

ANGIOSPERM WOOD STRUCTURE: GLOBAL PATTERNS IN VESSEL ANATOMY AND THEIR RELATION TO WOOD DENSITY AND POTENTIAL CONDUCTIVITY¹

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Woody stems comprise a large biological carbon fraction and determine water transport between roots and leaves; their structure and function can influence both carbon and hydrological cycles. While angiosperm wood anatomy and density determine hydraulic conductivity and mechanical strength, little is known about interrelations across many species. We compiled a global data set comprising two anatomical traits for 3005 woody angiosperms: mean vessel lumen area (\bar{A}) and number per unit area (N). From these, we calculated vessel lumen fraction ($F = \bar{A}N$) and size to number ratio ($S = \bar{A}/N$), a new vessel composition index. We examined the extent to which F and S influenced potential sapwood specific stem conductivity (K_S) and wood density (D ; dry mass/fresh volume). F and S varied essentially independently across angiosperms. Variation in K_S was driven primarily by S , and variation in D was virtually unrelated to F and S . Tissue density outside vessel lumens (D_N) must predominantly influence D . High S should confer faster K_S but incur greater freeze–thaw embolism risk. F should also affect K_S , and both F and D_N should influence mechanical strength, capacitance, and construction costs. Improved theory and quantification are needed to better understand ecological costs and benefits of these three distinct dimensions.

Key words: angiosperms; evolutionary divergences; potential conductivity; variances; vessel lumen fraction; vessel number; vessel size; wood density; xylem sapwood.

Much of the world's biomass is found in woody plants. In fact, old growth, tropical forests account for close to half of this biomass alone (Denman et al., 2007). If woody biomass is converted to amount of carbon, it contains an estimated 58% of the carbon found in the atmosphere (Chave et al., 2009). Rates of carbon release from woody plants should then have important influences on global carbon budgets. Hydrological cycles are also tied to vegetation cover via evapotranspiration (Denman et al., 2007). Because water exiting leaves must first traverse xylem sapwood in stems, flow rates from the plant are in part regulated by variation in xylem vessel anatomy (which largely determines flow rates through stems). Understanding variation in wood density and vessel anatomy is important for evaluating and integrating environmental and biotic influences on ecosystem and even global processes.

The cellular structure of xylem in plant stems is known to have important implications for whole-plant function (Carlquist and Hoekman, 1985; Tyree and Ewers, 1991; Carlquist, 2001;

Tyree and Zimmermann, 2002; Wheeler et al., 2007; Sperry et al., 2008; Martínez-Cabrera et al., 2009; Poorter et al., 2010). However, much is still unknown about the ways in which plants adjust the anatomy of xylem tissues to meet transpiration needs or increase mechanical stability, in part because studies have been based on relatively small numbers of species and/or limited geographic regions. Vessels in sapwood are the conduits through which most water in the transpiration stream of angiosperms must pass during its ascent to the canopy (Tyree and Zimmermann, 2002). To adjust rates of water supply through sapwood, plants can alter wood properties in several distinct ways, based on changes in: (1) fraction of sapwood occupied by vessel lumens (open conduit spaces), (2) vessel composition, from many narrow to few wide vessel lumens, and (3) total area of sapwood supplying a given unit of leaf. These adjustments are not necessarily mutually exclusive: plants can alter a combination of these traits, but the relative contribution of each to species-level differences in conductivity is not well known. In this paper, we examine four variables in basic vessel anatomy: mean vessel size (\bar{A}), vessel number per unit of sapwood (N), vessel lumen fraction (F), vessel size to number ratio or composition (S) (see Table 1 for a description of variables used), which are related as: $F = \bar{A}N$ and $S = \bar{A}/N$.

