

**CONTRASTING HYDRAULIC STRATEGIES IN TWO TROPICAL
 LIANAS AND THEIR HOST TREES¹**

DANIEL M. JOHNSON^{2,6}, JEAN-CHRISTOPHE DOMEQ^{2,3}, DAVID R. WOODRUFF⁴,
 KATHERINE A. MCCULLOH⁵, AND FREDERICK C. MEINZER⁴

²Nicholas School of the Environment, Duke University, Durham, North Carolina 27708, USA; ³Bordeaux Sciences AGRO, UMR 1220 TCEM INRA, 1 Cours du général de Gaulle, 33175 Gradignan Cedex, France; ⁴USDA Forest Service, Pacific Northwest Research Station, Corvallis, Oregon 97331, USA; and ⁵Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon 97331, USA

- *Premise of the Study:* Tropical liana abundance has been increasing over the past 40 yr, which has been associated with reduced rainfall. The proposed mechanism allowing lianas to thrive in dry conditions is deeper root systems than co-occurring trees, although we know very little about the fundamental hydraulic physiology of lianas.
- *Methods:* To test the hypothesis that two abundant liana species would physiologically outperform their host tree under reduced water availability, we measured rooting depth, hydraulic properties, plant water status, and leaf gas exchange during the dry season in a seasonally dry tropical forest. We also used a model to compare water use by one of the liana species and the host tree during drought.
- *Key Results:* All species measured were shallowly rooted. The liana species were more vulnerable to embolism than host trees and experienced water potentials that were predicted to result in substantial hydraulic losses in both leaves and stems. Water potentials measured in host trees were not negative enough to result in significant hydraulic losses. Model results predicted the liana to have greater gas exchange than its host tree during drought and nondrought conditions.
- *Conclusions:* The host tree species had a more conservative strategy for maintenance of the soil-to-leaf hydraulic pathway than the lianas it supported. The two liana species experienced embolism in stems and leaves, based on vulnerability curves and water potentials. These emboli were presumably repaired before the next morning. However, in the host tree species, reduced stomatal conductance prevented leaf or stem embolism.

Key words: *Anacardium excelsum*; drought stress; embolism; gas exchange; *Prionostemma aspera*; transpiration; *Trichostigma octandrum*; water relations.

Liana abundance is increasing across all tropical regions (Phillips et al., 2002; Schnitzer and Bongers, 2011), resulting in dramatically different forest composition and, potentially, forest functions (e.g., carbon, water, and nutrient cycling). Although lianas can account for as much as 40% of forest leaf biomass (Putz, 1984), thus potentially contributing to a large portion of the evaporative water loss and carbon gain in tropical forest canopies, we know substantially more about the physiological processes that regulate water transport and carbon acquisition for tropical forest trees than for lianas (Andrade et al., 1998; Malhi et al., 1999; James et al., 2003; Meinzer et al., 2008). Given that tropical forests constitute approximately one-third of global net terrestrial productivity (e.g., Field et al., 1998), it is important that we have a better understanding of the ecology and physiology of these understudied growth forms, and how they interact with each other and compete for the same resources.

Lianas typically have high capacity for water transport, transpiration, and photosynthesis (Gartner et al., 1990; Ewers et al.,

1991; Cai et al., 2009; Zhu and Cao, 2009). Previous studies have also suggested that compared to trees, lianas are highly sensitive to soil water depletion, as demonstrated by their low resistance to drought-stress-induced xylem embolism (e.g., Clearwater and Clark, 2003; Zhu and Cao, 2009). Paradoxically, many lianas appear to be able to fix more carbon during the dry seasons than co-occurring trees (Schnitzer et al., 2005; Cai et al., 2009). Although this does not appear to be the case in all systems (Andrade et al., 2005), it seems that some liana species have developed deeper root systems than co-occurring trees, thus allowing them access to deeper pools of water (Jackson et al., 1995).

Lianas compete with host trees both above and below ground for resources, and trees with heavy liana loads often show decreased growth and increased mortality (Schnitzer and Bongers, 2002). It has been proposed that belowground competition for water and nutrients is particularly intense between lianas and co-occurring trees (e.g., Pérez-Salicrup and Barker, 2000; Toledo-Aceves and Swaine, 2008) and is likely stronger than aboveground competition. However, aboveground competition can have deleterious effects on host trees. Leaves of lianas either shade or displace leaves of host trees, reducing the trees' overall ability to fix carbon (Kira and Ogawa, 1971). Lianas impose mechanical stress as well, which can result in trees allocating more resources to structural support (Schnitzer et al., 2005).

The underlying mechanism of lianas' faster growth and canopy colonization is related to maximizing carbon allocation efficiency by producing small stems with large leaf areas instead

¹Manuscript received 7 November 2012; revision accepted 4 December 2012.

This research was supported by National Science Foundation grant IOB-0919871. The authors thank S. Schnitzer and W. Carson for discussions that benefited this study. We also thank A. Roddy for daily critical discussions of ideas and for sharing his equipment and technical knowledge.

⁶Author for correspondence (e-mail: dan.johnson@duke.edu)

of structurally supportive organs, as compared to trees. As a consequence, lianas are typically characterized by low wood density (Ewers et al., 1991; Zhu and Cao, 2009), which is expected to result in differences in hydraulic traits such as greater xylem conductivity and a decrease in resistance to tension-induced embolism (Gartner et al., 1990; Hacke et al., 2001; McCulloh et al., 2011). However, there are several other potential mechanisms that can help in maintaining seasonal constancy of growth under limited soil moisture, including the utilization of stored water (e.g., Pratt et al., 2007; Meinzer et al., 2009), a more negative water potential at which leaves lose turgor, and the development of adaptive hydraulic traits at the leaf level (e.g., refilling mechanisms; Brodribb and Holbrook, 2004; Johnson et al., 2011).

The objective of the present study was to perform an analysis of the water relations and hydraulic properties of two co-occurring lianas and their host trees in the seasonal tropical rainforests of Panama, where liana biomass and abundance have been increasing over the past 40 yr (Ingwell et al., 2010). Specifically, our aims were to test the hypotheses that lianas rely on two features to protect themselves from catastrophic xylem embolism. (1) Leaves should be much more vulnerable to embolism than stems. Leaf embolism should prevent embolism in the stems upstream by causing stomatal closure, as has been observed in previous studies (Salleo et al., 2001; Brodribb et al., 2003; Woodruff et al., 2007), or by hydraulically disconnecting stomata from stems, and thereby preventing dangerously high transpiration-induced stem xylem tensions. (2) Given that xylem capacitance is related to wood density (e.g., Meinzer et al., 2009) and wood density is typically low in lianas (Putz and Holbrook, 1991), lianas may also rely on capacitance to avoid severe stem water potentials that could potentially induce xylem dysfunction. Furthermore, we hypothesized that (3) liana stems would have overall higher hydraulic conductivity (on a stem cross-sectional area basis) as compared to branches of their host trees, because of their reported larger vessel dimensions (Ewers, 1985; Ewers et al., 1991), and (4) that these contrasting hydraulic strategies would allow lianas to be more tolerant of reduced water availability than their host trees.

MATERIALS AND METHODS

Two abundant liana species, *Prionostemma aspera* (Lam.) Miers and *Trichostigma octandrum* (L.) H. Walter, were selected at the Parque Natural Metropolitano (8°59'08.23", 79°32'48.72"), Republic of Panamá, where there was access to multiple individuals from a 35-m-tall construction crane. The Parque site receives ~1800 mm of rainfall annually, but only ~150 mm during the dry season (January–April). Rainfall in 2010 was much greater than normal (~4000 mm), and there was 106 mm rain in the 30 d preceding the measurement period. All measurements were made during the dry season of 2011, between 17 January and 11 February. Lianas were sampled from two large individuals of *Anacardium excelsum* (Balb. ex Kunth) Skeels (91 and 104 cm diameter at breast height, DBH) at a height of 29 to 31 m, in the upper crowns of the trees. It was difficult to determine the number of distinct lianas sampled in the crown of the *A. excelsum*, because there were 16 liana stems below one tree crown and 21 below the other and they were all intertwined. However, there were only four different liana species present in the crowns of each tree, so our estimate is that we sampled 2–5 individuals of each liana species. Using the canopy crane, we were able to follow the stems of several individuals of *Trichostigma* (and were able to excavate roots—see section below on hydraulic conductivity and modeling) from the canopy to the ground, but were unable to follow any *Prionostemma* stems to the forest floor.

Field methods—Field measurements were performed on three to six leaves of each preselected individual on 2, 3, and 5 February 2011, at predawn,

midmorning, and midday on each date. Fully sunlit branches and leaves were chosen for measurement (with the exception of predawn measurements). Statistical analyses were performed using individuals as samples, and sample size (n) was equal to the number of trees or lianas sampled, which was 2 for *Anacardium* and an estimated 3 individuals of *Prionostemma* and *Trichostigma*.

