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Trade-offs Between Water Transport Capacity and Drought Resistance In Neotropical Canopy Liana and Tree Species

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Abstract

In tropical forest canopies, it is critical for upper shoots to efficiently provide water to leaves for physiological function while safely preventing loss of hydraulic conductivity due to cavitation during periods of soil water deficit or high evaporative demand. We compared hydraulic physiology of upper canopy trees and lianas in a seasonally dry tropical forest to test whether trade-offs between safety and efficiency of water transport shape differences in hydraulic function between these two major tropical woody growth forms. We found that lianas showed greater maximum stem-specific hydraulic conductivity than trees, but lost hydraulic conductivity at less negative water potentials than trees, resulting in a negative correlation and trade-off between safety and efficiency of water transport. Lianas also exhibited greater diurnal changes in leaf water potential than trees. The magnitude of diurnal water potential change was negatively correlated with sapwood capacitance, indicating that lianas are highly reliant on conducting capability to maintain leaf water status, whereas trees relied more on stored water in stems to maintain leaf water status. Leaf nitrogen concentration was related to maximum leaf-specific hydraulic conductivity only for lianas suggesting that greater water transport capacity is more tied to leaf processes in lianas compared to trees. Our results are consistent with a trade-off between safety and efficiency of water transport and may have implications for increasing liana abundance in neotropical forests.

Introduction

A current paradigm in plant hydraulics suggests a major trade-off between two indices of hydraulic function: maximum water transport capacity per unit cross-sectional sapwood area (K_s) or hydraulic efficiency, and resistance to drought-induced xylem cavitation or hydraulic safety (Pockman and Sperry 2000, Martínez-Vilalta et al. 2002). This trade-off is considered to be a major axis of plant strategy variation (Ackerly 2004, Choat et al. 2012), and is related to dynamic indices of hydraulic function including water acquisition, regulation of water use and water-use efficiency (Drake and Franks 2003, Santiago et al. 2004b, Bucci et al. 2009, Meinzer et al. 2009). A recent analysis across a broad range of species, including 335 angiosperms and 89 gymnosperms suggests that globally, this relationship is significant, but weak, and that although there are no species with both safe and efficient hydraulic systems, the numerous species with low efficiency and low safety present a curious conundrum to this paradigm (Gleason et al. 2015). Yet, correlations among traits at the global scale do not necessarily mean that the same relationships operate in regional or site-specific data sets (Santiago and Wright 2007). Within-site trait relationships likely reflect local resource availability and the identity of taxa that are present. Indeed, strong trade-offs between safety and efficiency have been observed within numerous single sites (Pockman and Sperry 2000, Martínez-Vilalta et al. 2002, Pratt et al. 2007) and among particular taxa (Wheeler et al. 2005, Hacke et al. 2007). We used this context to examine hydraulic differences between trees and lianas, the two main woody growth forms of tropical forest.

The safety-efficiency trade-off in plants is based on hydraulic theory and data demonstrating that the maximum rate of water flow through xylem vessels increases with the diameter of the vessel, and that wider vessels often cavitate at less negative water potentials than narrower vessels (Pockman and

Sperry 2000, Martínez-Vilalta et al. 2002, Wheeler et al. 2005). The vulnerability of large diameter vessels to freezing-induced cavitation is substantially increased (Tyree et al. 1994). However, for tropical plants, safety from cavitation by water stress is a greater constraint to vessel size than freezing. The pit area hypothesis suggests an increasing probability of the seal of inter-vessel pits failing as the total area of pits increases (Wheeler et al. 2005). The result is a complex trade-off between vessel size and vulnerability to cavitation by water stress that is too variable to allow physiologists to predict vulnerability to drought-induced cavitation based on vessel diameter, but strong enough to constrain xylem function to a limited range of operation (Tyree et al. 1994, Hacke et al. 2006, Sperry et al. 2008, Gleason et al. 2015).

Relatively little data comparing lianas and trees exist for the trade-off between K_s and vulnerability to xylem cavitation (Santiago et al. 2015). The emerging pattern suggests that lianas and trees fall along the same relationship of hydraulic safety versus efficiency, but that lianas show a tendency for greater maximum stem-specific conductivity and a less resistant xylem, and thus occupy the relatively less safe and more efficient side of the spectrum (Zhu and Cao 2009, Johnson et al. 2013, van der Sande et al. 2013, Santiago et al. 2015). If this pattern is robust, it would appear that the enhanced ability to transport water and support photosynthesis of canopy leaves may be more important than drought resistance in determining liana success. Reports generated through a variety of metrics indicate that the slender stems of lianas normally support a distal leaf area that is considerably greater than trees when normalized per unit stem area (Putz 1993, Gerwing and Farias 2000, Restom and Nepstad 2001, Feild and Balun 2008, Zhu and Cao 2009). There is also some evidence that lianas exhibit greater average stem-specific hydraulic conductivity than trees (Gartner et al. 1990, Patiño et al. 1995), supporting the idea that lianas utilize wide vessels to maintain efficient water transport to compensate for narrow stems (Ewers and Fisher 1991). Patterns of leaf-specific hydraulic conductivity (K_L) between lianas and trees, on the other hand, show more variation. For example, the studies of Feild and Balun (2008) and Zhu and Cao (2009) show lower K_L in lianas relative to trees. However, Patiño et al. (1995) and Santiago et al. (2015), both of which reviewed several studies, show higher K_L in lianas relative to trees. These data suggest that in general, greater water transport capacity in lianas promotes higher leaf photosynthetic potential than trees as has been observed in some studies (Zhu and Cao 2009, 2010, Asner and Martin 2012), indicating that interactions between water supply to leaves and photosynthetic carbon gain may be a critical component of the liana strategy.

