

Comparative hydraulic architecture of tropical tree species representing a range of successional stages and wood density

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Abstract Plant hydraulic architecture (PHA) has been linked to water transport sufficiency, photosynthetic rates, growth form and attendant carbon allocation. Despite its influence on traits central to conferring an overall competitive advantage in a given environment, few studies have examined whether key aspects of PHA are indicative of successional stage, especially within mature individuals. While it is well established that wood density (WD) tends to be lower in early versus late successional tree species, and that WD can influence other aspects of PHA, the interaction of WD, successional stage and the consequent

implications for PHA have not been sufficiently explored. Here, we studied differences in PHA at the scales of wood anatomy to whole-tree hydraulic conductance in species in early versus late successional Panamanian tropical forests. Although the trunk WD was indistinguishable between the successional groups, the branch WD was lower in the early successional species. Across all species, WD correlated negatively with vessel diameter and positively with vessel packing density. The ratio of branch:trunk vessel diameter, branch sap flux and whole-tree leaf-specific conductance scaled negatively with branch WD across species. Pioneer species showed greater sap flux in branches than in trunks and a greater leaf-specific hydraulic conductance, suggesting that pioneer species can move greater quantities of water at a given tension gradient. In combination with the greater water storage capacitance associated with lower WD, these results suggest these pioneer species can save on the carbon expenditure needed to build safer xylem and instead allow more carbon to be allocated to rapid growth.

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Introduction

The field of plant hydraulic architecture concerns the spatial distribution of various xylem properties throughout the individual. Properties of the xylem that have received considerable attention include vulnerability to embolism, hydraulic conductivity (volume flow rate per pressure gradient), and wood density (WD; dry mass per fresh volume). WD in particular has been linked to a wide variety of important ecological and physiological characteristics (Santiago et al. 2004; Chave et al. 2009). One of

the main ecological patterns that has been observed is that fast-growing pioneer species tend to have less dense wood than slower-growing species (Enquist et al. 1999; Muller-Landau 2004; King et al. 2005; Poorter et al. 2008, 2010). Physiologically, the consequences of higher WD on hydraulic architecture include lower hydraulic capacitance (water storage; Meinzer et al. 2003; Pratt et al. 2007; Scholz et al. 2007), lower hydraulic conductivity (Bucci et al. 2004a; Santiago et al. 2004), and greater resistance to drought-induced embolism (Hacke et al. 2001; Pratt et al. 2007).

All else being equal, a stem segment with low-density wood should have higher hydraulic conductivity than one with high-density wood because of differences in the proportion of xylem lumen volume. However, all else is rarely equal and stem segments with the same proportion of wood devoted to conduit volume can differ in density for various reasons. While cell wall density is a constant (1.53 g/cm^3), there are numerous ways to partition the material between fibers, rays, vessels and tracheids that result in different hydraulic conductivities. Furthermore, the dependence of hydraulic conductivity on conduit diameter to the fourth power complicates the relationship between WD and conductivity because the frequency distributions of conduit sizes can vary among stem segments with similar fractions of wood devoted to conduit lumen volume (McCulloh et al. 2010). Thus, WD alone is not necessarily a reliable predictor of a stem's conductivity. Yet, studies of co-occurring species with the same wood type often show strong inverse relationships between WD and hydraulic conductivity (Meinzer et al. 2008; Hacke et al. 2009; Gonzalez-Benecke et al. 2010).

Studies of hydraulic architecture in relation to species successional stage have largely focused on the hydraulic conductivity of small-diameter shoots and roots (Machado and Tyree 1994; Zotz et al. 1998; Phillips et al. 2001; Soriano 2003; Wang 2005), and have generally not attempted to measure or scale up to whole-plant, -shoot, or -root conductance. Leaf-specific hydraulic conductance (K_L) is a more appropriate measure to compare patterns of hydraulic architecture among species because it integrates the hydraulic conductivities of individual plant parts across the organism and has been shown to be proportional to stomatal conductance and photosynthetic rate (Meinzer and Grantz 1990; Sperry and Pockman 1993; Meinzer et al. 1995; Hubbard et al. 2001). Tyree et al. (1998) and Becker et al. (1999) determined that saplings of pioneer species had greater leaf-specific conductance than mature forest tropical species. Based on the widely observed trend in WD described above, the pioneer species in these studies probably had lower WD than the late successional species, but this was not measured; nor were the underlying xylem anatomical differences that may have contributed to these differences examined. The hydraulic architectures of many species can change greatly with tree size or age (Domec et al. 2009), but

previous work on pioneer versus late-seral species has focused on a single plant segment or on small trees or saplings. A better characterization of the hydraulic architecture of whole mature trees would improve our understanding of its ecological consequences.

Here, we examine the influence of WD and seral stage on various tree hydraulic parameters from the scale of vessels to stem segments in trunks and twigs, in order to explore how those parameters are integrated to influence in situ K_L , which has such significance for plant functioning. To accomplish these goals, we compared the hydraulic architecture and xylem sap flux of mature trees growing in two forests in Panama. The sites differed in seasonality of precipitation, with one site experiencing a more severe dry season; and in their successional stage, with the drier site being a relatively young secondary forest and the wetter site a mature forest. Whereas these forests differ in their seral stages, species found within each forest span the continuum of early to late successional stage. This continuum was particularly apparent at the mature forest site: gaps were populated by pioneer species, but the majority of trees were late seral species. At that site we were therefore able to examine a pioneer species in the same environment as the late successional species we sampled. We hypothesized that mean WD would be lower in pioneer than late successional species, and that this trend would be associated with greater vessel diameters in stems of pioneer species. We further hypothesized that the preceding properties would scale up to greater whole-tree K_L in pioneer species than late successional species.