Stomatal conductance (g_s) was measured with a steady-state porometer (LI-1600, LI-COR, Lincoln, Nebraska, USA) and leaf temperatures were measured concomitantly with a fine-wire thermocouple (located in the LI-1600 chamber). Leaf water potential (Ψ_L) was measured using a pressure chamber (PMS Instruments, Albany, Oregon, USA). Additionally, measurements of stem water potential were performed to estimate the amount of native embolism that occurred in stems of the measured individuals. Large disequilibria can exist between stem and leaf water potentials, especially at midday (Bucci et al., 2004). Therefore, it was necessary to bag and cover shoots (with a sealable plastic bag covered in aluminum foil) before dawn and then measure the midday water potential of bagged leaves to get an estimate of stem water potential. The integrated soil water potential over the entire soil depth where roots of an individual were present was taken as predawn Ψ_L corrected for the height at which the leaves were sampled. Additionally, soil water potential (Ψ_{soil}) was estimated by measuring predawn and midday water potentials of seedlings that had been covered with plastic bags before dawn to prevent transpiration. Those measurements allowed us to estimate Ψ_{soil} of the upper soil profile because seedling excavation indicated that their roots were located between 3 cm and 15 cm in depth. Because the nights prior to measurements had high relative humidity and, therefore, low vapor pressure deficits, the seedlings were assumed to have minimal water loss at night and to be in equilibrium with Ψ_{soil} (Dawson et al., 2007; Domec et al., 2010).

Stem and root hydraulic conductivity, vulnerability, capacitance, and wood density—Branches and roots 1 to 3 m in length were collected in the field, bagged, and transported to the laboratory. Estimates of longest vessel length were made using the compressed-air method of Ewers and Fisher (1989), whereby air is forced into the proximal end of the segment at 50–100 kPa and the distal end is submerged under water. Stem segments of 10 cm are cut from the distal end until air bubbles are seen, and the final length of the segment is then taken as the longest vessel length.

Before hydraulic measurements, segments of branches and roots that were $\geq 30\%$ longer than the mean longest vessel for that species and organ were cut under water and were flushed with filtered, distilled water at pH = 2 to prevent microbial growth. Mean shoot sample lengths for *Anacardium*, *Prionostemma*, and *Trichostigma* were 62, 143, and 153 cm, respectively, and mean root sample lengths for *Anacardium* and *Trichostigma* were 87 and 31 cm, respectively. Embolisms were removed by flushing the segments for 20 min at 100 kPa. To measure maximum hydraulic conductivity ($k_{h,max}$), a hydrostatic pressure head of 4 kPa, which was a low enough value to avoid refilling of the embolized vessels upon pressurization (for construction of the vulnerability curve), was used to induce flow through the segments. The resulting volume flow rate was measured by timing the intervals for water to reach successive gradations on a pipette attached with tubing to the distal end of the segment. Hydraulic conductivity (k_h) was calculated by dividing the volume flow rate of water flowing through the stem by the hydrostatic pressure gradient along the stem. Specific conductivity (k_s) was calculated by dividing k_h by the cross-sectional area of the section being measured. Leaf-specific conductivity (k_l) was calculated by dividing k_h by the downstream leaf area. The temperature of the solution was recorded before and after each specific conductivity measurement, and all conductivity calculations were corrected to 20°C to account for changes in fluid viscosity with temperature.

Vulnerability curves were constructed using the air-injection method (Sperry and Saliendra, 1994). Recent work has shown that reliable measurements of hydraulic vulnerability can be obtained by using this method, especially when using a small pressure sleeve (Ennajeh et al., 2011). Briefly, after determining $k_{h,max}$, stems were placed in a double-ended pressure sleeve (8 cm in length) and were pressurized for 2 min. The stem was then removed from the pressure sleeve and k_h was measured by the same method used for $k_{h,max}$. This process was repeated at 0.25- to 1-MPa increments (depending on species and organ) of increasing pressure until k_h had fallen to <10% of its maximum value. The percentage loss in hydraulic conductivity (PLC) was calculated as

$$PLC = 100 * \left(1 - \left(\frac{k_h}{k_{h,max}} \right) \right) \quad (\text{Eq. 1})$$

Wood density (ρ) taken as the dry mass per green volume was measured on a short segment (~3 cm long) that was cut from one end of the sample with the pith and bark removed. The fresh volume was determined by submerging the wood in a cup of water on a scale. The mass difference caused by the sample, which equals the volume of water displaced by the sample, was recorded and converted to volume based on the density of water as 1.0 g cm^{-3} at standard temperature and pressure (Archimedes' principle). The sample was then placed in a drying oven at 100°C overnight, and the dry mass was subsequently measured.

Small pieces (approximately $1 \times 1 \text{ cm}$) of stem (wood and pith) representing the range of diameters of the samples used for hydraulic measurements from both species were used to construct sapwood moisture release curves for estimating capacitance. Ten samples were measured for *Anacardium* stems, 13 for *Trichostigma* stems and 10 for *Prionostemma* stems. For roots of *Anacardium* and *Trichostigma*, six and five samples were used, respectively. For these measurements, the samples were vacuum-infiltrated overnight in water. The saturated samples were then blotted on a paper towel to remove excess water, weighed, and placed in screen-cage thermocouple psychrometer chambers (83 series; JRD Merrill Specialty Equipment, Logan, Utah, USA). These chambers were then double bagged and submerged in a cooler of water for 2–3 h to allow the sample to equilibrate with the chamber air. After the equilibration period, the millivolt readings were recorded using a 12-channel digital psychrometer reader (85 series; JRD Merrill). Following the measurement, the samples were removed from the chambers, weighed, and allowed to dry on the laboratory bench for approximately half an hour before repeating the process (except for the saturation step). The mV output of the psychrometer was converted to MPa based on calibration curves from salt solutions of known water potentials. Samples were measured repeatedly until water potential values reached approximately -4 MPa . Samples were then placed in the drying oven overnight before the dry mass was weighed. For each of the repeated measurements, the relative water content (RWC) was calculated as

$$\text{RWC} = \frac{M_f - M_d}{M_s - M_d} \quad (\text{Eq. 2})$$

where M_f is the sample mass for the measurement, M_d is the dry mass, and M_s is the saturated mass of the sample. From RWC, relative water deficit (RWD) was calculated as $1 - \text{RWC}$. The product of RWD and the mass of water per unit tissue volume at saturation (M_w) yielded the cumulative mass of the water lost at each measurement. M_w was calculated as

$$= \left(\frac{M_s}{M_d} * \rho \right) - \rho \quad (\text{Eq. 3})$$

where ρ is wood density. Then, by graphing moisture release curves, which compare the cumulative mass of water lost versus the sapwood water potential, the capacitance of the sample could be estimated by plotting a regression to the initial, nearly linear, phase of the plot, which encompassed the likely *in situ* physiological operating range of stem water potential (Meinzer et al., 2003, 2009).

Leaf hydraulic conductance and vulnerability—Leaf hydraulic conductance (K_{leaf} , $\text{mmol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$) was determined using a timed rehydration method described in Brodrick and Holbrook (2003), which is based on an analogy between rehydrating a leaf and discharging a capacitor:

$$K_{\text{leaf}} = C \ln(\Psi_o / \Psi_t) / t \quad (\text{Eq. 4})$$

where C = capacitance, Ψ_o = leaf water potential prior to partial rehydration, Ψ_t = leaf water potential after partial rehydration, and t = duration of rehydration. Branches approximately 30–50 cm long were collected from trees early in the morning prior to significant transpirational water loss and were transported to the laboratory, recut under water, and allowed to rehydrate for $\geq 4 \text{ h}$. Shoots were dried on the bench top for varying lengths of time, placed in a plastic bag and sealed, and then kept in the dark for $\geq 1 \text{ h}$ to equilibrate. Measurements of leaf rehydration kinetics were conducted over the next 3 d (shoots kept in the dark) on excised leaves for initial values of water potential (Ψ_o), and for final values (Ψ_t) after a period of rehydration of t seconds, which was between 15

and 120 s. Adjacent or paired leaves were used for each K_{leaf} measurement, and a total of 33–45 leaf pairs were used to construct each K_{leaf} vulnerability curve. Distilled water was used for rehydration of K_{leaf} samples, and water temperature was maintained between 21° and 23°C .

Pressure–volume curves were conducted on individual leaves for each species. Branch samples of approximately 30–50 cm were excised from the same individuals that were used for rehydration and measurement of K_{leaf} early in the morning and recut under water in the laboratory. Branches were allowed to rehydrate for $\geq 4 \text{ h}$ before pressure–volume analyses were performed. Pressure–volume curves were created by plotting the inverse of Ψ_L against RWC with alternate determinations of fresh mass and Ψ_L repeated during slow dehydration of the twig on the laboratory bench until values of Ψ_L exceeded the measuring range of the pressure chamber (-4.0 MPa).