It is well established that hydraulic efficiency controls maximum stomatal conductance (Meinzer and Grantz 1990, Meinzer et al. 1995, Pockman and Sperry 2000, Hubbard et al. 2001, Santiago et al. 2004a). Because stomatal conductance promotes CO_2 diffusion to the site of carboxylation, plants are expected to allocate relatively greater photosynthetic capacity as water supply to leaves increases in order to take advantage of a high supply of CO_2 for photosynthesis (Santiago et al. 2004a). Therefore, hydraulically efficient plant species are also predicted to occur on the fast-return on investment side of the leaf economics spectrum, including high rates of maximum photosynthesis, high leaf element concentrations and high specific leaf area (SLA), whereas species with low hydraulic efficiency are predicted to exhibit opposite traits (Wright et al. 2004b, Maire et al. 2015). Further linkages between stem and leaf coordination of hydraulic processes are evident in stable isotopic composition of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in leaves. Leaf $\delta^{13}\text{C}$ is related to intercellular CO_2 concentration (C_i) such that high rates of stomatal conductance are often associated with high C_i , high rates of discrimination by rubisco against $^{13}\text{CO}_2$ relative to $^{12}\text{CO}_2$, and low values of $\delta^{13}\text{C}$ (Farquhar et al. 1982). Leaf $\delta^{15}\text{N}$ in non- N_2 -fixing

species is related to the transpiration efficiency of N acquisition because nitrate reductase in the root preferentially reduces $^{14}\text{NO}_3^-$, leading to a pool enriched in ^{15}N that is transported to shoots through the transpiration stream (Cernusak et al. 2009). Thus hydraulic efficiency has implications for water, carbon and nutrient relations of leaves and appears to function as an overall constraint to leaf metabolic processes.

Trees and lianas are the two major woody growth forms in tropical forests, but several reports, mostly from the neotropics, indicate that the relative abundance of lianas compared to trees is increasing (Phillips et al. 2002, Wright et al. 2004a, Chave et al. 2008, Schnitzer and Bongers 2011, Laurance et al. 2014). Although increasing disturbance and forest fragmentation have been implicated in this change (Schnitzer and Bongers 2011), many of the reports of increasing liana abundance pertain to undisturbed or mature forest (Schnitzer and Bongers 2011, Laurance et al. 2014). Furthermore, other hypotheses to explain the relatively sudden increase in relative abundance of neotropical lianas include changes in precipitation patterns (Schnitzer and Bongers 2011, Schnitzer et al. 2015). Thus differences in the hydraulic function of trees and lianas could have important implications for the competitive balance between these two growth forms during climate change. We sought to compare the hydraulic physiology of upper canopy trees and lianas in a seasonally dry tropical forest to test whether trade-offs between safety and efficiency of water transport shape differences in hydraulic function between these two major tropical woody growth forms. Our main study questions were: How do stem hydraulic traits and wood biophysical properties differ between trees and lianas? Is there evidence of a trade-off between safety and efficiency of water transport? What are the relationships between leaf water usage and stem hydraulic traits? How do hydraulic traits affect leaf chemistry and photosynthetic potential?

Materials and methods

Study site and species

The study was conducted in a lowland tropical forest in Parque Natural Metropolitano, Panamá (8°59'N, 79°33'W). The site is a seasonally dry semi-deciduous forest with wet seasons occurring between May and November and a mean annual precipitation of 1865 mm. The soils are well-drained clays and composed of volcanic substrate (Santiago et al. 2004b). Measurements were conducted on six tree species and six liana species (Table 1) accessible from a canopy crane maintained by the Smithsonian Tropical Research Institute (STRI). The crane is equipped with a gondola suspended by cables from a rotating arm that enables access to approximately 0.85 ha of forest and 30–40 m canopy height. Measurements were made between 1 June and 8 September 2012, during the early and mid-wet season. All species were sampled at the top of the canopy. For each species, we measured six individuals except *Cordia alliodora* (Ruiz & Pav.) Cham. ex A. DC., which has only three individuals accessible from the crane.

Table 1. Plant species, growth form classification, family, symbol and phenology from Parque Metropolitano Natural. Phenology is based on Croat (1978).

Species	Family	Symbol	Phenology
Tree species:			
<i>Anacardium excelsum</i> (Bertero & Balb. ex Kunth) Skeels	Anacardiaceae	▲	Evergreen
<i>Annona spraguei</i> Saff.	Annonaceae	●	Semi-deciduous

<i>Antirrhoea trichantha</i> Hemsl.	Rubiaceae	■	Deciduous
<i>Astronium graveolens</i> Jacq.	Anacardiaceae	◆	Semi-deciduous
<i>Cordia alliodora</i> (Ruiz & Pav.) Cham. ex A. DC.	Boraginaceae	⬢	Deciduous
<i>Luehea seemanii</i> Triana & Planch.	Malvaceae	★	Evergreen
Liana species:			
<i>Arrabidaea patellifera</i> (Schltdl.) Sandwith	Bignoniaceae	△	Evergreen
<i>Combretum fruticosum</i> (Loefl.) Fawc. & Rendle	Combretaceae	○	Deciduous
<i>Dolioscarpus dentatus</i> (Aubl.) Standl.	Dilleniaceae	□	Evergreen
<i>Hiraea reclinata</i> Jacq.	Malpighiaceae	◇	Evergreen
<i>Mikania leiostachya</i> Benth.	Asteraceae	⬡	Evergreen
<i>Serjania mexicana</i> L. (Wild.)	Sapindaceae	☆	Evergreen

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Water potential and stomatal conductance

Three upper canopy leaves with full sun exposure from three individuals per species were cut at the petiole and then immediately bagged and stored in a dark cooler to prevent further transpiration. Sampling occurred between 1100 and 1300 h for midday bulk leaf water potential ($\psi_{\text{leaf md}}$; MPa) and between 0330 and 0630 h for pre-dawn bulk leaf water potential ($\psi_{\text{leaf pd}}$; MPa) on the same branches, and measurements were stratified among species in three rounds to avoid bias in timing of measurement. Measurements of $\psi_{\text{leaf md}}$ and $\psi_{\text{leaf pd}}$ were determined within 10 min of collection using a Scholander pressure chamber (Model 600D; Plant Moisture Stress Instruments, Albany, OR, USA). The diurnal range of ψ_{leaf} ($\Delta\psi_{\text{leaf}}$) was calculated from the difference between $\psi_{\text{leaf md}}$ and $\psi_{\text{leaf pd}}$. Maximum stomatal conductance ($g_{s \text{ max}}$) was measured with a steady-state porometer (SC-1 Leaf Porometer; Decagon Devices, Pullman, WA, USA) between 0900 and 1100 h.