Materials and methods

Study locations and species

Studies of large, adult trees were undertaken at two sites in the Republic of Panama, where there are canopy cranes operated by the Smithsonian Tropical Research Institute. One crane is located in the secondary forest of the Parque Natural Metropolitano near Panama City, which is estimated to be 100–150 years old (S. J. Wright, personal communication). This lowland tropical forest is seasonally dry and receives 1,800 mm of rain annually with a pronounced dry season from December to April (Meinzer et al. 2008). The second crane is located in mature forest in the Parque Nacional San Lorenzo on the Caribbean side of the isthmus that is estimated to be >300 years old (S.J. Wright, personal communication). This area receives 3,100 mm of rain per year and experiences a moderate dry season that is less intense and shorter than at the drier site (Meinzer et al. 2008).

The species studied for xylem anatomical characteristics at Parque Natural Metropolitano were *Anacardium excelsum* (Bentero & Balb. Ex Kunth) Skeels, *Cordia alliodora* (R. & P.)

Table 1 Morphological and anatomical characteristics for mature trees from ten species

Site/species	Ht (m)	DBH (m)	Branch <i>D</i> (mm)	Wood density (g/cm ³)		Vessel <i>D</i> (μm)		Vessel freq. (cells/mm ²)	
				Trunk	Branch	Trunk	Branch	Trunk	Branch
Early succ. forest									
<i>Anacardium excelsum</i>	38	0.98	20.5 (1.1)	0.39	0.39	142.7 (20.6)	79.1 (7.8)	2.7 (0.6)	14.6 (2.5)
<i>Cordia alliodora</i>	26	0.36	20.1 (1.1)	0.56	0.47	108.4 (13.5)	52.5 (11.1)	13.1 (2.4)	66.5 (4.6)
<i>Ficus insipida</i>	28.7	0.65	15.4 (2.2)	0.37	0.34	153.7 (24.9)	86.9 (4.4)	2.7 (0.4)	14.5 (0.8)
<i>Leuhea seemanii</i>	24.4	0.43	22.8 (3.3)	0.67	0.33	97.6 (27.4)	69.0 (14.8)	9.0 (1.2)	19.1 (7.5)
<i>Cecropia longipes</i>	20.2	0.15	43.4 (3.1)	0.35	0.32	173.1 (1.5)	112.1 (19.9)	3.9 (0.1)	14.8 (8.5)
Mature forest									
<i>Aspidosperma cruenta</i>	28.7	0.33	16.1 (1.6)	0.73	0.74	111.8 (8.8)	39.4 (2)	12.5 (3.3)	82.2 (5.6)
<i>Tachigalia versicolor</i>	23.2	0.40	15.4 (0.7)	0.57	0.64	163.8 (14.9)	45.6 (6.1)	5.3 (1.5)	48.7 (10.6)
<i>Tapirira guianensis</i>	34.5	0.70	15.3 (0.7)	0.54	0.50	105.9 (19.5)	41.0 (4.3)	15.4 (3.1)	60.9 (9.1)
<i>Vochysia ferruginea</i>	25.9	0.46	15.1 (2.0)	0.40	0.56	206.3 (22.9)	64.7 (9.1)	2.8 (0.6)	24.9 (5.9)
<i>Cecropia insignis</i> ^a	18.9	0.16	36.5 (4.4)	0.27	0.34	182.4 (32.6)	123.0 (23.1)	1.6 (0.2)	5.2 (2.2)

The numbers in parentheses indicate standard deviations between cores or branches ($n = 2-4$). Species are separated into groups based on the site from which they were collected: the Parque Natural Metropolitano (early successional forest) versus Parque Nacional San Lorenzo (mature forest) sites

^a Although this species was sampled at the mature forest site, it is a pioneer species that was found growing in the gap created by the installation of the canopy crane

Oken., *Ficus insipida* Willd., *Luehea seemanii* Triana & Planch, and *Cecropia longipes* Pittier (Table 1). At Parque Nacional San Lorenzo (formerly known as Fort Sherman), xylem anatomy was characterized in *Aspidosperma cruenta* Woods., *Tachigalia versicolor* Standl. and Wms, *Tapirira guianensis* Aubl., *Vochysia ferruginea* Mart., and *Cecropia insignis* Liebm. The *Cecropia insignis* was selected because although it was growing at the mature forest site, it is a pioneer species (Foster and Brokaw 1990; Condit et al. 1995), and was growing in the gap created when the canopy crane was installed. Thus, when we refer to the pioneer species, we are including *Ce. insignis* even though it grew at the mature forest site. When we refer to late successional species, we mean the other species at the mature forest site.