Values of leaf C were estimated from pressure–volume curves (Scholander et al., 1965; Tyree and Hammel, 1972). Briefly, the Ψ_L corresponding to turgor loss was estimated as the inflection point of the graph of the inverse of Ψ_L versus RWC. The slope of the curve prior to, and following turgor-loss provided C in terms of RWC (C_{wec}) for preturgor loss and post-turgor loss, respectively. For normalizing C on a leaf-area basis, leaf areas were obtained with a leaf area meter (LI-3100C, LI-COR). Five to six leaves of each species were used to construct pressure–volume curves and estimate C .

To test for significant differences between physiological measurements, individual t tests were performed (using the Bonferroni correction for multiple comparisons; Bland, 1995) between pairs of measurements.

Model methods—To estimate values of tree and liana transpiration (E) that would have occurred as soil dried, we used the hydraulic transport model developed by Sperry et al. (1998). The model also predicts the upper boundary for steady-state water transport, which is termed critical transpiration, E_{crit} , a surrogate for plant hydraulic limits as a function of soil water potential. The span of soil water potentials from zero to where it reaches E_{crit} represents the plant's "water use envelope." Once E exceeds the critical transpiration, there cannot be any further water uptake because of irreversible hydraulic dysfunction at some point in the soil–leaf hydraulic pathway (Sperry et al., 2002). Because we were able to find only *Anacardium* and *Trichostigma* roots, and root hydraulic vulnerability was needed to parameterize the model, those were the only species used with the model.

From the hydraulic properties of soil and xylem, the model predicts the relationship between steady-state E and the driving force in the soil–plant continuum ($E = K_{\text{plant}} (\Psi_{\text{soil}} - \Psi_L)$), where K_{plant} is the leaf-specific hydraulic conductance of the whole plant, and $\Psi_{\text{soil}} - \Psi_L$ is the water potential difference between soil and leaf. The drop in Ψ in the continuum is used to calculate the reduction in K_{plant} from the rhizosphere drying, root and stem embolism, and to determine E . The root components were assumed to comprise 50% of K_{plant} and stems; branches and leaves were assumed to represent the other 50% (Sperry et al., 1998). Midday Ψ_L was measured with the pressure chamber on the same days as Ψ_{soil} . The water-potential-dependent decrease in xylem hydraulic conductivity was calculated from a Weibull function fit to the root or stem vulnerability curve data. The model further divides root and shoot systems into lateral and axial components. We used the same fitting parameters for axial and lateral components within the root and shoot systems.

The water-potential-dependent decrease in rhizosphere conductance was calculated from soil conductivity, soil texture, and Ψ_{soil} , assuming a cylindrical rhizosphere sheath of 5 mm thickness from bulk soil to root surface (for details, see Sperry et al., 1998). The soils at the Parque Metropolitano site are well-drained clays high in nutrients, compared with other tropical soils (Bennett, 1929). There is hardly any humus layer or litter present. For each layer sampled, soil bulk density was measured as the dry weight over fresh volume (at field capacity; Table 1). Those soils are derived from the early to late Oligocene, generally andesitic in fine-grained tuff classified as Ultisol/Ustult from the Panama formation (Catapan, 1970; Woodring et al., 1980). Laboratory determination of clay content was unsuccessful because of the well-aggregated oxidic clays. We therefore used published soil-texture values for the model. Those soils were defined as Ancon clay with $\geq 25\%$ clay and $\geq 35\%$ silt (Bennett, 1929).

To convert rhizosphere conductance to a ground-area basis, we needed an estimate of the all-sided fine root area index (RAI). We therefore cored the soil at four locations and sampled roots at 0–15 cm and at 15–30 cm to determine change in root distribution and surface area with depth (Table 1). We sorted roots by diameter into two classes ($< 1 \text{ mm}$ and $> 1 \text{ mm}$) and determined the total dry mass of each size class. Root area was calculated from the total dry mass and from the relationships between dry mass and root area (specific root area = $0.015 \times \text{g cm}^{-2}$) calculated from 25 randomly selected roots. RAI usually shows an exponential decrease with soil depth (Jackson et al., 2000; Domec et al., 2010),

TABLE 1. Soil bulk density, water content, and root area index (RAI) in the top 30 cm of soil. Values are means \pm SE of averages measured using 4 samples during the early dry season of 2011.

	Soil bulk density (g cm ⁻³)	Water content (%)	RAI (m ⁻² m ⁻²)
0–15 cm	1.03 \pm 0.09	0.41 \pm 0.04	6.8 \pm 1.9
15–30 cm	1.38 \pm 0.21	0.52 \pm 0.08	4.5 \pm 1.5

so we fitted an exponential function to our two sampled depths and to the depth at which it was estimated that no roots were present. Deeper coring revealed that the deeper layers, consisting of water-logged, very fine-grained soil, were almost completely devoid of roots at a depth of 60 cm, so we used this depth as the lower point of our fitted curve. The fitted exponential decrease in RAI with depth revealed that between 30 and 60 cm, only 26% of remaining roots were present. The model divided the root system into two layers to correspond with the two depths where root area was measured. The root area used for each depth was a weighted average based on the relative cover of each species. Leaf area index (LAI) (trees and lianas vegetation combined) was determined on the basis of the MODIS-LAI product (Knyazikhin et al., 1998; Oak Ridge National Laboratory Distributed Active Archive Center, 2010), which is an 8-d interval time series and had a total of 39 scenes yr⁻¹ at the site. From 2010 to 2011, mean total LAI ranged from 4.2 to 5.1. It has been shown previously that 25% of the total LAI in the Parque Metropolitano is represented by lianas (Avalos and Mulkey, 1999), so we used an LAI of 1.1 for lianas and 3.4 for the trees when parameterizing the model.

RESULTS

Trichostigma stems had greater k_s than *Prionostemma* but were not statistically different from *Anacardium* (Table 2). There were no significant differences in k_L between species. Roots had greater k_s than stems ($t = 2.47$, $df = 3$, $P = 0.045$), with *Anacardium* and *Trichostigma* having 2.8 \times and 4.4 \times greater k_s in their roots than in their stems, respectively. *Trichostigma* roots had greater k_s than *Anacardium*, by a factor of 2.2.

Wood density was similar for all species and organs (0.43–0.49 g cm⁻³) tested, except for *Prionostemma* branches, which had wood density of 0.58 g cm⁻³ ($t = 3.45$, $df = 3$, $P = 0.02$; Table 2). Mean maximum vessel length was highly variable between species and organ. *Prionostemma* had the greatest branch mean maximum vessel length, which was 2.1 \times and 1.6 \times greater than *Anacardium* and *Trichostigma*, respectively; however, this relationship was not statistically significant.

Leaves were more vulnerable to embolism than stems in the two liana species but not in *Anacardium* (Fig. 1 and Table 3). Leaves and stems of *Anacardium* experienced 50% loss of conductivity (P_{50}) at water potentials of -1.49 and -1.45 MPa, respectively, but were not significantly different (overlapping 95% confidence intervals). Roots of both *Anacardium* and *Trichostigma* were less resistant to embolism than stems of the same species (Table 3 and Fig. 1). However, *Trichostigma* roots

($P_{50} = -1.31$ MPa) were much less vulnerable to embolism than *Anacardium* roots ($P_{50} = -0.76$ MPa).

Predawn leaf water potentials were similar for all species and ranged from -0.34 to -0.46 MPa (Fig. 2). Predawn soil water potential was -0.16 MPa and was estimated to have dropped to approximately -0.4 MPa by midday (this corresponds to a 3.5% drop in soil moisture in this type of clayey soil). Midday leaf and stem water potentials were much more negative in the two lianas than in *Anacardium* (respectively, leaf and stem t , df , and P values for *Anacardium* vs. *Prionostemma* and *Anacardium* vs. *Trichostigma* were $t = 4.53$, $df = 3$, $P = 0.01$; $t = 7.22$, $df = 3$, $P = 0.003$; $t = 22.9$, $df = 3$, $P = 0.001$; and $t = 20.8$, $df = 3$, $P = 0.002$). Midday leaf water potentials were -0.78 , -1.47 , and -1.44 MPa, and midday stem water potentials were -0.58 , -1.08 , and -0.95 MPa for *Anacardium*, *Prionostemma*, and *Trichostigma*, respectively. Predicted midday losses in conductance or conductivity (Table 3; based on vulnerability curves of leaves, stems, and roots, and measured midday water potentials) were especially high in leaves of the two liana species (73.9% and 78.3% loss in *Prionostemma* and *Trichostigma*, respectively), but near zero in *Anacardium* leaves. Similarly, stem hydraulic conductivity was predicted to decrease by 48.9% in *Prionostemma* and 19.1% in *Trichostigma*, but not at all in *Anacardium*. Roots of both species measured were predicted to experience losses in hydraulic conductivity (at the estimated midday soil water potential), although this loss was much greater in *Anacardium* (34.8% predicted loss) than *Trichostigma* (12.2% predicted loss).