Stem hydraulic conductivity, vulnerability curve, and safety margin

One sun exposed terminal branch (1.0–2.5 m in length) from each individual was collected from the top of the canopy between 0700 and 0900 h for measurements of hydraulic parameters. Cut ends of branches were sealed with parafilm and immediately placed in two layers of opaque plastic bags with moist paper towels to prevent further transpiration. Samples were transported to the STRI Earl S. Tupper Facility in Ancón, Panama within 1 h. In the laboratory, the recently collected 1.0 cm diameter stems were cut under water to a length of 20 cm. Liana samples were cut to include an internode and two nodes located between the cut ends (Jacobsen and Pratt 2012). Stem hydraulic conductivity (K_H ; $\text{kg m s}^{-1}\text{MPa}^{-1}$) was measured by connecting the stem to tubing filled with a degassed 20 mM KCl perfusion solution filtered through a 0.1- μm capsule filter (GE Water & Process Technologies, Trevose, PA, USA), with the basal end connected to an elevated fluid reservoir and the terminal end connected to a 1-ml pipette (KIMAX-51; Kimble Chase, Vineland, NJ, USA) to determine the flow rate from changes in volume over time. The pressure head was maintained below 2 kPa to avoid refilling open vessels (Jacobsen and Pratt 2012, Tobin et al. 2013). Before and after measurement, background flow was measured for 5 min without a pressure head to confirm that no stem passive water uptake occurred (Torres-Ruiz et al. 2012). K_H was measured as the pressure-driven flow divided by the pressure gradient (Sperry et al. 1988). Native stem hydraulic conductivity ($K_{H \text{ native}}$) was determined prior to removing emboli from stems. Stem ends were then cleanly shaved with a razor blade and the stem was cut to a standard sample length of 14.2 cm prior to determination of maximum K_H ($K_{H \text{ max}}$), after emboli were removed by vacuum infiltration under filtered water for at least 12 h.

Xylem vulnerability to cavitation was determined with vulnerability curves generated using the standard centrifugation method (Alder et al. 1997), in which conductivity is measured outside the centrifuge between inducing negative xylem pressures using the centrifuge. Several studies have demonstrated that no long-vessel artifact occurs with the static centrifugation method (Jacobsen and Pratt 2012, Sperry et al. 2012, Tobin et al. 2013, Hacke et al. 2015). Maximum xylem vessel lengths among our study species varied from 22 to 140 cm (Johnson et al. 2013, Louis Santiago, unpublished data). Stems were mounted in a 14.2-cm-diameter custom rotor in a refrigerated centrifuge (Sorvall RC-5C; Thermo Fisher Scientific, Waltham, MA, USA) with stem ends submerged in the 20 mM KCl perfusion solution contained in L-shaped reservoirs. Foam cosmetic sponges were added to the L-shaped reservoirs to soak up excess solution to keep stem ends in contact with solution even when the rotor was not spinning (Jacobsen and Pratt 2012, Tobin et al. 2013, Hacke et al. 2015). The solution volume in each reservoir

was maintained at the same volume to prevent induction of flow during centrifugation. K_H was measured after each spin and the process was repeated until >90% of stem K_H was lost.

We expressed K_H as sapwood-specific conductivity (K_S ; $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$), through normalizing values by sapwood area, calculated as the difference between xylem and pith cross-sectional area. We also expressed conductivity as leaf-specific conductivity (K_L ; $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) through normalizing values by total leaf area distal to the conducting stem. Accordingly, $K_{H \text{ max}}$ was expressed as maximum sapwood-specific hydraulic conductivity ($K_{S \text{ max}}$) and maximum leaf-specific conductivity ($K_{L \text{ max}}$). Resistance to drought-induced xylem cavitation was expressed as P_{50} , the water potential at which 50 percent loss of conductivity (PLC) occurs in vulnerability curves. Hydraulic safety margins were derived from the vulnerability to cavitation curve following Meinzer et al. (2009) where the air entry threshold (P_e) is calculated as the x-intercept of the line tangent to P_{50} . The change in PLC after P_e is reached was calculated as $P_e - P_{50}$, where high values indicate a more gradual increase in PLC when xylem water potential falls below P_e . Leaf area to sapwood area ratio (LA:SA) was calculated by dividing the total leaf area distal to the conducting stem by the sapwood area.

Xylem capacitance and wood biophysical properties

Stem samples 0.5 m long and 0.5–1.5 cm in diameter were collected from study individuals between 0700 and 0900 h. One subsample was immediately separated for measurement of native stem water potential ($\psi_{\text{stem native}}$) in a thermocouple psychrometer chamber (83-1V Large Chamber Thermocouple Psychrometer; Merrill Instruments, Logan, UT, USA) connected to a data logger (PSΨPRO; Wescor, Logan, UT, USA), whereas the rest of the branch was re-cut under water to a length of 20 cm and rehydrated overnight. For measurement of xylem water potential (ψ_x), stem samples were cut to 3 cm segments under water, the bark and pith were removed, samples were blotted with a paper towel, weighed on an analytical balance (Sartorius AG, Goettingen, Germany) to determine saturated mass, and immediately sealed in a thermocouple psychrometer chamber (83-3VC, Merrill Instruments). Three to six segments were used for each species to fill psychrometric chambers. The psychrometer chambers were allowed to equilibrate in an insulated water bath at room temperature (24 °C) for about 4 h, which was the amount of time to reach the first stable reading. ψ_x was measured in psychrometric mode using an automated multi-channel microvoltmeter (CR7; Campbell Scientific, Logan, UT). After the determination of ψ_x , the psychrometer chambers were removed from the water bath, partially dehydrated in a 40 °C oven, re-weighed, resealed in psychrometer chambers, and re-equilibrated in chambers for the next determination of ψ_x . This was repeated 7–10 times until the tissue reached ψ_x values of –3.0 to –7.0 MPa depending on the species. Following final determination of ψ_x , samples were dried at 100 °C for 1 h and then at 60 °C for 48 h and weighed to calculate tissue dry mass and water released. Capacitance (C ; $\text{kg m}^{-3} \text{MPa}^{-1}$) was calculated as the slope of the near linear portion in the initial part of the xylem water release curve (Meinzer et al. 2003, 2009). Wood density (ρ_{wood}) was calculated as dry mass divided by fresh tissue volume.