Besides water transport, another key function of wood is to provide mechanical support. However, much remains unknown about trade-offs between constructing mechanically strong wood and highly conductive wood. Notably, shifts to higher vessel lumen fraction (F) should lead to declining stem mechanical strength because increasing lumen fraction leads to lower support tissue for a given diameter stem (Jacobsen et al., 2005; Preston et al., 2006). Wood density (D), a trait frequently

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measured by ecologists and foresters (Green et al., 1999; Hacke and Sperry, 2001; Roderick and Berry, 2001; Chave et al., 2006, 2009; Preston et al., 2006; Jacobsen et al., 2007; Swenson and Enquist, 2007; Chao et al., 2008; Martínez-Cabrera et al., 2009; Poorter et al., 2010), is a good predictor of stem mechanical strength. Since vessel lumens do not contribute to dry mass, wood density can be partitioned into the proportion of stem that is not vessel lumen ($1 - F$) (for brevity referred to in the text as non-lumen fraction, although it does contain smaller lumens from other tissue types such as fibers and tracheids) and density of this non-lumen component (D_N), using $D = D_N(1 - F)$. Empirically, wood density may be negatively correlated with lumen fraction, although this relationship is typically fairly weak and often not found at all (Preston et al., 2006; Jacobsen et al., 2007; Pratt et al., 2007; Martínez-Cabrera et al., 2009; Poorter et al., 2010).

Here, on the basis of global-scale data compilations across angiosperms, we examine interspecific variation in wood anatomy and its relationships with correlates of conductivity and mechanical strength of xylem tissues. Variables frequently described across species in the literature (Baas et al., 2004; Preston et al., 2006; Wheeler et al., 2007; Sperry et al., 2008; Fan et al., 2009; Martínez-Cabrera et al., 2009; Poorter et al., 2010) are mean cross-sectional lumen diameter (mm) or area averaged over the vessel size distribution (\bar{A} ; mm²), number of vessels per unit area of sapwood (N ; number-mm⁻²), and wood density, as dry mass per fresh volume (D ; g-cm⁻³). Across species, \bar{A} and N are strongly negatively correlated (Carlquist and Hoekman, 1985; Wiemann et al., 1998; Baas et al., 2004; Preston et al., 2006; Wheeler et al., 2007; Sperry et al., 2008; Fan et al., 2009; Martínez-Cabrera et al., 2009; Poorter et al., 2010). A negative correlation makes sense in part because the relationship between \bar{A} and N is constrained by lumen fraction F ($=\bar{A}N$; unitless) being bounded by a value somewhat less than 1 (the “packing limit”, allowing for vessel walls) (Sperry et al., 2008).

Although \bar{A} and N are useful descriptors of vessels, they do not, in themselves, distinguish among the different ways stem conductivity may be altered. To this end, we propose two alternative metrics as descriptors of vascular strategy related to vessels, both of which can be calculated from known values of \bar{A} and N . Lumen fraction F (McCulloh et al., 2004; McCulloh and Sperry, 2005; Preston et al., 2006; Pratt et al., 2007) measures the relative amount of transport space, while a new metric S ($=\bar{A}/N$; mm⁴) measures variation in the vessel composition within this space. Higher values of S indicate that conducting area is comprised of few large vessels. These vessels should be efficient at fast water transport but potentially at greater risk of embolisms, particularly under freeze-thaw conditions, with less redundancy if any one vessel fails (Tyree et al., 1994; Tyree and Zimmermann, 2002; Schenk et al., 2008). Low values of S indicate a more conservative strategy with many small vessels. In some previous work, the slope of \bar{A} vs. N in a log-log plot has been -1 (Baas, 1973; Baas et al., 2004; Preston et al., 2006), meaning S and F may also vary orthogonally across species, representing independent axes of xylem sapwood function. A particular advantage of S and F being orthogonal is that it allows us to examine their independent influences on transport efficiency. However, because previous studies were confined to individual sites or relatively few species, the generality of these patterns has not been established. These large data compilations can be further useful in determining whether traits show coordinated evolutionary divergences broadly across taxa or whether correlations between traits are driven by shifts in a few clades.