Stem hydraulic capacitance was over twice as great in *Anacardium* than in either liana species (Fig. 3; $t = 4.74$, $df = 3$, $P = 0.01$ for *Prionostemma* vs. *Anacardium*; $t = 7.0$, $df = 3$, $P = 0.003$ for *Trichostigma* vs. *Anacardium*). Measured capacitance was 346 kg m⁻³ MPa⁻¹ in *Anacardium* stems, and 154 and 157 kg m⁻³ MPa⁻¹ in *Prionostemma* and *Trichostigma*, respectively. Root capacitance was not significantly different between *Anacardium* and *Trichostigma*. Root capacitance was 3.2 \times greater than stem capacitance in *Trichostigma* ($p = 0.03$), but root and stem capacitance were not significantly different in *Anacardium*.

Maximum stomatal conductance and transpiration were much greater in *Trichostigma* than in either *Prionostemma* or *Anacardium* (Table 4; respectively, stomatal conductance and transpiration t , df , and P values for *Trichostigma* vs. *Anacardium* and *Trichostigma* vs. *Prionostemma* were $t = 8.55$, $df = 3$, $P = 0.002$; $t = 3.52$, $df = 3$, $P = 0.02$; $t = 11.12$, $df = 4$, $P = 0.0002$; and $t = 4.18$, $df = 4$, $P = 0.01$). Transpiration was 2.5 \times and 3.6 \times greater in *Trichostigma* than in *Anacardium* and *Prionostemma*, respectively. Additionally, maximum leaf hydraulic conductance was nearly 2 \times greater in *Trichostigma* than in *Anacardium* and *Prionostemma* ($t = 4.34$, $df = 3$, $P = 0.01$ for *Trichostigma* vs. *Anacardium*; $t = 4.76$, $df = 4$, $P = 0.005$ for *Trichostigma* vs. *Prionostemma*). Midday leaf water potential

TABLE 2. Branch- and root-specific conductivity (k_s), leaf-specific conductivity (k_L), wood density, mean longest vessel length, and mean sample diameter for *Anacardium excelsum* (ANEX), *Prionostemma aspera* (PRAS), and *Trichostigma octandrum* (TROC). Numbers in parentheses are standard errors.

Species organ	k_s (kg MPa ⁻¹ m ⁻¹ s ⁻¹)	k_L (kg MPa ⁻¹ m ⁻¹ s ⁻¹)	Wood density (g cm ⁻³)	Mean longest vessel (cm)	Mean sample diameter (mm)
ANEX branch	1.10 (0.34)	5.1×10^{-3} (2.8×10^{-3})	0.43 (0.03)	48.7 (4.1)	3.42 (0.23)
PRAS branch	0.71 (0.27)	1.5×10^{-3} (6.4×10^{-4})	0.58 (0.03)	103.0 (11.7)	5.03 (1.00)
TROC branch	1.58 (0.38)	3.1×10^{-3} (8.2×10^{-4})	0.49 (0.04)	64.0 (6.6)	9.07 (0.67)
ANEX root	3.12 (0.34)		0.43 (0.04)	69.1 (11.3)	7.95 (0.36)
TROC root	6.92 (1.66)		0.47 (0.04)	25.1 (5.5)	7.68 (0.62)

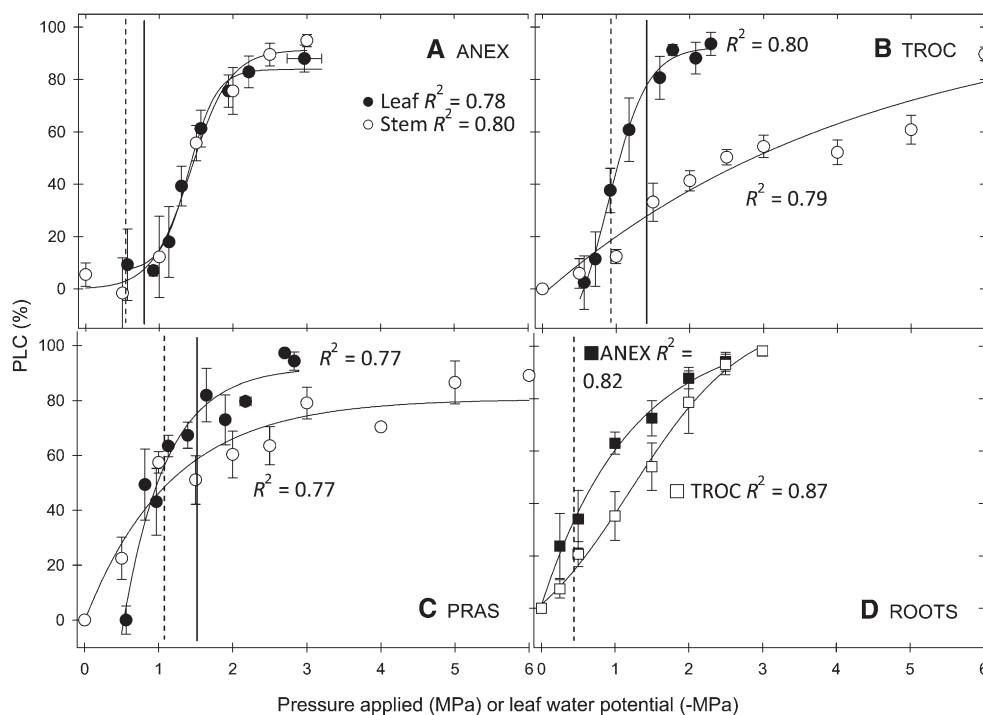


Fig. 1. Percent loss (PLC) of leaf hydraulic conductance (closed circles) and stem hydraulic conductivity (open circles) across a range of water potentials for the tree species (A) *Anacardium excelsum* (ANEX) and the two liana species (B) *Prionostemma aspera* (PRAS) and (C) *Trichostigma octandrum* (TROC) and for (D) roots of ANEX (closed squares) and TROC (open squares). Midday minimum leaf water potentials and stem water potentials are indicated by vertical solid and dashed lines, respectively, except for panel D, where the dashed line indicates minimum estimated soil water potential. Error bars represent standard errors.

measurements indicated that neither *Anacardium* nor *Prionostemma* ever reached water potentials approaching their turgor loss points (Table 4) but that midday leaf water potentials in *Trichostigma* were very close the leaf turgor loss point.

The hydraulic model yielded accurate estimates of leaf-level transpiration based on measured gas exchange (Fig. 4). The model predicted that *Trichostigma* would have higher transpiration rates and higher E_{crit} than *Anacardium*. The former can be explained by the *Trichostigma* roots being more resistant to embolism and the latter by the higher values of K_{plant} (2.7 ± 0.3 and 2.0 ± 0.2 $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$, for *Trichostigma* and *Anacardium*, respectively). Modeled droughts (i.e., soil drying) were associated with declines in E , with a higher relative magnitude seen in the lianas than in the tree with a 50% reduction in E at soil water potentials of -0.22MPa for *Trichostigma* and -0.35MPa for *Anacardium*.

Plotting E_{crit} against Ψ_{soil} yielded a water use envelope (Sperry et al., 2002), which characterizes the potential for soil water extraction as soils dry. The maximum transpiration rates were modeled to be $4.2 \text{mmol m}^{-2} \text{s}^{-1}$ in *Trichostigma* and $2.6 \text{mmol m}^{-2} \text{s}^{-1}$ in *Anacardium*. The model predicted that as opposed to the liana species, *Anacardium* never closely approached E_{crit} as soil water potential dropped (Fig. 4A, B). In *Trichostigma*, the predicted soil water potential at which E was within 5% of E_{crit} was estimated to be -0.75MPa . However, over the range of soil water potentials measured, *Trichostigma* was predicted to use $2.7\times$ more water (per leaf area) than *Anacardium* (Fig. 4C; y axis is log scale). The model also predicted that between -0.25 and -1.75MPa , water use by both species would only represent 14% of the water use between 0 and -0.25MPa . The soil water potentials at which water use by *Trichostigma*

and *Anacardium* would be reduced by 50% were -0.19MPa and -0.30MPa , respectively.

DISCUSSION

Although many studies have assessed physiological properties of tropical tree species, little work has been done on tropical lianas. Our study indicated that even under significant water stress (soil water potential lower than -1.0MPa), the liana species (*Trichostigma*) was predicted to have a competitive advantage over the host trees by maintaining a higher rate of water uptake. In fact, the soil water potential of -0.75MPa at which

TABLE 3. Water potentials at which 50% of hydraulic conductivity (stems and roots) or conductance (leaves) has been lost (P_{50}), and the predicted percent loss in hydraulic conductivity or conductance at midday in organs of *Anacardium excelsum* (ANEX), *Prionostemma aspera* (PRAS), and *Trichostigma octandrum* (TROC). Numbers in parentheses are boundaries of 95% confidence intervals. Asterisks indicate values that are not significantly different from zero.

