Becker P, Rabenold PE, Idol JR, Smith AP (1988) Water potential gradients for gaps and slopes in a Panamanian tropical moist forest's dry season. *J Trop Ecol* 4:173–184

- Carlquist S (1985) Observations on functional wood histology of vines and lianas: vessel dimorphism, tracheids, vasicentric tracheids, narrow vessels, and parenchyma. *Aliso* 11:139–157
- Castellanos AE (1991) Photosynthesis and gas exchange of vines. In: Putz FE, Mooney HA (eds) *The biology of vines*. Cambridge University Press, Cambridge, pp 181–204
- Chiarello NR, Field CB, Mooney HA (1987) Midday wilting in a tropical pioneer tree. *Funct Ecol* 1:3–11
- Clearwater MJ, Meinzer FC, Andrade JL, Goldstein G, Holbrook NM (1999) Potential errors in measurements of non-uniform sap flow using heat dissipation probes. *Tree Physiol* 19:681–687
- Dawson TE (1996) Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: the roles of tree size and hydraulic lift. *Tree Physiol* 16:263–272
- Dawson TE, Pate JS (1996) Seasonal water uptake and movement in root systems of Australian phraeatophytic plants of dimorphic root morphology: a stable isotope investigation. *Oecologia* 107:13–20
- Ehleringer JR, Dawson TE (1992) Water uptake by plants: perspectives from stable isotopes. *Plant Cell Environ* 15:1073–1082
- Ehleringer JR, Osmond CB (1989) Stable isotopes. In: Percy RW, Ehleringer JR, Mooney HA, Rundel PW (eds) *Plant physiological ecology. Field, methods and instrumentation*. Chapman and Hall, London, pp 281–300
- Ewers FW, Carlton MR, Fisher JB, Kolb KJ, Tyree MT (1997) Vessel diameters in roots versus stems of tropical lianas and other growth forms. *IAWA J* 18:261–279
- Ewers FW, Fisher JB, Fichtner K (1991) Water flux and xylem structure in vines. In: Putz FE, Mooney HA (eds) *The biology of vines*. Cambridge University Press, Cambridge, pp 127–160
- Fichtner K, Schulze E-D (1990) Xylem water flow in tropical vines as measured by a steady state heating method. *Oecologia* 82:351–361
- Flanagan LB, Ehleringer JR, Marshall JD (1992) Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland. *Plant Cell Environ* 15:831–836
- Forseth IN, Teramura AH (1987) Field photosynthesis, microclimate and water relations of an exotic temperate liana, *Pueraria lobata*, kudzu. *Oecologia* 71:262–267
- Gartner BL, Bullock SH, Mooney HA, Brown VB, Whitbeck JL (1990) Water transport properties of vine and tree stems in a tropical deciduous forest. *Am J Bot* 77:742–749
- Gentry AH (1991) The distribution and evolution of climbing plants. In: Putz FE, Mooney HA (eds) *The biology of vines*. Cambridge University Press, Cambridge, pp 3–49
- Goldstein G, Andrade JL, Meinzer FC, Holbrook NM, Cavelier J, Jackson P, Celis A (1998) Stem water storage and diurnal patterns of water use in tropical forest canopy trees. *Plant Cell Environ* 21:397–406
- Granier A (1985) Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. *Ann Sci For* 42:193–200
- Granier A (1987) Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiol* 3:309–320
- Holbrook NM, Putz FE (1996) Physiology of tropical vines and hemiepiphytes: plants that climb up and plants that climb down. In: Mulkey SS, Chazdon RL, Smith AP (eds) *Tropical forest plant ecophysiology*. Chapman & Hall, New York, pp 363–394
- Hubbell SP, Foster RB (1983) Diversity of canopy trees in a neotropical forest and implications for conservation. In: Sutton SJ, Whitmore TC, Chadwick AC (eds) *Tropical rainforest: ecology and management*. Blackwell Scientific, Oxford, pp 25–41
- Jackson PC, Cavelier J, Goldstein G, Meinzer FC, Holbrook NM (1995) Partitioning of water resources among plants of a lowland tropical forest. *Oecologia* 101:197–203
- Jackson PC, Meinzer FC, Bustamante M, Goldstein G, Franco A, Rundel PW, Caldas L, Iglér E, Causin F (1999) Partitioning of soil water among tree species in a Brazilian Cerrado ecosystem. *Tree Physiol* 19:717–724
- James SA, Clearwater MJ, Meinzer FC, Goldstein G (2002) Heat dissipation sensors of variable length for the measurement of sap flow in trees with deep sapwood. *Tree Physiol* 22:277–283
- James SA, Meinzer FC, Goldstein G, Woodruff D, Jones T, Restom T, Mejia M, Clearwater M, Campanello P (2003) Axial and radial water transport and internal water storage in tropical forest canopy trees. *Oecologia* 134:37–45
- Leigh EGJ Jr, Wright SJ (1990) Barro Colorado Island and tropical biology. In: Gentry AH (ed) *Four neotropical rainforests*. Yale University Press, New Haven, pp 28–47
- Le Roux X, Bariac T, Mariotti A (1995) Spatial partitioning of the soil water resource between grass and shrub components in a West African humid savanna. *Oecologia* 104:147–155
- Meinzer FC, Andrade JL, Goldstein G, Holbrook NM, Cavelier J, Wright SJ (1999) Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia* 121:293–301
- Meinzer FC, Goldstein G, Andrade JL (2001) Regulation of water flux through tropical forest canopy trees: do universal rules apply? *Tree Physiol* 21:19–26
- Nobel PS (1991) *Physicochemical and environmental plant physiology*. Academic, San Diego
- Oberbauer SF, Strain BR, Riechers GH (1987) Field water relations of a wet-tropical tree species, *Pentaclethra macroloba* (Mimosaceae). *Oecologia* 71:369–374
- Putz FE (1984) The natural history of lianas of Barro Colorado Island, Panama. *Ecology* 65:1713–1724
- Restom TG, Nepstad DC (2001) Contribution of vines to the evapotranspiration of a secondary forest in eastern Amazonia. *Plant Soil* 236:155–163
- Richards PW (1996) *The tropical rain forest: an ecological study*. Cambridge University Press, Cambridge
- Schnitzer SA, Bongers F (2002) The ecology of lianas and their role in forest. *Trends Ecol Evol* 17:223–230
- Smith BN, Ziegler H (1990) Isotopic fractionation of hydrogen in plants. *Bot Acta* 103:335–342
- Teramura AH, Gold WG, Forseth IN (1991) Physiological ecology of mesic, temperate woody vines. In: Putz FE, Mooney HA (eds) *The biology of vines*. Cambridge University Press, Cambridge, pp 245–285
- Tyree MT, Ewers FW (1996) Hydraulic architecture of woody tropical plants. In: Mulkey SS, Chazdon RL, Smith AP (eds) *Tropical forest plant ecophysiology*. Chapman & Hall, New York, pp 217–243
- Windsor DM (1990) Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panama. *Smithsonian Contributions to the Earth Sciences* No. 29, Smithsonian Institution Press, Washington, D.C.
- Wright SJ (1996) Phenological responses to seasonality in tropical forest plants. In: Mulkey SS, Chazdon RL, Smith AP (eds) *Tropical forest plant ecophysiology*. Chapman & Hall, New York, pp 440–460
- Zimmermann MH (1983) *Xylem structure and the ascent of sap*. Springer, Berlin Heidelberg New York