The data compilation reported here is unprecedented in terms of species coverage and geographic spread (3005 species distributed globally, although the majority of analyses were done on 2230 of these species for which we had both \bar{A} and N values for the same specimen: Fig. 1, Table 1; Appendix S1, see Supplemental Data with online version of this article). The data set is available in the Dryad data repository (<http://hdl.handle.net/10255/dryad.1139>). These species represent 43 of the 62 angiosperm orders (69%) and 128 of the 425 angiosperm families (30%). This paper investigates worldwide patterns both across present-day species and across independent phylogenetic divergences. Our goals were to (1) partition variation in vascular design (\bar{A} and N) across species into its components, changes in lumen fraction (F) and changes in vessel composition (S), (2) test whether S and F represent independent (orthogonal) axes of vascular design, as would be predicted from a slope of -1 between \bar{A} and N , (3) determine the relative contributions of cross-species variation in F and S to variation in potential conductivity (K_S ; g-mm⁻¹·MPa⁻¹·s⁻¹), (4) examine the degree to which non-vessel lumen fraction ($1 - F$) contributes to cross-species variation in wood density D , and (5) determine whether correlations between traits are due to repeated evolutionary divergences.

MATERIALS AND METHODS

Data sets collated—For woody angiosperm species, we compiled data from the literature on average vessel diameter (mm) and vessel number (N , mm⁻²) (see Table 1 for a description of variables used), and matched these species to an existing data set of wood density (D , dry mass per fresh volume; g-cm⁻³) (Chave et al., 2009; Zanne et al., 2009). Both data sets are available in the Dryad data repository (<http://datadryad.org/repo>; National Evolutionary Synthesis Center). Data were collected for stems of mature individuals from species growing in their native regions, and data collected from juvenile (e.g., seedlings) or plantation-grown individuals (and thus outside of their native range) were not included. Average vessel area \bar{A} (also referred to here as vessel size; mm²) was calculated from diameters, assuming a circular cross section. Lumen fraction was calculated as the product of vessel size and number ($F = \bar{A}N$; unitless) and vessel composition index as vessel size divided by number ($S = \bar{A}/N$; mm⁴), also referred to as the vessel size to number ratio. When vessel data were reported as a range, we took the midpoint value, and when multiple records per species were available, we took geometric means to obtain species averages for each of the variables. We assembled data on vessel anatomy for 3005 species. However, the main analyses were run on data for 2230 species from 128 families where \bar{A} and N came from the same specimen. Wood density data were matched to 584 of these species. Species names were converted to recently accepted nomenclature using the programs TaxonScrubber (version 2.1; http://www.salvias.net/pages/salvias_news.html) and Phylomatic (<http://www.phylodiversity.net/phyloomatic/>) and the Angiosperm Phylogeny Website (Stevens, 2001 onward). Subspecies and varieties were not considered.

We recognize that compilations of data from disparate literature sources need to be interpreted with care for several reasons. The most important is that primary sources record vessel diameters in various ways (e.g., as a true average of all the vessels in a section of wood, as a range, as an average of the larger and/or smaller vessels). These potential sources of error may have led to a wider range of lumen fraction than is physically possible. We removed 12 species ($\sim 0.5\%$ of data) for which lumen fraction values were estimated to be >1.0 . Another potential problem in the data are that wood density has usually been measured on a different specimen from the vessel measurements. To give additional certainty to our analyses, we explored the sensitivity of results to these potential problems by analyzing two subsets of the data: (1) subsetting for only those data that are true averages of vessel size, (2) subsetting for only diffuse-porous species, with diffuse-porous species information taken from the InsideWood database (InsideWood, 2004 onward). Diffuse-porous species are those with similar size vessels across the growth ring, as opposed to ring-porous species with larger vessels in the early springwood and smaller vessels in the later summerwood. In ring-porous species, average vessel size is often reported separately for the larger and smaller vessel classes. In these analyses of data