Species and organ	P_{50}	Percent loss at midday
ANEX leaf	-1.49 ($-1.32, -1.61$)	7.9*
ANEX stem	-1.45 ($-1.28, -1.70$)	1.3*
ANEX root	-0.76 ($-0.59, -0.97$)	34.8
PRAS leaf	-0.98 ($-0.89, -1.09$)	73.9
PRAS stem	-1.14 ($-0.85, -1.48$)	48.9
TROC leaf	-1.05 ($-0.95, -1.23$)	78.3
TROC stem	-2.90 ($-2.51, -3.46$)	19.1
TROC root	-1.31 ($-1.12, -1.52$)	12.2

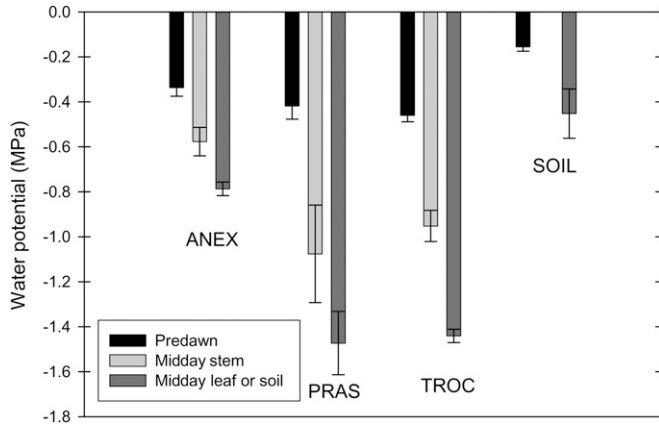


Fig. 2. Predawn leaf, midday leaf, and midday stem water potentials in *Anacardium excelsum* (ANEX), *Prionostemma aspera* (PRAS), and *Trichostigma octandrum* (TROC) and estimated predawn and midday soil (SOIL) water potentials.

predicted soil water extraction approaches E_{crit} in the liana has, to our knowledge, never been measured at this dry site. However, if future changes in climatic conditions reduce precipitation, we may expect soils to fall below this predicted threshold value. It is interesting to note, on the basis of vulnerability curves, that a soil water potential of -0.75 MPa would induce only 20% loss of root conductivity, which indicates that on this type of soil, rhizosphere drying—and not water transport within the plant—becomes the limiting factor for the lianas to extract water as soil dries (Sperry et al., 1998).

Performance of the hydraulic model was limited by the lack of detailed representation of Ψ_{soil} from all depths and by limited data of fine-root xylem vulnerability to embolism, which has been shown to be more limiting than branch and coarse root xylem (Hacke et al., 2000). We speculate that the inclusion of additional xylem components in the model might narrow the safety margins for each species but that it would not have different effects between species and, thus, would not change our overall conclusions of hydraulic failure.

There is a strong positive correlation between the length of the dry season and liana abundance (DeWalt et al., 2010; Schnitzer and Bongers, 2011), as well as much evidence for increasing liana abundance in the tropics over the past 40 yr. These trends have been attributed to access to deeper water sources by lianas than by co-occurring trees. Similarly, one of the principal explanations for the increasing abundance of lianas through time is more frequent and severe drought and the competitive edge that lianas benefit from owing to their deeper root systems (e.g., Schnitzer, 2005). Many lianas have remarkably deep and extensive root systems, with some going deeper than 10 m (Holbrook and Putz, 1996; Restom and Nepstad, 2004), and it has been shown that lianas, especially in areas where many trees lose their leaves in the dry season, have access to deeper water sources than co-occurring trees (Jackson et al., 1995). However, in the present study, the lianas (as well as trees) were shallowly rooted, with almost no roots found below 60 cm. In fact, Andrade et al. (2005) found evidence that the majority of water use by lianas, including *Prionostemma aspera*, at a nearby site (Barro Colorado Island, Panama) was greatest between 30 and 60 cm depth during the dry season. However, it appeared that two of the species of lianas studied by Andrade et al. were able to extract water from deeper sources.

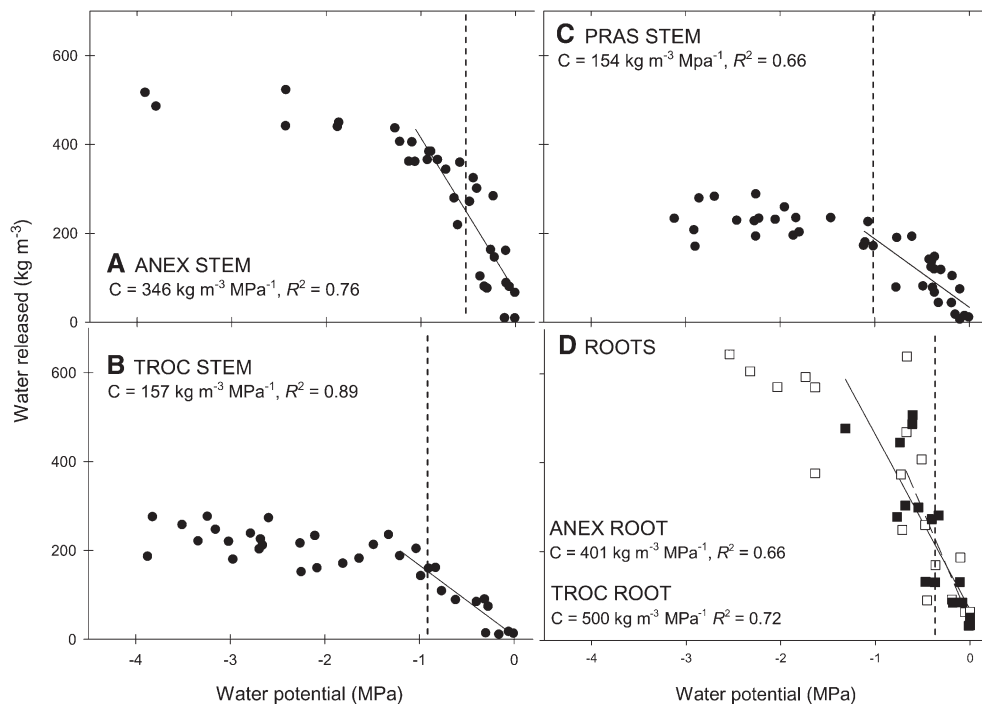


Fig. 3. Volumetric moisture release curves for stems of the tree species (A) *Anacardium excelsum* (ANEX) and the two liana species (B) *Prionostemma aspera* (PRAS) and (C) *Trichostigma octandrum* (TROC) and (D) roots of ANEX (closed squares) and TROC (open squares). Midday minimum stem water potentials and estimated minimum soil water potentials are indicated by vertical lines in A through C and D, respectively.

TABLE 4. Mean maximum stomatal conductance (g_s), transpiration (E), and leaf hydraulic conductance ($K_{\text{leaf max}}$), along with preturgor loss leaf hydraulic capacitance (C_{leaf}) and leaf turgor loss point (TLP) in *Anacardium excelsum* (ANEX), *Prionostemma aspera* (PRAS), and *Trichostigma octandrum* (TROC). Numbers in parentheses are standard errors.

Species	g_s (mmol m ⁻² s ⁻¹)	E (mmol m ⁻² s ⁻¹)	$K_{\text{leaf max}}$ (mmol m ⁻² s ⁻¹ MPa ⁻¹)	C_{leaf} (mol m ⁻² MPa ⁻¹)	TLP (MPa)
ANEX	64.8 (7.9)	1.73 (0.56)	24.5 (1.5)	0.87 (0.13)	-1.13 (0.06)
PRAS	38.2 (6.2)	1.23 (0.24)	22.7 (1.2)	0.57 (0.04)	-2.07 (0.09)
TROC	153 (10.3)	4.41 (0.76)	43.1 (3.0)	0.96 (0.03)	-1.49 (0.07)

It is possible that a few deep roots in the species in the present study provide access to deeper pools of water and that these roots were not detected during sampling.