In several species at each site we also measured sap flux in trunks and upper canopy branches and the water potential of upper canopy leaves to estimate whole-tree K_L and to examine relationships between sap flux, tree successional stage and xylem biophysical characteristics. Sap flux and leaf water potential were measured in *Anacardium excelsum*, *Cordia alliodora*, *Ficus insipida*, and *Schefflera morototoni* (Aubl.) Maguire, Steyer and Frodin at the Parque Natural Metropolitano site and in *Aspidosperma cruenta*, *Protium panamense* (Rose) I.M. Johnst., *Tachigalia versicolor*, *Tapirira guianensis*, and *Vochysia ferruginea* at the Parque Nacional San Lorenzo site.

Collections for xylem anatomy

Branch samples were collected from twigs in the canopy and cores were taken from the bases of trees at the two forest sites

during February 2005 and 2007. Three or four branches were collected from the upper crown of each individual, except the two species of *Cecropia*, because they had very few branches. Instead, 5-mm diameter cores were made of two branches from each individual in an attempt to minimize damage. Branches for all ten species were accessed using crane gondolas and taken from morphologically equivalent locations (i.e., the same number of branch junctions proximally from the leaves) for all species except *Cecropia*, which had very few junctions. For *Cecropia*, branches were taken from roughly the same distance proximally from the leaves as the other species. Two to four 12.5-mm diameter cores were collected from the bases of these trees at breast height (1.3 m) for all species except *F. insipida*, for which we sampled at 2.2 m (above its large buttresses). Branch and trunk diameters are listed in Table 1. Before coring the trunk, we allowed stain to ascend into the core through the transpiration stream. To introduce the stain, holes were drilled using a 4 mm-diameter bit at a downward angle (approximately 15–20° from the horizontal) into the trunk to a depth of 12–15 cm or approximately half the diameter of the trunk (whichever was longer) at about 5 cm below the 2–4 locations targeted for core removal. Into the bottom half of each hole was inserted a thin piece of tubing that had been cut in half length-wise, and 0.5% filtered aqueous safranin O was injected with a syringe to fill the holes. The tubing minimized dye flow downwards in the trunk. More dye was added regularly to replace the volume that was absorbed. After 15 min, we bored 12.5 mm cores. The functional xylem area was assumed to be between the cambium and the innermost stained vessel.

Sapwood anatomy and density

Vessel dimensions from trunks and distal branches were assessed in all species listed in Table 1. Images of transverse sections of branch segments and cores were taken using a Photometrics Coolsnap camera (Tucson, AZ, USA) mounted on a Nikon Eclipse E400 microscope connected to a PC using Metavue software (Universal Imaging Corp., Downingtown, PA, USA). Images were analyzed using the freeware software ImageJ (NIH, USA, <http://rsb.info.nih.gov/ij/>). For branch samples, lumen areas were measured on all vessels within three pie piece-shaped areas spanning from the bark to the pith (averaging $4.8 \times 10^{-6} \text{ m}^2$). If fewer than 100 vessels were measured in three combined areas, more pie piece-shaped areas were added until >100 vessels had been measured. Cores from tree trunks were divided into 1–1.5-cm-long segments from the bark to the last dyed vessel. Each of these segments was sampled by taking several thin transverse sections, and vessels were measured until a total of >100 vessels were sampled per tree from the trunk. For all sampling locations, each vessel diameter (D) was determined by calculating the diameter of a circle of the given lumen area. A second measure, the area-weighted vessel diameter, was also calculated as $D_A = (\sum D^2/n)^{0.5}$, where n is the number of vessels measured from a sample. The xylem area defined by the nearest two adjacent sets of radial ray cells surrounding the vessels that were measured for D estimates was also measured, including one line of ray cells, to calculate the vessel packing density as the number per mm^2 . Further, the fraction of vessel lumens was calculated using the area-weighted average diameter as $= (D_A/2)^2 \pi F$, where F is the number of vessels per mm^2 .

Wood density (dry mass per fresh volume in g/cm^3) was measured on branches and cores for all species. For each branch, a small segment (≤ 3 cm in length) was cut from the samples, and the bark and pith were removed and discarded. For the cores, the outer 2 cm of wood was measured for WD. Fresh volume was measured using Archimedes' principle as described in Hacke et al. (2000). Samples were then dried for 3–5 days in an oven at 60°C and weighed for dry mass.

Sap flux measurements

Variable length heat dissipation sap flow probes with a heated and reference sensor measuring length of 10 mm at the probe tip (James et al. 2002) determined sap flux ($\text{g m}^{-2} \text{ s}^{-1}$) at different radial depths and vertical positions in each tree. Two replicate sets of probes were installed on opposite sides of the trunk near the base of each tree. Pairs of sensors were placed in an upward spiral around the trunk, 10 cm apart vertically and 10 cm apart

circumferentially, at 3–5 successive depths between 1.3 and 24 cm depending on the trunk diameter. The trunk sensors were installed at heights of about 1.3–3.1 m depending on the degree of root buttressing near the base of the tree. Pairs of sensors were also installed with their tips at a sapwood depth of approximately 1.3 cm in each of 3–5 branches in the upper crown of each tree (branch diameter ≈ 3 –5 cm). For probe installation, two 38-gauge (2.58 mm diameter) holes, separated axially by 10 cm, were drilled into the sapwood. The sensors were coated with thermally conductive silicone heat sink compound prior to insertion. All probes were protected from direct sunlight and rainfall by reflective insulation, and additional foam insulation was used on the branches. Concurrent differential voltage measurements across the copper thermocouple leads were converted to a temperature difference between the heated and reference sensor. Signals from the sap flow probes were scanned every minute, and 10 min means were recorded with a data logger (CR10X, Campbell Scientific, Logan, UT, USA) equipped with a 32-channel multiplexer (AM416, Campbell Scientific). The temperature difference between the heated and reference sensors (ΔT) was converted to sap flux ($\text{g m}^{-2} \text{ s}^{-1}$) based on the calibration of Granier (1985) re-validated for tropical species (Clearwater et al. 1999; McCulloh et al. 2007).