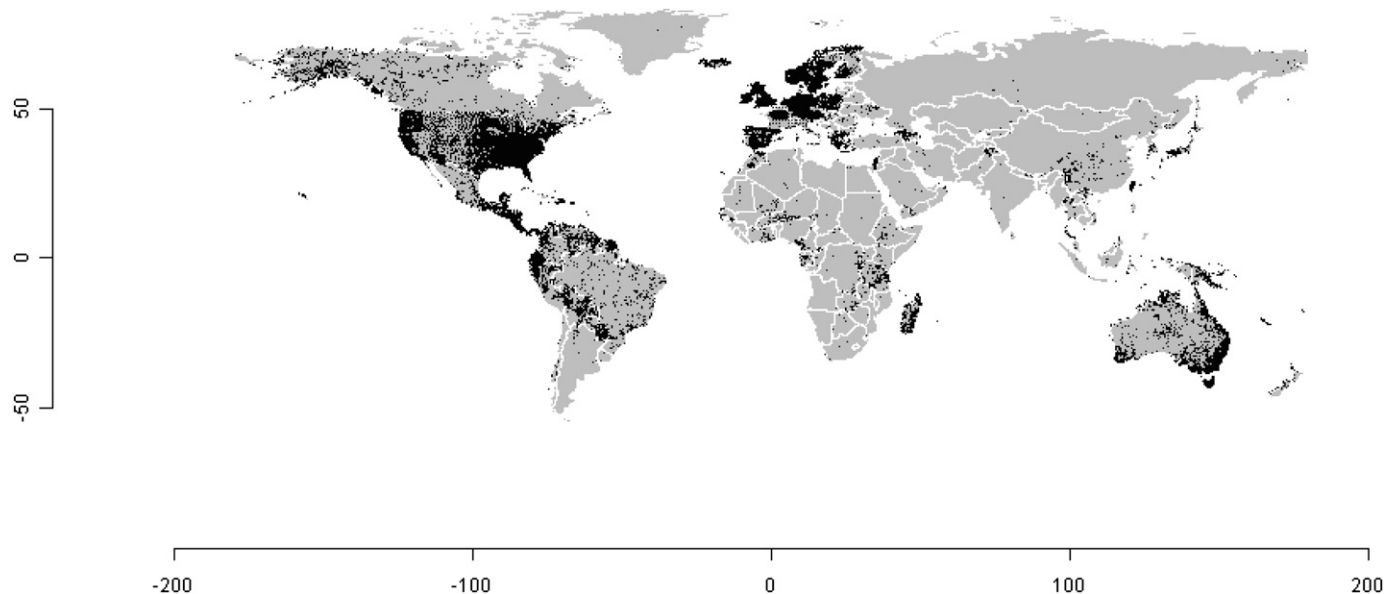


Fig. 1. Distributions of species from this study around the world based on individual record locations from the Global Biodiversity Information Facility (GBIF) (<http://data.gbif.org/species/>). Each point represents a specimen location from the GBIF database. Only 1282 (57%) of the species in the analyses had location data listed in GBIF, so this is an under-representation of our total sampling.

subsets, we have not discovered cases where the subsets behaved differently from the full data set. Accordingly, the full data set is used for the main narrative of results.

Analyses—Vessel size \bar{A} , vessel number N , lumen fraction F , and size to number ratio S all showed log-normal distributions, and wood density D performed similarly when log-transformed or untransformed. Analyses were conducted on log-transformed sapwood trait data, unless otherwise noted. Using the program R (version 2.8.1, <http://cran.r-project.org/>), Pearson product-moment correlations were used to examine expected relationships (or lack of a relationship) between particular vessel traits (\bar{A} vs. N ; S vs. F ; D vs. $1 - F$) as described in our goals. We also examined whether traits showed phylogenetic signal and coordinated evolutionary divergences. A phylogenetic tree was built using Phylomatic (version 2; <http://www.phylodiversity.net/phyloomatic/>) with the R20080417.new backbone tree, using branch lengths of 1. This work was completed before the release of the most recent Angiosperm Phylogeny Group classification (APG III) and did not incorporate these phylogenetic revisions (Haston

et al., 2009). We used the aot package in Phylocom (version 4.0.1b; <http://www.phylodiversity.net/phylocom/>) to obtain phylogenetic signal and phylogenetically independent contrast values for the sapwood traits. To examine coordinated divergences, we analyzed contrast values using Pearson product-moment correlations with the intercept fit through 0, using R (version 2.8.1, <http://cran.r-project.org/>).