On the basis of Sperry et al.'s (1998, 2002) model, we would predict that *Trichostigma* should outperform *Anacardium* (greater gas exchange and water extraction) both when soil water is abundant and during drought (Fig. 4). This is in direct support of the finding of increased photosynthesis in lianas during the dry season (as compared to co-occurring trees; Schnitzer et al., 2005; Cai et al., 2009). *Prionostemma aspera* is very abundant around Parque Metropolitan and Barro Colorado Island (Putz, 1984; Andrade et al., 2005), but absent at Parque Nacional San Lorenzo (S. Schnitzer, personal communication), which is only 55 km from Parque Metropolitan but receives 3300 mm of precipitation per year. At this point, we are unsure about whether there has been an increase or decrease in *Prionostemma* abundance over time because census data are incomplete. However, on the basis of recent census data from Barro Colorado Island, *Prionostemma* appears to have a strong affinity for drier sites (S. Schnitzer, personal communication). Although there is little information on the ecology of *Trichostigma*, it appears to be very tolerant of a wide range of precipitation regimes (900–2500 mm yr⁻¹; USDA Forest Service, International Institute of Tropical Forestry) and soil types.

Earlier work has shown that when using a combination of vulnerability curves and *in situ* water potential measurements, predicted loss of conductance is very similar to actual loss of conductance in leaves and branches (Domec et al., 2005, 2006; Johnson et al., 2009). In the present study, *Trichostigma* had very high stomatal conductance and transpiration (and presumably photosynthesis), which was supported by high K_{leaf} , stem k_L , and root k_s . However, *Trichostigma* was predicted to lose 78% of K_{leaf} at midday, but with little concurrent loss of root or stem conductivity. Conversely, *Anacardium* had much lower stomatal conductance and transpiration but lost no K_{leaf} at midday. *Anacardium* had very high stem k_L supplying leaf tissues. This combination of high k_L and lower stomatal conductance allowed *Anacardium* to retain its leaf hydraulic conductance at midday. *Prionostemma* had the lowest stomatal conductance and transpiration in the present study but, owing to highly vulnerable leaves and stems and low k_L , lost a large portion of leaf (74% loss) and stem (49% loss) hydraulic conductance or conductivity, respectively, at midday. These results are in good agreement with earlier work by Andrade et al. (2005) that reported very low sap flux in *Prionostemma* and work by James et al., (2002) that showed very high water use in *Anacardium*.

In general, water potentials, especially at midday, were much more negative in the lianas than in *Anacardium*. On a volumetric basis, sapwood capacitance was also lower in the lianas than in *Anacardium*, which could result in more negative water potentials in the lianas for a given transpiration flux (e.g., Meinzer et al., 2003). On the basis of an absolute volume of water, the smaller amount of wood in the liana stems than in the boles of

the trees means that a smaller absolute volume of water would be released in the lianas. Our hypothesis that lianas would have greater capacitance than *Anacardium* and would not suffer large negative water potentials resulting in embolism was not supported. However, no roots or stems of the species measured ever experienced water potentials that were more negative than the initial, linear portion of the moisture release curve. The observed low midday water potentials in the two liana species may also be due to the reduced stem hydraulic conductivity in the liana species as compared to *Anacardium*. It appears that the liana species measured here experience embolism in leaves, stems, and roots on a daily basis during the dry season, and there must be a mechanism(s) that allows emboli to be repaired. The loss and recovery of hydraulic function on a daily time scale has been observed in leaves of several species (Bucci et al., 2003; Brodribb and Holbrook, 2004; Johnson et al., 2009, 2011) and in stems of *Vitis* (Brodersen et al., 2010), *Quercus* (Taneda and Sperry, 2008; Christman et al., 2012), and *Laurus* (Salleo and Lo Gullo, 1993; Hacke and Sperry, 2003). In another recent study, Zhu and Cao (2009) found that dry-season leaf water potentials in three lianas were between 0 and 0.2 MPa more negative than the P₅₀ of the associated stems. Therefore, even with a difference of 0.5 MPa between leaf and stem water potentials, there would have been daily embolism in the liana stems that they measured. Lianas (*Vitis*) have been shown to exhibit the ability to repair petiole and stem embolisms over daily time scales (Brodersen et al., 2010; Zufferey et al., 2011). In general, root pressures are quite low in most tropical vines (Ewers et al., 1997), and maximum measured root pressure in *Trichostigma octandrum* (from Mexico) was 7 kPa (Fisher et al., 1997). In the species examined here, a pressure of nearly 300 kPa would be required to refill embolized conduits of the uppermost branches. It could be hypothesized that the large proportional amount of living parenchyma tissue in liana stems (as compared to trees, which have most of their stems devoted to xylem conduits and/or fibers) or their many anomalous vascular structures (e.g., multiple cambia producing interxylary phloem; Isnard and Silk, 2009) may allow them to efficiently refill embolized conduits. If current thinking on the mechanism(s) of embolism repair is correct (Zwieniecki and Holbrook, 2009; Brodersen et al., 2010; Nardini et al., 2011; Secchi et al., 2011), having extra parenchyma and/or phloem per xylem area would be very advantageous for repairing embolized conduits (Johnson et al., 2012).

Although we are aware of increasing abundance of lianas with climate change, the mechanisms responsible for this trend remain unclear. Much work is needed on the physiological ecology of liana species to determine what characteristics determine their ability to thrive as dry seasons get drier. On the basis of the two examples here, as well as several other examples (Clearwater and Clark, 2003; Zhu and Cao, 2009), lianas appear to be highly vulnerable to hydraulic dysfunction. Therefore, their increase in abundance with increased dry-season

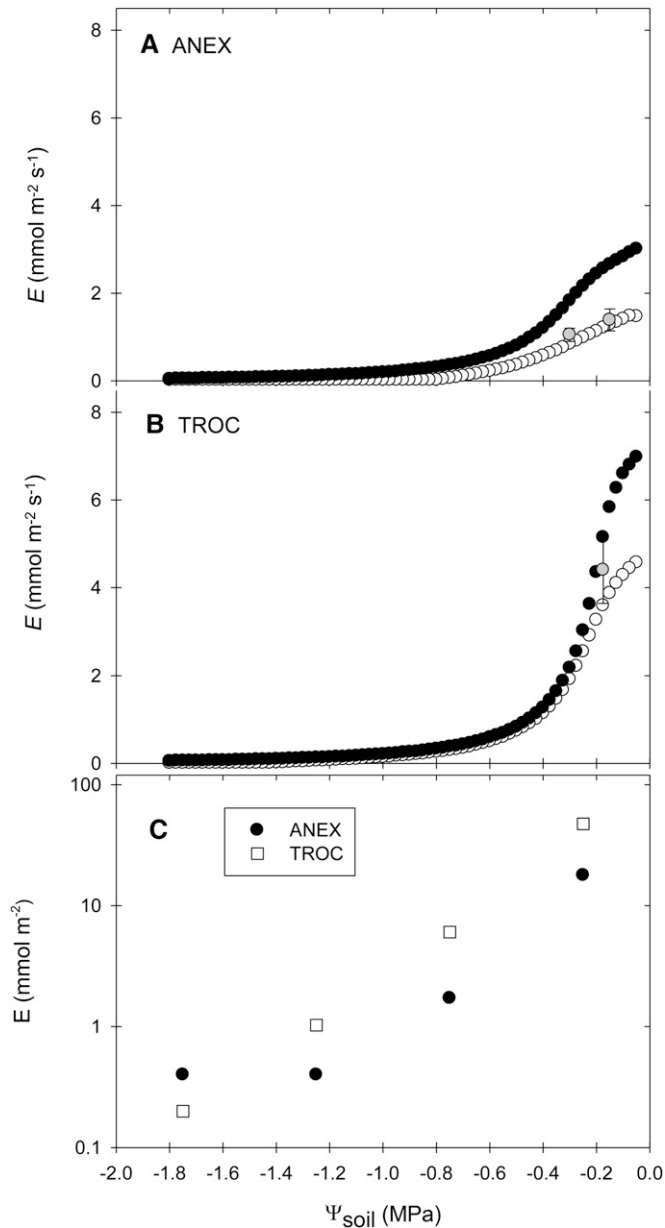


Fig. 4. Modeled and measured transpiration vs. soil water potential for the tree (A) *Anacardium excelsum* (ANEX) and the liana (B) *Trichostigma octandrum* (TROC). Closed circles represent the upper value for transpiration that would result in critical hydraulic failure (E_{crit}). Open circles represent predicted transpiration at a given soil water potential, and gray circles indicate measured values. Panel C is an estimate of plant water use integrated across ranges of soil water potentials (0 to -0.5 MPa, -0.5 to -1 , -1 to -1.5 , and -1.5 to -2.0). Closed circles represent ANEX, and open squares represent TROC.

length or drought seems paradoxical. The answer may lie in their ability to rapidly repair embolism.

LITERATURE CITED

ANDRADE, J. L., F. C. MEINZER, G. GOLDSTEIN, N. M. HOLBROOK, J. CAVELIER, P. JACKSON, AND K. SILVERA. 1998. Regulation of water flux through trunks, branches and leaves in trees of a lowland tropical forest. *Oecologia* 115: 463–471.