Maximum trunk and branch sap fluxes were estimated over three or more diurnal cycles corresponding to clear, dry conditions during February/March 2004 at the Parque Nacional San Lorenzo site and February/March 2001 and 2002 at the Parque Natural Metropolitano site. Estimates of maximum trunk sap flux were based on measurements at sensor depths yielding the highest fluxes along the sapwood radial profile, typically within 5 cm of the cambium. Maximum branch sap fluxes were estimated from the 3–5 branches showing the greatest fluxes. Occasionally one or more branches showed substantially different maximum fluxes than the others because of partial shading during the morning when branch sap flux peaked (~ 0900 – 1030 h) or sensor malfunction, and the values from these sensors were not used. The times at which maximum branch and trunk sap fluxes occurred were not synchronous because of internal capacitance (Meinzer et al. 2003, 2008).

Whole-tree hydraulic conductance

Soil-to-leaf hydraulic conductance (K_L ; $\text{mmol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$) was estimated as the ratio of branch transpiration per unit leaf area to the difference between soil and leaf water potentials during the same time period (~ 1000 – 1400 h) and on the same days as the transpiration measurements. Leaf xylem pressures were measured with a pressure chamber (PMS Instrument Company, Albany, OR, USA) on 3–4 leaves per species at 1–2 h intervals throughout the day. To

obtain the net driving force for transpiration, these values were corrected to ground level based on the estimated height of branches above the ground and a vertical gravitational gradient of 0.01 MPa m^{-1} . Soil water potential was estimated from early morning ($\sim 0630\text{--}0730 \text{ h}$) measurements of water potential on covered, nontranspiring leaves (Bucci et al. 2004b). When these values were corrected to ground level, they were not significantly different from zero at both sites, so soil water potential was taken to be zero for the purpose of estimating K_L . Branch transpiration was calculated by multiplying the sap flux by the sapwood cross-sectional area and then dividing by the total leaf area distal to the point of sap flow measurement. Branch leaf areas were estimated by multiplying the total number of leaves by the mean area per leaf obtained from a subsample of 50–200 leaves.

Statistical analyses

Student *t* tests were used to compare means of anatomical and physiological data between the successional groups. Relationships between variables were compared with standard major axis (SMA) line-fitting methods using SMATR freeware (Warton et al. 2006; <http://www.bio.mq.edu.au/ecology/SMATR/>). Probability levels of $p < 0.05$ were considered significant.

Results

As has been observed in other studies, the vessel diameters increased with stem diameter and were widest in trunks, but showed no consistent trend with trunk diameter (Table 1, Fig. 1a). The vessel diameters in the branches ranged from $39 \mu\text{m}$ in *A. cruenta* to $123 \mu\text{m}$ in *C. insignis*. In the trunks, vessel diameters were generally greater and ranged from $98 \mu\text{m}$ in *L. seemannii* to $206 \mu\text{m}$ in *V. ferruginea*. There were no statistical differences between trunk vessel diameters in species from different successional stages (Table 1) or in the relationship between vessel and stem diameter between the groups (Fig. 1a). Vessel diameters in branches were smaller in mature-forest species than early successional species (p value = 0.02), which was consistent with a non-significant trend towards narrower branches in late successional species (p value = 0.08).

As has also been previously observed in other species, the packing density of vessels (number of vessels/ mm^2) decreased with increasing vessel diameter in all species (Table 1; Fig. 1b). On average, there were approximately four times as many vessels/ mm^2 in branches versus trunks