Leaf traits and chemistry

Samples of 1–10 young fully mature leaves, depending on the leaf sizes of different species, distal to the section used for hydraulic measurements were collected from each of the sample branches of each species. For measurement of SLA (area divided by dry mass), 5–30 leaves were measured with an area meter and dried in an oven for 60 °C for 48 h and weighed. For chemical analysis, leaves were placed in a coin envelope and dried in an oven at 60 °C for 48 h. For large leaved species, intercostal tissue was

collected between the mid-rib and the periphery at the centre of the leaf. Samples were ground and homogenized using a mill (8000D Dual Mixer/Mill; SPEX SamplePrep, Metuchen, NJ, USA). Homogenized samples of 1–2 mg were weighed and rolled in foil capsules. Samples were sent to the Facility for Isotope Ratio Mass Spectroscopy (FIRMS), University of California, Riverside, for analysis of total leaf nitrogen concentration (N), and isotopic composition of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$). Leaf N was expressed per unit leaf mass (N_{mass}) and per unit area (N_{area}) by dividing the mass-based values by SLA.

Statistical analysis

Student's t -tests were used to evaluate differences of trait means between tree and liana species in R (R Core Team 2015). Mann–Whitney U tests were used for comparisons with non-normal distribution. We evaluated bivariate trait relationships with Pearson product–moment correlation using the Hmisc package in R . The leverage potential of x -variable outliers was analyzed with the hat matrix procedure (Neter et al. 1990). Phylogenetic independent contrasts (PIC) were analyzed using Phylocom (Webb et al. 2008). Alpha was set at 0.05 for all comparisons. Normality tests were conducted prior to testing correlations. Non-normally distributed data were \log_{10} -transformed and absolute values were calculated prior to transformation for values that are normally reported as negative. Principal components analysis (PCA) was done with PAST statistical software (Hammer et al. 2001), using the 21 physiological variables on the 12 canopy liana and tree species (see Table S1 available as Supplementary Data at [Tree Physiology Online](#)). We determined values for P_{50} using the best-fit non-linear regression to a Weibull function.

Results

We observed statistically significant variation between lianas and trees in 13 out of 21 physiological traits studied. Xylem vulnerability curves indicated that trees had more negative mean P_{50} values than lianas (Table 2), indicating greater resistance to drought-induced cavitation. Values for C were greater in trees than lianas (Table 2), indicating a greater ability to supply the water needed to limit rapid drops in water potential. However, water transport capacity expressed as $K_{S \text{ max}}$, and $K_{L \text{ max}}$ were significantly higher in lianas than in trees. Values for $K_{S \text{ native}}$ were also greater in lianas than in trees, but values for $K_{L \text{ native}}$ were statistically indistinguishable (Table 2).

Table 2. Summary of traits for tree and liana growth forms. The values are reported as mean \pm SE. Test statistics reported are from either Student's t -test or Mann–Whitney U test.

Variable	Tree	Liana	Test statistic	P -value
P_{50} (MPa)	-0.70 ± 0.08	-0.35 ± 0.04	4.06	<0.001
C ($\text{kg m}^{-3} \text{MPa}^{-1}$)	453 ± 41	273 ± 23	-3.83	<0.001
$K_{S \text{ max}}$ ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$)	5.31 ± 0.73	10.50 ± 1.75	2.87	0.007
$K_{L \text{ max}}$ ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$)	$0.60 \times 10^{-3} \pm 0.09 \times 10^{-3}$	$0.99 \times 10^{-3} \pm 0.15 \times 10^{-3}$	2.27	0.026
$K_{S \text{ native}}$ ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$)	1.63 ± 0.29	3.82 ± 0.75	2.73	0.009
$K_{L \text{ native}}$ ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$)	$0.23 \times 10^{-3} \pm 0.05 \times 10^{-3}$	$0.39 \times 10^{-3} \pm 0.08 \times 10^{-3}$	1.78	0.079
$\Delta\Psi_{\text{leaf}}$ (MPa)	0.69 ± 0.10	0.98 ± 0.08	2.38	0.023
$\Psi_{\text{leaf pd}}$ (MPa)	-0.30 ± 0.03	-0.33 ± 0.03	145	0.591
$\Psi_{\text{leaf md}}$ (MPa)	-0.99 ± 0.09	-1.31 ± 0.08	-2.72	0.010
$\Psi_{\text{stem native}}$ (MPa)	-0.62 ± 0.06	-0.81 ± 0.07	-2.06	0.043
P_e (MPa)	$59 \times 10^{-3} \pm 17 \times 10^{-3}$	$56 \times 10^{-3} \pm 19 \times 10^{-3}$	652	0.696
$P_e - P_{50}$ (MPa)	0.72 ± 0.07	0.39 ± 0.04	304	<0.001