- ANDRADE, J. L., F. C. MEINZER, G. GOLDSTEIN, AND S. A. SCHNITZER. 2005. Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest. *Trees (Berlin)* 19: 282–289.
- AVALOS, G., AND S. S. MULKEY. 1999. Seasonal changes in liana cover in the upper canopy of a Neotropical dry forest. *Biotropica* 31: 186–192.
- BENNETT, H. H. 1929. Soil reconnaissance of the Panama Canal Zone and contiguous territory. U.S. Department of Agriculture Technical Bulletin No. 94.
- BLAND, M. 1995. An introduction to medical statistics. Oxford University Press, Oxford, UK.
- BRODERSEN, C. R., A. J. McELRONE, B. CHOAT, M. A. MATTHEWS, AND K. A. SHACKEL. 2010. The dynamics of embolism repair in xylem: In vivo visualizations using high-resolution computed tomography. *Plant Physiology* 154: 1088–1095.
- BRODRIBB, T. J., AND N. M. HOLBROOK. 2003. Stomatal closure during leaf dehydration, correlation with other leaf physiological traits. *Plant Physiology* 132: 2166–2173.
- BRODRIBB, T. J., AND N. M. HOLBROOK. 2004. Diurnal depression of leaf hydraulic conductance in a tropical tree species. *Plant, Cell & Environment* 27: 820–827.
- BRODRIBB, T. J., N. M. HOLBROOK, E. J. EDWARDS, AND M. V. GUTIÉRREZ. 2003. Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. *Plant, Cell & Environment* 26: 443–450.
- BUCCI, S. J., G. GOLDSTEIN, F. C. MEINZER, F. G. SCHOLZ, A. C. FRANCO, AND M. BUSTAMANTE. 2004. Functional convergence in hydraulic architecture and water relations of tropical savanna trees: From leaf to whole plant. *Tree Physiology* 24: 891–899.
- BUCCI, S. J., F. G. SCHOLZ, G. GOLDSTEIN, F. C. MEINZER, AND L. DA S. L. STERNBERG. 2003. Dynamic changes in hydraulic conductivity in petioles of two savanna tree species: Factors and mechanisms contributing to the refilling of embolized vessels. *Plant, Cell & Environment* 26: 1633–1645.
- CAI, Z. Q., S. A. SCHNITZER, AND F. BONGERS. 2009. Seasonal differences in leaf-level physiology give lianas a competitive advantage over trees in a tropical forest. *Oecologia* 161: 25–33.
- CATAPAN. 1970. Soil maps 1:100 000 and 1:200 000. Jacobs and Co for CRA-Catapan, MIDA, Santiago, Panama.
- CHRISTMAN, M. A., J. S. SPERRY, AND D. D. SMITH. 2012. Rare pits, large vessels, and extreme vulnerability to cavitation in a ring-porous tree species. *New Phytologist* 193: 713–720.
- CLEARWATER, M. J., AND C. J. CLARK. 2003. In vivo magnetic resonance imaging of xylem vessel contents in woody lianas. *Plant, Cell & Environment* 26: 1205–1214.
- DAWSON, T. E., S. S. O. BURGESS, K. P. TU, R. S. OLIVEIRA, L. S. SANTIAGO, J. B. FISHER, K. A. SIMONIN, AND A. R. AMBROSE. 2007. Nighttime transpiration in woody plants from contrasting ecosystems. *Tree Physiology* 27: 561–575.
- DEWALT, S. J., S. A. SCHNITZER, J. CHAVE, F. BONGERS, R. J. BURNHAM, Z. CAI, G. B. CHUYONG, ET AL. 2010. Annual rainfall and seasonality predict pan-tropical patterns of liana density and basal area. *Biotropica* 42: 309–317.
- DOMEC, J.-C., J. S. KING, A. NOORMETS, E. A. TREASURE, M. J. GAVAZZI, G. SUN, AND S. G. MCNULTY. 2010. Hydraulic redistribution of soil water by roots affects whole stand evapotranspiration and net ecosystem carbon exchange. *New Phytologist* 187: 171–183.
- DOMEC, J.-C., M. PRUYN, AND B. L. GARTNER. 2005. Axial and radial xylem conductivities, water storage and native embolism in trunks of young and old ponderosa pine trees. *Plant, Cell & Environment* 28: 1103–1113.
- DOMEC, J.-C., F. G. SCHOLZ, S. J. BUCCI, F. C. MEINZER, G. GOLDSTEIN, AND R. VILLALOBOS-VEGA. 2006. Diurnal and seasonal variation in root xylem embolism in Neotropical savanna woody species: Impact on stomatal control of plant water status. *Plant, Cell & Environment* 29: 26–35.
- ENNAJEH, M., F. SIMÕES, H. KHEMIRAA, AND H. COCHARD. 2011. How reliable is the double-ended pressure sleeve technique for assessing xylem vulnerability to cavitation in woody angiosperms. *Physiologia Plantarum* 142: 205–210.