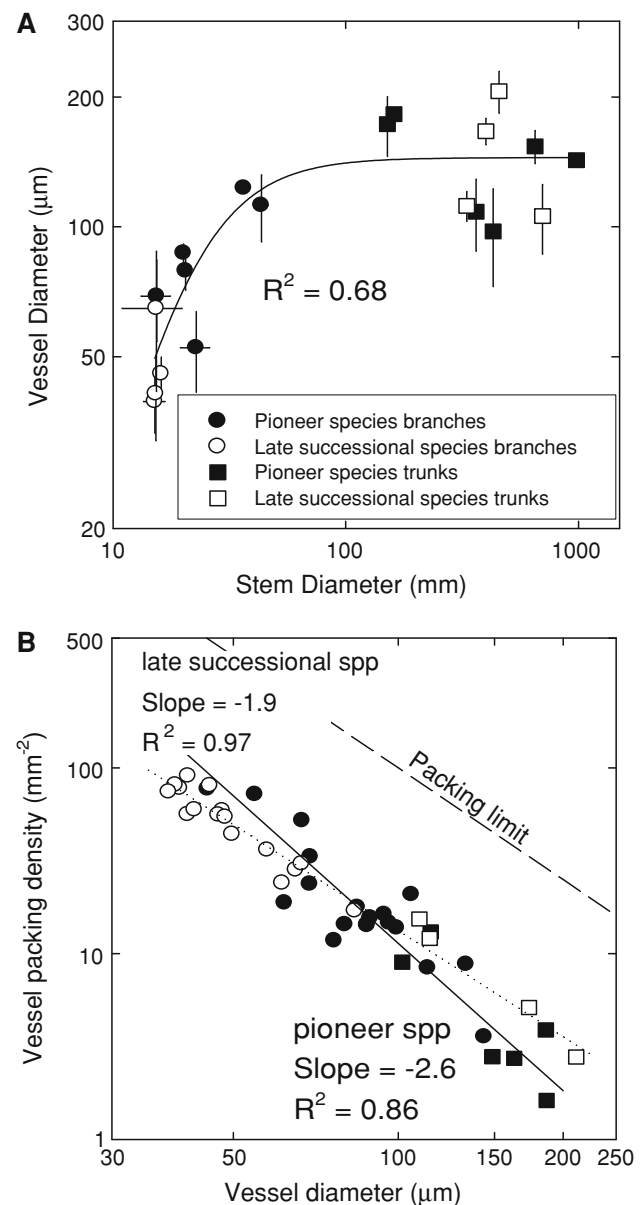


Fig. 1 **a** The relationship between mean vessel diameter and stem diameter in branches and trunks of ten tropical tree species plotted on a log–log scale. Symbols signify grand means of measurements between branches ($n = 2\text{--}4$) or cores of the trunk ($n = 2\text{--}4$) taken from one individual. Error bars indicate standard errors between branches or cores. Sigmoidal, three-parameter regressions were not different between the pioneer and late successional species, so only a single function fitted to the pooled data is shown. **b** The number of vessels per mm^2 (packing density) versus the mean area-weighted vessel diameter on a log–log plot. Symbols indicate means from individual branches or grand means from 2–4 cores of trunks from trees indicated by the legend in **a**. The “packing limit” indicates the maximum number of vessels of a given diameter that could fit into a square millimeter, and was calculated as $1/d^2$. Lines indicating SMA relationships were significantly different between the groups (p value = 0.002)

in pioneer species, but six times as many in late successional species. While the vessel packing densities of species from different successional stages were marginally different (p value = 0.06), the decline in packing density with vessel diameter was much less steep in late successional than pioneer species (SMA slopes = -1.9 vs. -2.6 , respectively, p value comparing slopes = 0.002).

WD did not differ among branches and trunks within individuals (two-way ANOVA comparing all samples with sampling location (branch or trunk), and successional stage as fixed effects and species as a random effect, type III sum of squares, p value = 0.11). The same statistical test showed that trunk wood densities did not differ among the two successional groups (p value = 0.11). However, these analyses showed that branch wood was denser ($p = 0.005$) in late successional species ($0.61 \pm 0.05 \text{ g cm}^{-3}$) than pioneer species ($0.36 \pm 0.02 \text{ g cm}^{-3}$). Across all species, increases in WD were associated with greater vessel packing densities and narrower vessels in both trunks and branches (Fig. 2a, b). The slopes of relationships for trunks and branches were similar for the comparison of vessel diameter versus WD (Fig. 2b; p value = 0.49), but the slope was greater for branches than trunks when packing density was compared with WD (Fig. 2a; p value = 0.001).

The greater trunk-to-branch tapering of vessels associated with the morphologically equivalent but marginally narrower branches in late successional species was not proportional to the increase in packing density, and resulted in a decline in vessel lumen fraction (proportion of vessel lumen area to total wood area) in branches relative to trunks (Fig. 3). The ratio of the vessel lumen fraction in branches:trunks of pioneer species was greater than 1, indicating that a given area of wood in branches had more lumen area than in trunks of these species, and this value was greater than for late successional species (p value = 0.001), which had a ratio of <1 . The lumen fraction ratio of pioneer species exceeded 1 even when the large-branched *Cecropia* species were excluded. The lumen fraction ratios are also reflective of the slopes of the relationships in Fig. 1b. The log–log plot of this graph means a lumen ratio of 1 would be predicted if packing density scaled with vessel diameter to the power of -2 . The slightly shallower slope than -2 (although not significantly different: p value = 0.2) of late successional species resulted in a lumen fraction ratio <1 , while the significantly steeper relationship (p value comparing pioneer species slope to $-2 = 0.002$) seen in the pioneer species had a ratio >1 .

Along the observed gradient of increasing branch WD from pioneer to mature species, strong linear declines were observed in anatomical and functional relationships (Fig. 4). The greater tapering of conduits in late successional species