$g_{s \max}$ (mmol m ⁻² s ⁻¹)	169 ± 15	193 ± 19	0.978	0.335
ρ_{wood} (g cm ⁻³)	0.34 ± 0.01	0.43 ± 0.03	2.74	0.009
LA:SA (m ² m ⁻²)	8323 ± 611	14498 ± 1987	720	0.042
SLA (cm ² g ⁻¹)	138 ± 8.8	148 ± 7.8	-0.697	0.489
d_{branch} (mm)	8.58 ± 0.33	5.75 ± 0.15	-7.79	<0.001
$\delta^{15}\text{N}$ (‰)	1.35 ± 0.20	0.79 ± 0.21	-1.90	0.061
$\delta^{13}\text{C}$ (‰)	-29.9 ± 0.23	-30.3 ± 0.21	-1.08	0.283
N_{mass} (mg g ⁻¹)	23.5 ± 1.15	21.3 ± 0.72	503	0.202
N_{area} (g cm ⁻²)	0.18 ± 0.009	0.16 ± 0.009	-2.08	0.042

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$\delta^{13}\text{C}$ (‰)	-29.9 ± 0.23	-30.3 ± 0.21	-1.08	0.283
N_{mass} (mg g ⁻¹)	23.5 ± 1.15	21.3 ± 0.72	503	0.202
N_{area} (g cm ⁻²)	0.18 ± 0.009	0.16 ± 0.009	-2.08	0.042

Lianas experienced a greater daily change in water potential, with greater $\Delta\psi_{\text{leaf}}$ than trees and this was driven by more negative $\psi_{\text{leaf md}}$ and $\psi_{\text{stem native}}$ in lianas, because there were no differences between trees and lianas for $\psi_{\text{leaf pd}}$ (Table 2). There were no differences in air entry threshold (P_e), but hydraulic safety margin ($P_e - P_{50}$) was greater in trees than in lianas (Table 2). There was no difference between the two growth forms in $g_{s \max}$ (Table 2). Lianas showed greater values of ρ_{wood} and LA:SA than trees, but had narrower terminal stem diameters (d_{branch} ; Table 2). We also measured greater N_{area} in trees than in lianas, but there were no differences in $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, N_{mass} or SLA (Table 2).

Vulnerability curves were 's' shaped for *Antirrhoea trichantha* and *Anacardium excelsum*, and 'r' shaped for all other species (Figure 1). Whereas liana species showed high (>-1.0 MPa) values for P_{50} , they also had very high values of $K_{S \max}$ up to 27.8 kg m⁻¹ s⁻¹ MPa⁻¹ such that most of these species still had a K_S above 5 kg m⁻¹ s⁻¹ MPa⁻¹ as loss of hydraulic conductivity rose above 50% (Figure 1). Tree species showed lower values of K_S at 50% loss of conductivity and overall more gradual loss of hydraulic conductivity as water potential decreased compared to lianas (Figure 1). We found evidence of a significant correlation and trade-off between water transport capacity and resistance to drought-induced xylem cavitation, as species with high $K_{S \max}$ tended to exhibit less negative P_{50} (Figure 2, Table 3). Values for $K_{S \max}$ were also positively correlated with LA:SA ($P = 0.02$; Table 3), whereas K_L

native was negatively correlated with LA:SA only among tree species ($r = -0.85$, $P = 0.03$). P_{50} was negatively correlated with LA:SA ($P = 0.03$; Table 3) and P_e was negatively correlated with ρ_{wood} ($P = 0.04$; Table 3). Among tree species, $P_e - P_{50}$ was negatively correlated with LA:SA ($r = -0.93$, $P = 0.008$).

Table 3. Pearson product–moment correlation coefficients (r) for species traits are given in the upper right section of the matrix ($n = 12$).

	ρ_{wood}	C	P_{50}	K_S max	K_L max	P_e	Ψ_{leaf} pd	Ψ_{leaf} md	g_s max	LA:SA	d_{branch}
ρ_{wood}		-0.508	-0.068	-0.216	0.053	-0.600	-0.386	-0.534	-0.250	-0.201	-0.279
C	-0.496		0.209	-0.011	-0.003	0.443	-0.039	0.590	-0.066	-0.045	0.242
P_{50}	-0.041	0.260		0.650	0.512	0.534	-0.111	-0.238	0.305	0.630	-0.540
K_S max	-0.061	-0.142	0.727		0.800	0.403	0.186	-0.268	0.232	0.653	-0.243
K_L max	0.271	-0.008	0.718	0.841		0.349	0.106	-0.432	0.327	0.207	-0.329
P_e	-0.597	0.382	0.620	0.442	0.433		-0.079	0.334	0.744	0.292	-0.063
Ψ_{leaf} pd	-0.410	-0.147	-0.564	0.270	0.390	-0.184		-0.064	-0.110	-0.037	0.279
Ψ_{leaf} md	-0.601	0.494	-0.301	-0.375	-0.553	0.273	-0.278		0.073	-0.225	0.661
g_s max	-0.309	-0.260	0.337	0.335	0.368	0.790	-0.197	0.127		0.155	-0.291
LA:SA	-0.217	-0.173	0.605	0.813	0.361	0.333	-0.475	-0.332	0.141		-0.426
d_{branch}	-0.225	0.090	-0.625	-0.354	-0.424	-0.181	0.633	0.619	-0.237	-0.555	

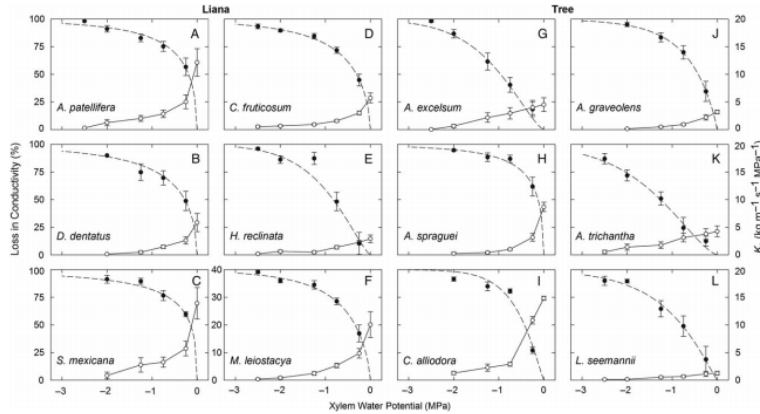
Correlation coefficients for independent contrasts are given in the lower left section of the matrix ($n = 12$). Bold type indicates significant correlations ($P \leq 0.05$).