- EWERS, F. W. 1985. Xylem structure and water conduction in conifer trees, dicot trees, and lianas. *International Association of Wood Anatomists Bulletin* 6: 309–317.
- EWERS, F. W., H. COCHARD, AND M. T. TYREE. 1997. A survey of root pressures in vines of a tropical lowland forest. *Oecologia* 110: 191–196.
- EWERS, F. W., AND J. B. FISHER. 1989. Techniques for measuring vessel lengths and diameters in stems of woody plants. *American Journal of Botany* 76: 645–656.
- EWERS, F. W., J. B. FISHER, AND K. FICHTNER. 1991. Water flux and xylem structure in vines. In F. E. Putz and H. A. Mooney [eds.], *The biology of vines*, 73–98. Cambridge University Press, Cambridge, UK.
- FIELD, C. B., M. J. BEHRENFELD, J. T. RANDERSON, AND P. FALKOWSK. 1998. Primary production of the biosphere: Integrating terrestrial and oceanic components. *Science* 281: 237–240.
- FISHER, J. B., G. ANGELES, F. W. EWERS, AND J. LOPEZ-PORTILLO. 1997. Survey of root pressure in tropical vines and woody species. *International Journal of Plant Sciences* 158: 44–50.
- GARTNER, B. L., S. H. BULLOCK, H. A. MOONEY, V. B. BROWN, AND J. L. WHITBECK. 1990. Water transport properties of vine and tree stems in a tropical deciduous forest. *American Journal of Botany* 77: 742–749.
- HACKE, U. G., AND J. S. SPERRY. 2003. Limits of xylem refilling under negative pressure in *Laurus nobilis* and *Acer negundo*. *Plant, Cell & Environment* 26: 303–311.
- HACKE, U. G., J. S. SPERRY, B. E. EWERS, D. S. ELLSWORTH, K. V. R. SCHÄFER, AND R. OREN. 2000. Influence of soil porosity on water use in *Pinus taeda*. *Oecologia* 124: 495–505.
- HACKE, U. G., J. S. SPERRY, W. T. POCKMAN, S. D. DAVIS, AND K. A. MCCULLOH. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126: 457–461.
- HOLBROOK, N. M., AND F. E. PUTZ. 1996. Physiology of tropical vines and hemiepiphytes: Plants that climb up and plants that climb down. In S. S. Mulkey, R. L. Chazdon, and A. P. Smith [eds.], *Tropical forest plant ecophysiology*, 363–394. Chapman and Hall, New York, New York, USA.
- INGWELL, L. L., S. J. WRIGHT, K. K. BECKLUND, S. P. HUBBELL, AND S. A. SCHNITZER. 2010. The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. *Journal of Ecology* 98: 879–887.
- ISNARD, S., AND W. SILK. 2009. Moving with climbing plants from Charles Darwin's time into the 21st century. *American Journal of Botany* 96: 1205–1221.
- JACKSON, P. C., J. CAVELIER, G. GOLDSTEIN, F. C. MEINZER, AND N. M. HOLBROOK. 1995. Partitioning of water resources among plants of a lowland tropical forest. *Oecologia* 101: 197–203.
- JACKSON, R. B., J. S. SPERRY, AND T. E. DAWSON. 2000. Root water uptake and transport: Using physiological processes in global predictions. *Trends in Plant Science* 5: 482–488.
- JAMES, S. A., M. J. CLEARWATER, F. C. MEINZER, AND G. GOLDSTEIN. 2002. Heat dissipation sensors of variable length for the measurement of sap flow in trees with deep sapwood. *Tree Physiology* 22: 277–283.
- JAMES, S. A., F. C. MEINZER, G. GOLDSTEIN, D. WOODRUFF, T. JONES, T. RESTOM, M. MEJIA, M. J. CLEARWATER, AND P. CAMPANELLO. 2003. Axial and radial water transport and internal water storage in tropical forest canopy trees. *Oecologia* 134: 37–45.
- JOHNSON, D. M., K. A. MCCULLOH, F. C. MEINZER, AND D. R. WOODRUFF. 2011. Hydraulic patterns and safety margins, from stem to stomata, in three eastern US tree species. *Tree Physiology* 31: 659–668.
- JOHNSON, D. M., K. A. MCCULLOH, D. R. WOODRUFF, AND F. C. MEINZER. 2012. Hydraulic safety margins and embolism reversal in stems and leaves: Why are conifers and angiosperms so different? *Plant Science* 195: 48–53.
- JOHNSON, D. M., D. R. WOODRUFF, K. A. MCCULLOH, AND F. C. MEINZER. 2009. Leaf hydraulic conductance, measured in situ, declines and recovers daily: Leaf hydraulics, water potential and stomatal conductance in four temperate and three tropical tree species. *Tree Physiology* 29: 879–887.
- KIRA, T., AND H. OGAWA. 1971. Assessment of primary production in tropical and equatorial forests. In P. DuVigneaud [ed.], *Productivity of forest ecosystems*, 309–321. UNESCO, Paris, France.
- KNYAZIKHIN, Y., J. V. MARTONCHIK, R. B. MYENI, D. J. DINER, AND S. W. RUNNING. 1998. Synergistic algorithm for estimating vegetation canopy leaf area index and fraction of absorbed photosynthetically active radiation from MODIS and MISR data. *Journal of Geophysical Research* 103: 32257–32274.
- MALHI, Y., D. D. BALDOCCHI, AND P. G. JARVIS. 1999. The carbon balance of tropical, temperate and boreal forests. *Plant, Cell & Environment* 22: 715–740.
- MCCULLOH, K. A., F. C. MEINZER, J. S. SPERRY, B. LACHENBRUCH, S. L. VOELKER, D. R. WOODRUFF, AND J.-C. DOMEQ. 2011. Comparative hydraulic architecture of early and late successional tropical tree species. *Oecologia* 167: 27–37.
- MEINZER, F. C., P. I. CAMPANELLO, J.-C. DOMEQ, M. G. GATTI, G. GOLDSTEIN, R. VILLALOBOS-VEGA, AND D. R. WOODRUFF. 2008. Constraints on physiological function associated with branch architecture and wood density in tropical forest trees. *Tree Physiology* 28: 1609–1617.
- MEINZER, F. C., S. A. JAMES, G. GOLDSTEIN, AND D. R. WOODRUFF. 2003. Whole-tree water transport scales with sapwood capacitance in tropical forest canopy trees. *Plant, Cell & Environment* 26: 1147–1155.
- MEINZER, F. C., D. M. JOHNSON, B. LACHENBRUCH, K. A. MCCULLOH, AND D. R. WOODRUFF. 2009. Xylem hydraulic safety margins in woody plants: Coordination of stomatal control of xylem tension with hydraulic capacitance. *Functional Ecology* 23: 922–930.
- NARDINI, A., M. A. LO GULLO, AND S. SALLEO. 2011. Refilling embolized xylem conduits: Is it a matter of phloem unloading? *Plant Science* 180: 604–611.
- OAK RIDGE NATIONAL LABORATORY DISTRIBUTED ACTIVE ARCHIVE CENTER. 2010. MODIS subsetted land products, collection 5 [<http://daac.ornl.gov/MODIS/modis.html>] from ORNL DAAC, Oak Ridge, Tennessee, USA.
- PÉREZ-SALICRUP, D. R., AND M. G. BARKER. 2000. Effect of liana cutting on water potential and growth of adult *Senna multijuga* (Caesalpinioideae) trees in a Bolivian tropical forest. *Oecologia* 124: 469–475.
- PHILLIPS, O. L., R. VÁSQUEZ MARTÍNEZ, L. ARROYO, T. R. BAKER, T. KILLEEN, S. L. LEWIS, Y. MALHI, ET AL. 2002. Increasing dominance of large lianas in Amazonian forests. *Nature* 418: 770–774.
- PRATT, R. B., A. L. JACOBSEN, F. W. EWERS, AND S. D. DAVIS. 2007. Relationships among xylem transport, biomechanics, and storage in stems and roots of nine Rhamnaceae species of the California chaparral. *New Phytologist* 174: 787–798.
- PUTZ, F. E. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65: 1713–1724.
- PUTZ, F. E., AND N. M. HOLBROOK. 1991. Biomechanical studies of vines. In F. E. Putz and H. A. Mooney [eds.], *The biology of vines*, 73–98. Cambridge University Press, Cambridge, UK.
- RESTOM, T. G., AND D. C. NEPSTAD. 2004. Seedling growth dynamics of a deeply-rooting liana in a secondary forest in eastern Amazonia. *Forest Ecology and Management* 190: 109–118.
- SALLEO, S., AND M. A. LO GULLO. 1993. Drought resistance strategies and vulnerability to cavitation of some Mediterranean sclerophyllous trees. In M. Borghetti, J. Grace, and A. Raschi [eds.], *Water transport in plants under climatic stress*, 99–113. Cambridge University Press, Cambridge, UK.
- SALLEO, S., M. A. LO GULLO, F. RAIMONDO, AND A. NARDINI. 2001. Vulnerability to cavitation of leaf minor veins: Any impact on leaf gas exchange? *Plant, Cell & Environment* 24: 851–859.
- SCHNITZER, S. A. 2005. A mechanistic explanation for global patterns of liana distribution and abundance. *American Naturalist* 166: 262–276.
- SCHNITZER, S. A., AND F. BONGERS. 2002. The ecology of lianas and their role in forests. *Trends in Ecology & Evolution* 17: 223–230.
- SCHNITZER, S. A., AND F. BONGERS. 2011. Increasing liana abundance and biomass in tropical forests: Emerging patterns and putative mechanisms. *Ecology Letters* 14: 397–406.
- SCHNITZER, S. A., M. KUZEE, AND F. BONGERS. 2005. Disentangling above- and below-ground competition between lianas and trees in a tropical forest. *Journal of Ecology* 93: 1115–1125.
- SCHOLANDER, P. F., H. T. HAMMEL, E. D. BRADSTREET, AND E. A. HEMMINGTON. 1965. Sap pressure in vascular plants. *Science* 148: 339–346.
- SECCHI, F., M. E. GILBERT, AND M. A. ZWIENIECKI. 2011. Transcriptome response to embolism formation in *Populus trichocarpa* provides

- insight into signaling and biology of refilling. *Plant Physiology* 157: 1419–1429.
- SPERRY, J. S., F. R. ADLER, G. S. CAMPBELL, AND J. P. COMSTOCK. 1998. Limitation of plant water use by rhizosphere and xylem conductance: Results from a model. *Plant, Cell & Environment* 21: 347–359.
- SPERRY, J. S., U. G. HACKE, R. OREN, AND J. P. COMSTOCK. 2002. Water deficits and hydraulic limits to leaf water supply. *Plant, Cell & Environment* 25: 251–263.
- SPERRY, J. S., AND N. Z. SALIENDRA. 1994. Intra- and inter-plant variation in xylem cavitation in *Betula occidentalis*. *Plant, Cell & Environment* 16: 279–287.
- TANEDA, H., AND J. S. SPERRY. 2008. A case-study of water transport in co-occurring ring- versus diffuse-porous trees: Contrasts in water-status, conducting capacity, cavitation and vessel refilling. *Tree Physiology* 28: 1641–1651.
- TOLEDO-ACEVES, T., AND M. D. SWAINE. 2008. Above- and below-ground competition between the liana *Acacia kamerunensis* and tree seedlings in contrasting light environments. *Plant Ecology* 196: 233–244.
- TYREE, M. T., AND H. T. HAMMEL. 1972. The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. *Journal of Experimental Botany* 23: 267–282.
- WOODRING, W., R. STEWARD, AND J. STEWARD. 1980. Geological map of the Panama Canal. U.S. Geological Survey, Reston, Virginia, USA.
- WOODRUFF, D. R., K. A. MCCULLOH, J. M. WARREN, F. C. MEINZER, AND B. LACHENBRUCH. 2007. Impacts of tree height on leaf hydraulic architecture and stomatal control in Douglas fir. *Plant, Cell & Environment* 30: 559–569.
- ZHU, S.-D., AND K.-F. CAO. 2009. Hydraulic properties and photosynthetic rates in co-occurring lianas and trees in a seasonal tropical rainforest in southwestern China. *Plant Ecology* 204: 295–304.
- ZUFFEREY, V., H. COCHARD, T. AMEGLIO, J.-L. SPRING, AND O. VIRET. 2011. Diurnal cycles of embolism repair and formation in petioles of grapevine (*Vitis vinifera* cv. Chasselas). *Journal of Experimental Botany* 62: 3885–3894.
- ZWIENIECKI, M. A., AND N. M. HOLBROOK. 2009. Confronting Maxwell's demon: Biophysics of xylem embolism repair. *Trends in Plant Science* 14: 530–534.