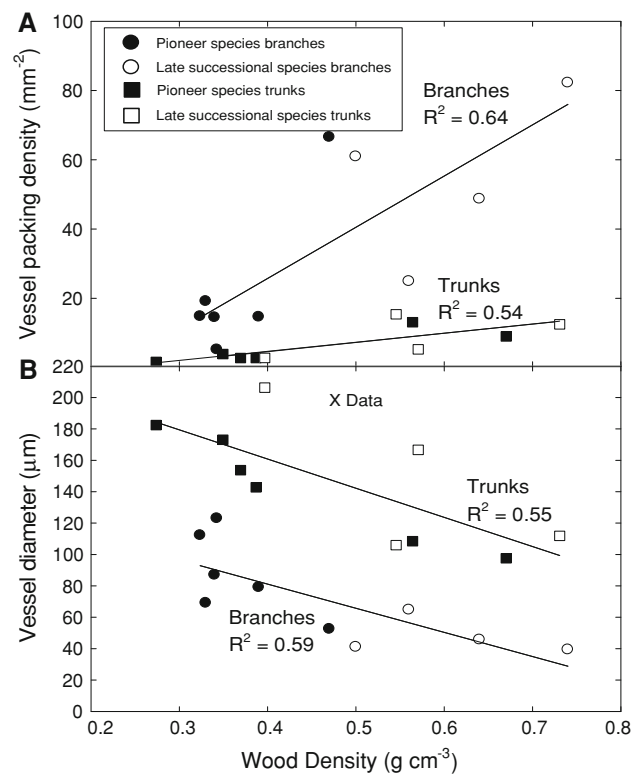


Fig. 2 Wood density versus the frequency of vessels (a) and the mean vessel diameter (b) for branches and trunks from ten species. All four SMA analyses were significant (p value < 0.001 , except for trunks in a in which the p value = 0.025)

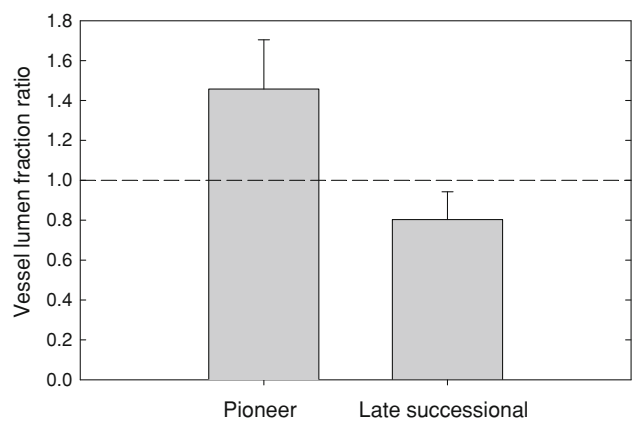


Fig. 3 The average ratio of the vessel lumen fraction of wood in pioneer versus late successional species. The ratio was calculated as the branch:trunk lumen fraction. The fraction of vessel lumens was calculated using the area-weighted average diameter as $= (D_A/2)^2 \pi F$, where F is the number of vessels per mm^2 . Results from a t test indicated significant differences between the two groups (p value = 0.001). Error bars show one standard deviation. Dashed line indicates constant lumen fraction between trunk and branches

segregated those species from pioneer species when vessel diameter ratio (branch:trunk mean vessel diameter) was compared (Fig. 4a). Branch sap flux was greater in pioneer

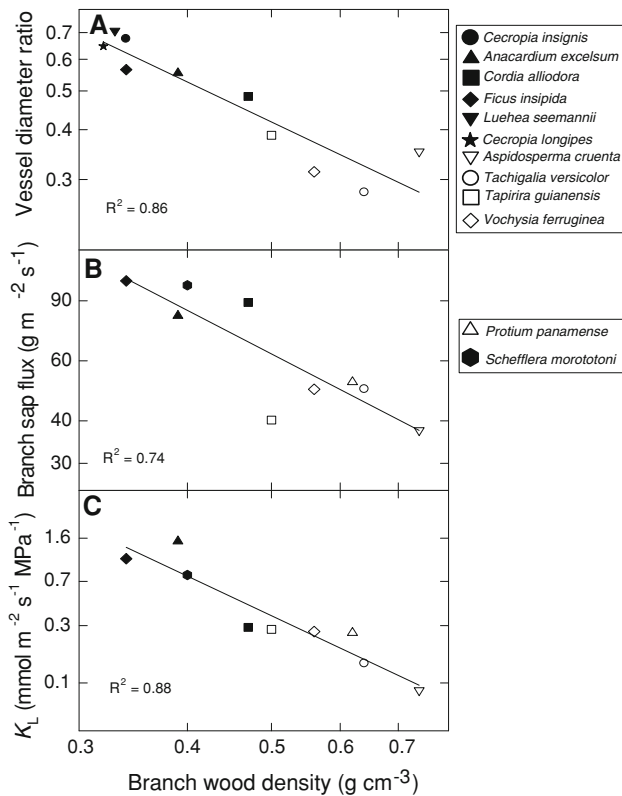


Fig. 4 The branch wood density compared with the vessel diameter ratio (branch:trunk mean vessel diameter) (a), the branch sap flux (b), and the leaf-specific hydraulic conductance (c) for pioneer (solid symbols) and late successional (open symbols) species. *P* values for the regressions were <0.001 in a and c and $=0.002$ in b

species (Fig. 4b), as was leaf-specific, whole-tree hydraulic conductance (K_L ; Fig. 4c). Across the near-twofold range in wood densities sampled, K_L had a tenfold range. This variation was associated with the average K_L of pioneer species being approximately four times that of late successional species (p value = 0.02).

The segregation of branch sap flux of pioneer versus late successional species with WD (Fig. 4b) was accompanied by distinct differences between groups in trunk sap flux, with pioneer species having greater trunk sap flux ($p = 0.006$). The relationship between branch and trunk sap flux across all species was strongly linear ($R^2 = 0.84$), with a y-intercept that was not different from zero (Fig. 5). On average, branch sap flux was 2.1 times greater than trunk sap flux (compare the regression line in Fig. 5 with the dashed 1:1 line).