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	ρ_{wood}	C	P_{50}	K_S max	K_L max	P_e	Ψ_{leaf} pd	Ψ_{leaf} md	g_s max	LA:SA	d_{branch}
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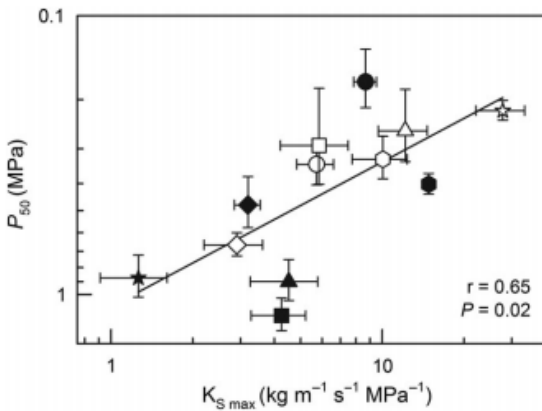
Correlation coefficients for independent contrasts are given in the lower left section of the matrix ($n = 12$). Bold type indicates significant correlations ($P \leq 0.05$).

Figure 1.



Xylem vulnerability to cavitation curves of lianas (A–F) and trees (G–L) during the wet season (June – August 2012; mean \pm SE; $n = 6$, except for *C. alliodora* with $n = 3$) expressed as PLC (closed circle symbol and broken line) and expressed as hydraulic conductivity values (K_s , open circle symbol and solid line). Only *S. mexicana* (C) has a different K_s scale, which is indicated to the right of the plot.

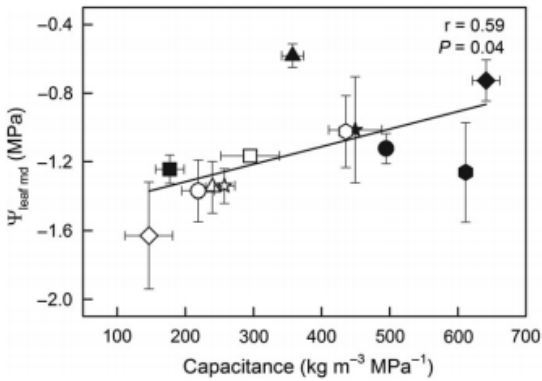
Figure 2.



Relationship between maximum sapwood-specific conductivity and pressure causing 50% loss in hydraulic conductivity. Each symbol represents the mean \pm SE for each species ($n = 6$, $n = 3$ for *C. alliodora*). Corresponding species and symbols are found in Table 1. Closed symbols represent tree species and open symbols represent liana species.

There was a positive correlation between C and $\psi_{\text{leaf md}}$ (Figure 3, Table 3), indicating that high values for C buffer sapwood reached more negative values of ψ_{leaf} . We found that C was significantly correlated with P_{50} within the tree growth form ($r = 0.81$, $P = 0.05$), but did not vary significantly with P_{50} within lianas or across all species (Table 3). Among lianas, C was negatively correlated with ρ_{wood} ($r = -0.91$, $P = 0.01$), but not among trees or across all species (Table 3).

Figure 3.

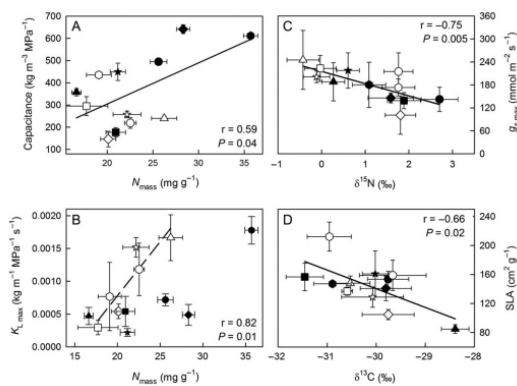


Relationship between capacitance and midday leaf water potential. Each symbol represents the mean \pm SE for each species ($n = 3$). Corresponding species and symbols can be found in Table 1. Closed symbols represent tree species and open symbols represent liana species.

We found evidence of coordination between leaf water status and stem traits. d_{branch} was positively correlated with $\Psi_{\text{leaf md}}$ ($P = 0.02$; Table 3) across species, and within lianas $\Psi_{\text{leaf md}}$ was positively correlated with ρ_{wood} ($r = 0.88$, $P = 0.02$) and SLA ($r = -0.82$, $P = 0.05$). We also found evidence of coordination between gas exchange and stem traits where $g_{s \text{ max}}$ was positively correlated with P_e ($P = 0.006$; Table 3). Within the liana growth form, $g_{s \text{ max}}$ was positively correlated with P_{e-50} ($r = 0.88$, $P = 0.02$). Within lianas, $\delta^{13}\text{C}$ was positively correlated with ρ_{wood} ($r = 0.82$, $P = 0.05$) and $\Psi_{\text{leaf md}}$ ($r = 0.84$, $P = 0.04$), and negatively correlated with C ($r = -0.85$, $P = 0.03$).

Among leaf traits, N_{mass} was positively correlated with C ($P = 0.04$; Figure 4A) across all species and with $K_{L \text{ max}}$ within lianas ($P = 0.03$; Figure 4B), but no relationship was found within trees because the point for *C. alliodora* failed the hat matrix procedure test for outliers. $\delta^{15}\text{N}$ was negatively correlated with $g_{s \text{ max}}$ ($r = -0.75$, $P = 0.005$; Figure 4C), and $\delta^{13}\text{C}$ was negatively correlated with SLA ($P = 0.02$; Figure 4D). N_{area} was also negatively correlated with SLA ($r = -0.64$, $P = 0.02$). Among lianas N_{area} was positively correlated with $\Psi_{\text{leaf md}}$ ($r = 0.90$, $P = 0.01$) and was negatively correlated with C ($r = -0.89$, $P = 0.01$).