The contribution of S and F to global variation in \bar{A} and N can be determined directly from variances of the different terms. Using log-transformed variables, $\text{var}(\bar{A}) + \text{var}(N) = 0.5[\text{var}(S) + \text{var}(F)]$, the relative contributions of S and F to total variation in vascular design, given by $\text{var}(\bar{A}) + \text{var}(N)$, were then calculated using this formula.

To determine whether S and F were orthogonal, there are three equivalent statistical tests. First, we used a direct correlation between the two variables, testing for a difference from 0 (orthogonality). Second, it can be shown analytically (see Appendix S1 with the online version of this article) that S and F are orthogonal only when the variances of \bar{A} and N are equal. Equality of variances would normally be tested with an F -test, but in this case it is inappropriate, as the two variables, \bar{A} and N , do not represent independent samples. Thus, we were unable to use this second method. Third, a test for a standardized major axis (SMA) slope of 1 or -1 corresponds exactly to the other two tests (Warton et al., 2006) and is the same as running a principal component analysis (PCA) on just two variables. Recovered axes in a PCA are by definition orthogonal. We also ran a PCA on \bar{A} and N and tested the strength of the correlation between S and F and the first and second PCA axes. If S and F are indeed orthogonal, then they should be perfectly correlated with the two recovered PCA axes.

We estimated the relative contributions of cross-species variation in F and S to variation in potential conductivity using a formula that includes influences of lumen, using Hagen-Poiseuille law for laminar flow through pipes (Tyree and Zimmermann, 2002), and end-wall resistivities on flow through stems (see Appendix S1 with the online version of this article). Our derivations suggest that average vessel size \bar{A} and number N (or variables derived from these such as S and F) provide reliable estimates of whole-stem conductivity even when other sources of variation (e.g., end-wall resistivity and distribution of vessel sizes) are present (see online Appendix S1 for more details).

RESULTS

Trait variation and phylogenetic conservatism—All the anatomical traits varied considerably across species (Table 2); S showed the most variation, followed by \bar{A} and N , with both F and D showing modest amounts of variation. There was also substantial phylogenetic conservatism, with trait values tending

TABLE 1. List of commonly used variables, including their descriptions and units. It should be noted that lumen is used throughout the paper in reference to vessel lumens, as we have no other measures of lumens. We recognize that other tissues have lumens (e.g., fibers, tracheids), but these are included in the non-lumen component. Additionally, measures of vessel lumens do not include measures of vessel walls. These are also included in the non-lumen component.

Variable	Description	Units
A	Individual vessel cross-sectional area	mm ²
\bar{A}	Mean individual vessel cross-sectional area (i.e., average vessel size)	mm ²
D	Wood density (i.e., wood specific gravity)	g·cm ⁻³
D_N	Non-lumen wood density (i.e., non-lumen density)	g·cm ⁻³
F	Lumen fraction ($= N\bar{A}$)	Unitless
$1 - F$	Non-lumen fraction, including vessel walls ($= 1 - N\bar{A}$)	Unitless
K_S	Estimated total conductivity per stem cross-sectional area or sapwood specific conductivity	g·mm ⁻¹ ·MPa ⁻¹ ·s ⁻¹

to be more similar in species that were more closely related ($P \leq 0.001$). Nevertheless, all correlations were similar when considered as phylogenetic divergences, using independent contrasts, and when considered across present-day species (Table 3).

Shifts in vessel composition contribute much more to variation in vascular design than changing lumen fraction— \bar{A} and N varied approximately equal amounts across species (Table 2). As expected from previous studies, vessel size \bar{A} was strongly negatively correlated with vessel number N (Table 3). As a result of this correlation, most variation in \bar{A} and N was distributed along a single axis closely aligned with S (Fig. 2). Overall, vessel composition (S) accounted for 95.2% of total variation described by measured values of \bar{A} and N , compared to only 4.8% accounted for by variation in lumen fraction (F). Thus despite concern (see Materials and Methods) that our data may overestimate variation in lumen fraction, variation in F represented less than 5% of total variance in vascular design.