Discussion

We had hypothesized that early successional species would have less dense wood than late successional species, and that this difference would be reflected in xylem anatomical

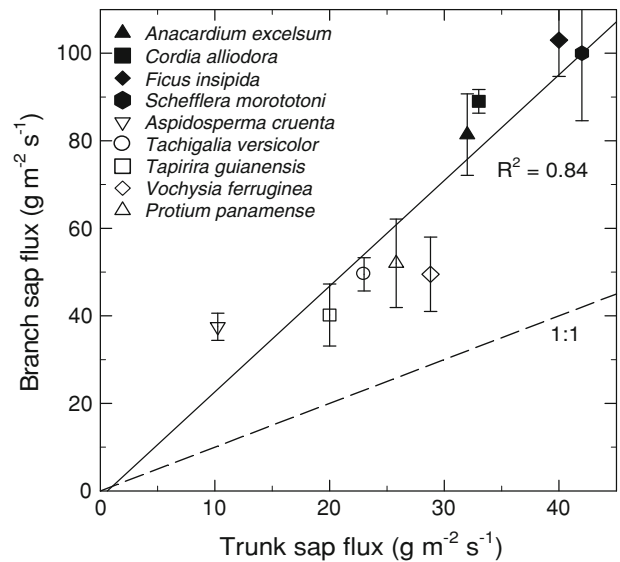


Fig. 5 Maximum trunk sap flux versus maximum branch sap flux for pioneer (solid symbols) and mature forest (open symbols) species. Vertical bars represent standard errors ($n = 3-5$). The dashed 1:1 line indicates equal sap flux within branches and trunks. The solid line fitted to the data is a linear regression (p value <0.001)

differences with associated consequences for hydraulic conductance. Specifically, we predicted that the lower density wood of pioneer species would have wider vessels that would result in greater K_L than late successional species. Our hypothesis regarding WD was not supported in the trunks of species with different successional stages; nor did we observe differences in vessel diameters in trunks (Table 1). Although wood densities were indistinguishable at the depths of sapwood we examined, it is possible differences in WD were present at depths closer to the pith that we did not detect. However, branches of pioneer species did have lower density wood than late successional species, which was consistent with the early successional species having wider vessels than the late successional species. Nevertheless, this difference in vessel diameter could also have been marginally confounded by the morphologically equivalent yet slightly wider stems taken from the pioneer species. The steeper slope in the vessel diameter versus packing density relationship for the pioneers (Fig. 1b) resulted in greater ratios of lumen fraction (Fig. 3) and vessel diameter (Fig. 4a) in pioneer species than late successional species. A major functional consequence of these anatomical differences was greater whole-tree hydraulic conductance in the early versus late successional species (Fig. 4c). Despite slightly wider branches at the equivalent distance from the leaves, the leaf to sapwood area ratios ($A_L:A_S$) have been shown to be lower in pioneer versus late successional species in a group of species that largely overlap with the species examined here (Meinzer et al. 2008), and these differences could explain part of

the greater K_L we observed in pioneer species. However, the range in $A_L:A_S$ between groups was roughly $5\times$ lower than the range in K_L , suggesting that this morphological trait cannot fully explain the functional difference between the groups.

A second and related correspondence of these anatomical differences is the higher sap flux observed in pioneer species than in late successional species (Fig. 5). Functionally, greater K_L values were associated with greater sap fluxes (Figs. 4c, 5), which means that pioneer species would be expected to transport more water per unit xylem area for a given tension gradient than late successional species. This result is supported by previous work showing that, in a comparison of many of the same species examined here, transpiration per unit leaf area was greater in pioneer species (Meinzer et al. 2008). Equivalent xylem water tension and greater capacitance in species with lower density wood (Meinzer et al. 2003, 2008, 2009; Pratt et al. 2007; Scholz et al. 2007) thus ameliorates the requirement for extra investment in xylem structural features that make the wood more embolism resistant. In the environments where these trees grow, capacitance is sufficient to buffer diurnal fluctuations in xylem tensions such that each species investigated avoids the threshold of loss in conductivity that might otherwise be expected to cause catastrophic embolism (Meinzer et al. 2009, 2010). This suite of traits may allow more carbon to be allocated to more rapid growth (wood production and display of leaf area).

Assuming a constant total sapwood area from trunk to twigs, the observed vessel lumen area ratio (Fig. 3) of pioneer species suggests that sap flux should decline along this trajectory, because when the same volume of water is transported in a network with increasing total lumen cross-sectional area, flux slows (McCulloh and Sperry 2005). However, the opposite trend in sap flux was observed (Fig. 5), suggesting that while the lumen area per sapwood area increases in twigs relative to the trunk, the total sapwood area must decline. There are at least three non-mutually exclusive explanations for this decrease in sapwood area. If total cross-sectional stem diameter is constant from trunk to twigs (da Vinci's rule), the fraction of stem devoted to sapwood area could decline from the bottom to the tops of trees. Alternatively, if the sapwood fraction remains constant from trunk to branch, total stem cross-sectional area could decline, contradicting da Vinci's rule. For one species for which we were able to measure the total cross-sectional area of the trunk and all branches (*Cecropia insignis*), the trunk area was more than three times greater than the total branch cross-sectional area. This result suggests a strong deviation from da Vinci's rule in this species and supports the second explanation. However, a third possibility is that because all branches are never drawing

water from the trunk equally (i.e., some branches will always be shaded relative to others), the communal trunk area will be mainly servicing the subset of sunlit branches. Thus, the effective area for flow to sunlit branches will be much greater in the trunk than the area of those branches, and flow in branches will be much faster than the trunk. Essentially, the trunk is hydraulically overbuilt for the branches at any given time.