Figure 4.



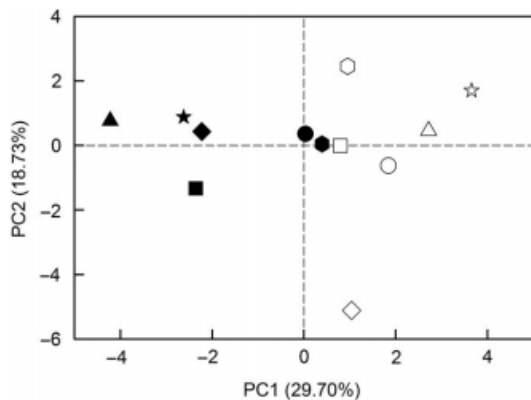
The relationship between leaf nitrogen per mass (N_{mass}) and (A) capacitance and (B) maximum leaf-specific hydraulic conductivity ($K_{L \text{ max}}$); between (C) leaf N isotopic composition ($\delta^{15}\text{N}$) and maximum stomatal conductance ($g_{s \text{ max}}$); and between (D) leaf C isotopic composition ($\delta^{13}\text{C}$) and SLA. No relationship occurred for trees

between N_{mass} and $B K_{L \text{ max}}$ due to failing the outlier test. Corresponding species and symbols are found in Table 1. Closed symbols represent tree species and open symbols represent liana species. Each symbol represents the mean \pm SE for each species ($n = 6$, $n = 3$ for *C. alliodora*). Solid line represent correlations that include both trees and lianas while broken line represent correlation for lianas only.

All of the cross-species correlations, except the relationship between $\Psi_{\text{leaf md}}$ and C were also significant when evaluated as PICs (Table 3). We found more correlations in PICs than in cross-species correlations, especially those related to ρ_{wood} , P_{50} and d_{branch} , indicating that these correlations are the products of repeated evolutionary divergences in plant traits through evolutionary time, as well as being functionally correlated among extant species today. In addition to the significant relationship with $K_{S \text{ max}}$, P_{50} was also related to $K_{L \text{ max}}$ and P_e in PICs (Table 3). PIC analysis also showed significance in $\rho_{\text{wood}}-\Psi_{\text{leaf md}}$, $d_{\text{branch}}-P_{50}$ and $d_{\text{branch}}-\Psi_{\text{leaf md}}$ relationships, which were not observed in cross-species analysis (Table 3).

The first PCA axis accounted for 29.70% of the variance (Figure 5). The highest absolute eigenvector scores for the negative range of the first PCA axis were the hydraulic safety margin P_e-P_{50} , $\Psi_{\text{leaf md}}$, and d_{branch} , whereas more vulnerable P_{50} values, $\Delta\Psi_{\text{leaf}}$, and $K_{S \text{ max}}$ loaded on the positive range of the first PCA axis. The second PCA axis accounted for 18.73% of the variance (Figure 5). The highest absolute eigenvector scores for the negative range of the second PCA axis were ρ_{wood} and P_e , whereas $K_{S \text{ native}}$ and $g_{S \text{ max}}$ loaded on the positive range of the second PCA axis.

Figure 5.



Principal components analysis ordination for tree species (closed symbols) and liana species (open symbols) based on 21 traits measured. The percentages in the axis labels indicate the variance explained by the axis. Corresponding species and symbols are found in Table 1.

Discussion

Our physiological measurements support the existence of a trade-off between efficiency, in the form of water transport capacity ($K_{S \text{ max}}$) and safety, in the form of resistance to drought-induced xylem cavitation (P_{50}) in trees and lianas. We found that trees exhibited greater resistance to water-stress-induced cavitation with more negative P_{50} values, higher capacitance, and a greater safety margin. In comparison lianas exhibited higher conductive capabilities than coexisting tree species, based on greater values of $K_{S \text{ max}}$, $K_{L \text{ max}}$, and $K_{S \text{ native}}$. Our PCA analysis confirmed that trees and lianas separate along a principal axis determined by P_{50} and $K_{S \text{ max}}$, among other variables. These results demonstrate that trees use more conservative strategies to maintain the soil-to-leaf hydraulic pathway than do lianas (Johnson

et al. 2013). Indeed our data demonstrate that most lianas exhibit higher absolute conductivity than trees even as they lose a higher percentage of conductive capability with declining water potential. The interspecific negative bivariate relationship between P_{50} and $K_{S \max}$ agrees with previous findings of trade-offs between drought resistance and hydraulic transport (Pockman and Sperry 2000, Maherali et al. 2004, Gleason et al. 2015), and illustrates how this relationship may structure a diverse assemblage of hydraulic strategies and competitive balance of trees and lianas in neotropical forest with regards to site water balance.

Plotting the reduction in K_S with declining water potential in vulnerability curves revealed patterns that are obscured by only examining PLC. Although lianas show a rapid decrease in K_S with declining water potential and P_{50} values ranging from -0.22 to -0.66 MPa, their high values of $K_{S \max}$ result in relatively high values of K_S remaining even after losing more than 50% of hydraulic conductivity. For example, all liana species except *H. reclinata* showed K_S values above $5 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ after losing more than 50% of hydraulic conductivity, which is greater than 90% of the angiosperms investigated in the recent global meta-analysis of hydraulic safety versus efficiency (Gleason et al. 2015). This pattern is likely due to heteroxily in lianas, in which a wide variation in vessel sizes can be found in individual stems (Gentry 1996, Rowe and Speck 2005). The rapid decrease in hydraulic conductivity with declining water potential in lianas could represent the cavitation of a few of the largest vessels which might contribute disproportionately to high K_S , but might also be more vulnerable to cavitation by water stress. By contrast, trees showed a more gradual increase in PLC with declining water potential, resulting in a more conservative strategy than lianas. Our findings are consistent with previous studies at this site comparing lianas and trees. In comparing the tree species *A. excelsum* and two liana species, Johnson et al. (2013) also found lianas to be more vulnerable to cavitation. Yet, they reported similar values for K_S and ρ_{wood} between lianas and trees, which differs from our study because, when we added five other tree species and four other liana species to the comparison, we found that lianas had greater K_S and denser wood than trees.