S and F are essentially independent axes of variation—Formal testing using correlations showed that S and F were significantly correlated (Table 3). We believe this result is of limited biological significance for the following reasons. First, the strength of the correlation between S and F is very low ($r^2 = 0.006$), meaning S and F are orthogonal for all practical purposes. Second, the main and various “clean” subsets of the data showed different results: the Full and Subset for diffuse porosity data sets had slight negative correlations, while the Subset for averages and phylogenetically independent contrast values (PICs) had slight positive correlations. The correlations detected always accounted for <5% of the variation. Overall, this pattern is consistent with random correlations due to sampling error fluctuating around a true value of 0. Third, when we correlated S and F with the first and second principal component axes (which are by definition orthogonal) recovered from a PCA of \bar{A} and N , S was perfectly correlated with PCA axis 1 ($r^2 = 1.000$, $N = 2230$, $P < 0.001$) and F was closely correlated with PCA axis 2 ($r^2 = 0.994$, $N = 2230$, $P < 0.001$). Thus S and F are very close to the axes representing the orthogonal patterns of these data.

Variation in conductivity is more strongly influenced by S than by F —Assuming independence of S and F , conductivity can be expressed as powers of S and F (see online Appendix S1) such that with variables untransformed:

$$K_s \propto F^{1.5} S^{0.5} \quad (1)$$

(This formulation is more informative than the corresponding formulation based on \bar{A} and N because the relative independent contributions of shifts in lumen fraction (F) and shifts in vessel composition (S) to conductivity can be estimated.) Equation 1 implies that a 10-fold increase in S at a given lumen fraction confers a 3.2-fold increase in conductivity (the increased width of each vessel outweighing the reduced numbers), while a 10-fold increase in lumen fraction at a given S confers a 31.6-fold increase in conductivity. Thus conductivity is more sensitive to changes in lumen fraction F than to changes in the size to number ratio S , all else being equal. Accordingly, isolines of equal conductivity (Fig. 2) increase more steeply in the F direction than in the S direction.

Despite conductivity being more sensitive to changes in lumen fraction, S had a much stronger influence on differences across species because S varied over a much wider range than F (4.4×10^4 -fold vs. 11-fold, respectively; Table 2). These results lead to differences in conductivity of 200-fold through variation in vessel size to number ratio, compared to only 30-fold through variation in lumen fraction. Using the equation for conductivity (Eq. 5 in online Appendix S1), we found that 69% of the total variation in K_s that results from the observed variation in S and F is contributed by S , whereas F contributes only 31%.

Weak correlation between non-lumen fraction and wood density—The non-lumen fraction ($1 - F$) was only weakly correlated with wood density (D) (Table 3, Fig. 3), accounting for 0.7–4.7% of the variation in the data, depending on the data set chosen. Given that $D = D_N(1 - F)$ (for untransformed variables), it follows that non-lumen density D_N must be the main factor determining wood density, not the amount of lumen. We do not have independent measures of D_N so can only estimate the amount of variation contributed by $1 - F$ but not that contributed by D_N . There was 1.75-fold variation in $1 - F$ across species. Based on the above equation for D , it follows that a maximum of 15% of variation in wood density could possibly be accounted for by the $1 - F$ term (see online Appendix S1). These results support our conclusions of a weak linkage between wood density and non-lumen fraction, and the importance of the heretofore under-appreciated variable, D_N .

DISCUSSION

The influence of vessel size and vessel number on conductivity has long been recognized, as has the negative relationship between vessel size and number (Baas, 1973; Tyree and Ewers, 1991; Tyree and Zimmermann, 2002; Baas et al., 2004; Preston et al., 2006; Sperry et al., 2008; Fan et al., 2009; Poorter et al., 2010). However, this is the first study we know of to decouple

TABLE 2. Summary characteristics of vessel traits in the main data set. Mean, low, and high values (calculated as mean \pm 2 SD) are shown. These were calculated on log-transformed variables then back-transformed to give raw values. Also shown for each trait are the n -fold variation (given by the ratio of high to low values) of the raw values and variance of log-transformed values.