Across the greater than 2.5-fold range in WD, the anatomical and functional characteristics examined scaled similarly across all species (Figs. 2, 4, 5). These shared scaling relationships occurred despite these species representing different successional stages and growing in environments that varied considerably in their rainfall quantity and seasonality. Given the number of species studied, we were unable to carry out conclusive tests for differences in scaling of functional traits against WD for the pioneer versus late successional species (e.g., Fig. 4). However, when single regressions were fitted to pooled data sets for both groups, they were highly significant and explained 54–88% of the variation in y -variables (e.g., Figs. 2, 4). The scaling observed in Fig. 5 shows the greatest potential for differences along the successional continuum, because the slope for late successional species could be smaller. However, it would be biologically and physically unexpected for the intercept of this type of relationship to be different from zero under steady state conditions (i.e., there cannot be branch sap flux without trunk sap flux), which supports our conclusion that both groups scale similarly. The relationships with WD observed here would not be expected to hold among the species we examined and species with coniferous and ring-porous wood, or even across temperate diffuse-porous species, because of differences in conduit diameters associated with climate and wood type (McCulloh et al. 2010). They would also not be expected when comparing saplings with adults of the same species, because basal conduit diameters increase with plant size (Zobel and van Buijtenen 1989; Lei et al. 1996; Gartner et al. 1997; Lei et al. 1997). However, it is possible that the anatomical and functional attributes examined here would scale with WD similarly across species, but with different slopes depending on wood type and climate.

An exception to the pattern of similar scaling relationships across early and late successional species was found in the dependence of packing density on vessel diameter, where packing density was greater in pioneer species at smaller vessel diameters and greater in late successional species at larger vessel diameters (Fig. 1b). The consequences of this difference in vessel packing within the wood were the scaling relationships along the axis in WD. Given that the WD of the trunks and the vessel packing density of either the trunks or the twigs were indistinguishable between the two groups, this indicates that the

gradient in packing density and WD from trunk to twigs may be more important in determining functional traits such as hydraulic conductance than these parameters at one point in the continuum from roots to distal branches. This result is especially important to consider when WD from only one organ is used to compare functional traits from a wide variety of species across or within habitats (e.g., Chave et al. 2009; Russo et al. 2010).

As mentioned, the main difference among species, other than their successional stage, was that they grew at sites differing considerably in the quantity and seasonality of rainfall, with the early successional site receiving much less rain and experiencing consistently greater vapor pressure deficits (http://striweb.si.edu/esp/physical_monitoring/downloads_intro.htm). These site differences raise the question of whether the greater branch sap flux and K_L observed in pioneer species could be due to adaptations to environmental differences between the sites and not inherent differences in suites of functional traits between the groups associated with their successional stage. Perhaps the observed xylem anatomical differences between groups, and their consequent functional segregation, were determined largely by differences in their growth environment. Contrary to this hypothetical is *Cecropia insignis*, a pioneer species (Foster and Brokaw 1990) that was sampled at the mature forest site. Hydraulic traits of this species were consistently closer to those of the pioneer species and not its cohabitants at the mature forest, which supports the original hypothesis that the observed differences reflect successional stage.

Similar to the pattern Tyree et al. (1998) reported for whole-shoot conductance in saplings, we found that mature trees of pioneer species had greater K_L values than late successional species. Given the relationship between hydraulic function and plant productivity (Domec and Gartner 2003; Tyree 2003; Lovelock et al. 2004; Zhang and Cao 2009; Poorter et al. 2010), it seems reasonable to predict that high K_L is one of the primary mechanisms pioneer species use to initially outgrow late successional species. The subsequent shift in forest species from early to late successional has been related to factors that are largely independent of hydraulic architecture, such as seedling and sapling shade tolerance (e.g., Shirley 1945; Kobe et al. 1995; Oliver and Larson 1996).

Although this study was not conducted as a phylogenetically independent contrast, the groups did represent a wide variety of tropical families. In the two cases in which the same family or genus were sampled, these species grouped within the same successional stage with respect to anatomical and functional traits, rather than by family or genus. For example, *Tapirira guianensis* and *Anacardium excelsum* are both in the Anacardiaceae, yet they were separated into the mature forest and pioneer groups,

respectively, which was consistent with their successional stage. Similarly, both *Cecropia* species grouped with the pioneer species, despite growing at different sites, which was also consistent with their successional stage. It appears that the overarching structure–function relationships and mechanisms superseded phylogenetic relationships, and that the types of biophysical constraints examined here could be expected to be universal.

In conclusion, we found that suites of morphological and anatomical traits among early and late successional species resulted in different operating ranges along a continuum of functional traits such as whole-plant hydraulic conductance and axial trends in sap flux from trunks to branches. The pioneer species had lower branch WD and fewer but larger conduits that promoted higher K_L , all of which are consistent with the general pattern of pioneer species exhibiting rapid growth relative to late successional species. In scaling from anatomical measurements to whole-plant functioning, this study was able to link form directly to function in adult trees.

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