Our findings that lianas had greater LA:SA than trees and that $K_{L \max}$ was related to N_{mass} only for lianas suggest potential benefits in terms of photosynthetic productivity with high K_S in lianas in this seasonally dry forest. Both LA:SA and $K_{L \max}$ are indices of water supply to leaves and the increase in N_{mass} with $K_{L \max}$ in lianas supports the idea that plants are expected to allocate relatively greater photosynthetic capacity as water supply to leaves increases in order to take advantage of a high supply of CO_2 for photosynthesis (Santiago et al. 2004a). Greater K_L in lianas than in trees has been found in previous analyses comparing hydraulic capacity of lianas and trees (Patiño et al. 1995, Santiago et al. 2015), and is consistent with lianas as a hydraulically efficient growth form that occur on the fast-return side of the leaf economics spectrum (Wright et al. 2004, Maire et al. 2015). The extension of greater K_L to greater photosynthetic potential is also consistent with an analysis demonstrating greater concentrations of metabolically active elements in lianas and trees across 48 tropical forest sites (Asner and Martin 2012). However, at high precipitation sites ($>2500 \text{ mm rainfall yr}^{-1}$), lianas may lose their elevated leaf elemental concentration advantage to trees (Santiago and Wright 2007, Asner and Martin 2012). Further linkages between stem and leaf coordination of water loss and potential carbon gain were not evident in results of leaf $\delta^{13}\text{C}$ as there were no significant differences between lianas and trees. The only pattern in leaf $\delta^{13}\text{C}$ was a significant negative relationship with SLA indicating that thicker leaves incorporated more ^{13}C likely due to reduced CO_2 diffusion rates and low C_i in thick leaves (Vitousek et al. 1990). Leaf $\delta^{15}\text{N}$ showed a significant negative relationship with $g_{S \max}$ and significantly lower values in

lianas than in trees, consistent with greater transpiration efficiency of N uptake in trees with lower rates of stomatal conductance (Cernusak et al. 2009).

Our study produced several striking results concerning biophysical properties of wood. First, lianas showed greater wood density than trees. We originally expected greater wood density in trees because of the well-known presence of large vessels in liana stems (Ewers and Fisher 1991). However, it is critical to note that not only large vessels characterize liana stems, but also heteroxyle, the presence of a broad distribution of vessel sizes (Rowe and Speck 2005). Furthermore, wood density is determined by the sum of vessels, fibers, and parenchyma cells, not only vessel size. The high number of vessels packed in liana stems, which is possible due to less investments in fibers for mechanical support, may determine the high wood density in lianas (Ewers et al. 2015). Indeed, high vessel density has been shown to increase wood density (Martínez-Cabrera et al. 2011). Our data are also consistent with at least one study from Parque Natural Metropolitano which reported dense wood in lianas (Johnson et al. 2013), and also consistent with a previous finding that high wood density results in greater fluctuations in leaf water potential (Meinzer 2003). Therefore, although wood density as a functional trait is generally related to growth and water transport capacity (Santiago et al. 2004a, Poorter et al. 2008), actual measures of stem anatomy are likely to determine the physiological roles of wood density and vessel size in hydraulic architecture.

The second striking result from our study illustrates that C is greater in trees than in lianas, is related to $\psi_{\text{leaf md}}$ and is also related to N_{mass} . Thus, C appears to buffer leaves from rapid drops in water potential during high rates of transpiration. Additionally, C plays an important role in supplying water in species with a deciduous leafing habit (Wolfe and Kursar 2015) and might also provide a physical space for a large reservoir of N needed for rapidly developing new leaves, and thus requires further investigation in seasonally dry tropical forests where many species, particularly trees, tend to be drought deciduous. Significantly lower LA:SA in trees also appears to promote a strong buffering effect on $\psi_{\text{leaf md}}$. Finally, trees have greater terminal canopy stem diameters, a common denominator that is positively correlated with pre-dawn and midday water potential and negatively with P_{50} , and generally reduces shifts in leaf water potential and augments time lags of trees due to stem water storage (Goldstein et al. 1998, Phillips et al. 1999).

In terms of increasing liana relative abundance in neotropical forests, our study represents the first comprehensive analysis of hydraulic safety and efficiency of a group of naturally established mature canopy tree and liana species. Our finding that lianas exhibit greater water transport capacity at the expense of vulnerability to drought-induced xylem cavitation suggests that hydraulic physiology could be a mechanism contributing to changes in relative abundance of lianas and trees in neotropical forests, especially if changes in temperature and precipitation patterns produce substantial alterations of water balance. Several studies document increases in liana density that coincide with long-term reductions in precipitation (Wright et al. 2004a, Wright and Calderón 2006, Ingwell et al. 2010, Schnitzer et al. 2012), yet a new long-term study shows increased liana relative abundance in undisturbed Amazonian forest with no significant change in local precipitation (Laurance et al. 2014). Thus, whether it is changes in temperature, evaporative demand, precipitation, or other factors that are driving liana increases in the neotropics, the greater water transport capacity in lianas than in trees, along with greater potential belowground resource acquisition in lianas (Chen et al. 2015, Collins et al. 2016), represent mechanisms that could promote liana increases relative to trees. Yet, if climate change continues unabated, we are likely to see the development of tropical environments not previously observed in Earth's history

(Chambers et al. 2013), with habitats receiving greater than 3000 mm of precipitation with mean annual temperatures >30 °C. As temperatures and evaporative demand increase, greater vulnerability to drought-induced cavitation in lianas might become detrimental to their growth and survival, which could shift the competitive advantage back to trees. Overall, it appears that the hydraulic safety versus efficiency trade-off may shape differences in hydraulic function between lianas and trees with major implications for their relative abundance during climate change.

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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