X	Sapwood trait	Units	n	Range			n-fold variation	Variance
				Mean	Low	High		
\bar{A}	Vessel size	mm ²	2230	3.62E-03	2.44E-04	5.36E-02	219	0.343
N	Vessel number	mm ⁻²	2230	3.77+01	2.33E+00	6.09E+02	262	0.365
S	Vessel size to number ratio	mm ⁴	2230	9.62E-05	4.58E-07	2.02E-02	44056	1.348
F	Lumen fraction	mm ² -mm ⁻²	2230	1.36E-01	4.11E-02	4.52E-01	11	0.068
D	Wood density	g-cm ⁻³	584	6.00E-01	3.36E-01	1.07E+00	3	0.016

TABLE 3. Relationships between vessel traits \bar{A} vs. N , S vs. F , and $1 - F$ vs. D for the full data set, for a subset with only true averages for vessel dimensions, for a subset with only diffuse-porous species, and for the phylogenetically independent contrast values (PICs) for the full data set. All analyses were performed on log-transformed variables. For more information on subsetting, see Materials and Methods. Significant relationships at $P \leq 0.05$ are in boldface.

Data set used	Sign	N	r^2	P
\bar{A} vs. N				
Cross species: Full	–	2230	0.818	<0.001
Cross species: Subset for averages	–	307	0.805	<0.001
Cross species: Subset for diffuse porosity	–	617	0.839	<0.001
PICs: Full	–	565	0.543	<0.001
S vs. F				
Cross species: Full	–	2230	0.006	<0.001
Cross species: Subset for averages	+	307	0.050	<0.001
Cross species: Subset for diffuse porosity	–	617	0.003	0.179
PICs: Full	+	565	0.027	<0.001
$1 - F$ vs. D				
Cross species: Full	+	584	0.012	0.009
Cross species: Subset for averages	+	56	0.054	0.085
Cross species: Subset for diffuse porosity	+	313	0.021	0.011
PICs: Full	+	255	0.007	0.198

influences of vessel composition S , along an axis from few big to many small vessels, vs. the plant's total fraction of sapwood cross-sectional area occupied by vessels F . Through this decoupling, we were able to examine the influences of S and F on potential conductivity K_S and $1 - F$ on wood density D . Our evidence indicates three independent axes of trait variation in angiosperm sapwood anatomy across species, (1) vessel composition (or vessel size to number ratio) S , (2) vessel lumen fraction F , and (3) non-lumen wood density D_N . Furthermore, conductivity K_S was more strongly driven by the vessel composition, than by the overall amount of vessel lumen because the vessel size to number ratio varied much more widely across species.

What do these trait axes tell us?—Vessel size to number ratio, S —The presumed advantage of high S is high hydraulic conductivity. Potential conductivity increased by more than three orders of magnitude from the lower right to upper left along the vessel size to number spectrum S in Fig. 2. Although mathematically a proportional change in F has greater influence on conductivity than a similar change in S , S varied much more widely across species than did F and therefore was the major factor driving variation in potential conductivity. While hydraulic conductivity is influenced by many factors, we show in the modeling exercise (see online Appendix S1) that the influence of varying S should be distinctly detectable from variation in other components. Furthermore, it is both logical from an evolutionary standpoint and observed empirically that different components of vessels contributing to conductivity scale together (e.g., vessel diameters increase with increasing vessel lengths) (Hacke et al., 2006).

A clear disadvantage of high S , and thus wide vessels, is an increased risk of freeze-induced embolisms (Davis et al., 1999; Hacke and Sperry, 2001; Tyree and Zimmermann, 2002). Species with high S may also be more vulnerable to drought-induced embolisms, although the mechanism is indirect and the relationship typically weak (Tyree and Zimmermann, 2002; Baas et al., 2004; Sperry et al., 2005; Wheeler et al., 2005). It remains unclear though, whether embolism should be understood as a severe hazard leading to increased plant mortality, or whether different species accommodate themselves to different

levels of embolism. For example, might species with very different values for S nevertheless have similar effective conductivities across the year after accounting for their different levels of embolism in the field? Or, might the costs of refilling embolized vessels in some species be sufficiently moderate that fluctuating levels of embolism have limited impact on performance? S may also be influenced by the relative construction costs of building a few big vs. many small vessels. For instance, at a fixed F , smaller vessels will have greater total surface area than

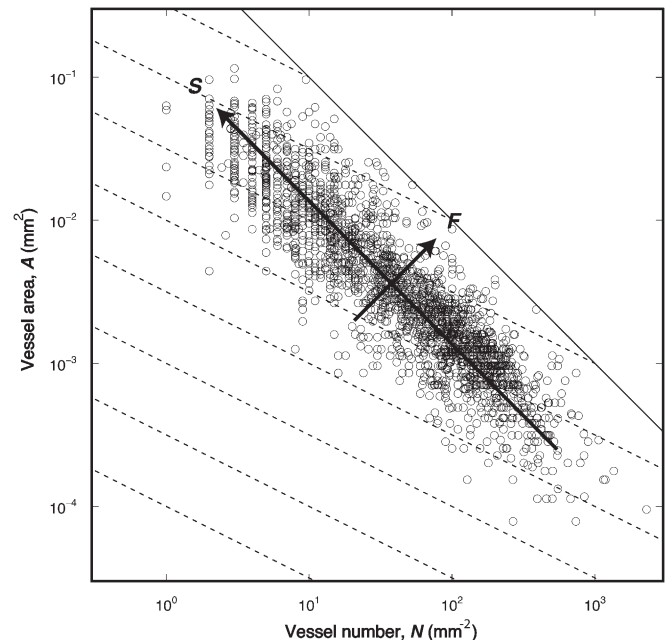


Fig. 2. Vessel area \bar{A} vs. vessel number N for 2230 species plotted on log-scaled axes. Bold lines with arrows show orientation of vessel size to number ratio S and lumen fraction F , where lengths of lines represent ± 2 SD from mean values (Table 2). Dashed lines denote isolines representing constant values of conductivity K_S , with adjacent lines signifying a one order of magnitude change in K_S . The solid line represents the constraint of lumen fraction $F \leq 1$.

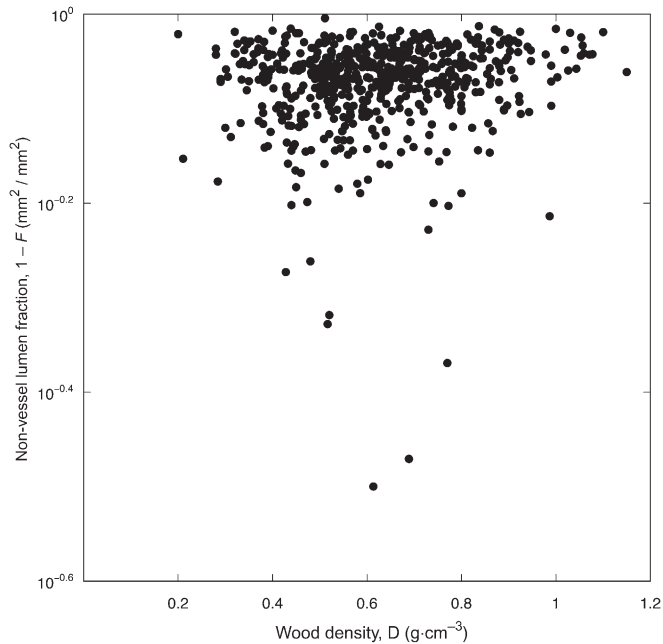


Fig. 3. Wood density D vs. log non-vessel lumen fraction ($1 - F$) for 584 species.

larger vessels and thus require more wall material. However, the construction costs of more or less wall surface area can be modified by the relationship between A and vessel wall thickness (Hacke and Sperry, 2001).

Lumen fraction, F —Lumen fraction is an interesting property, but an understanding of what drives its variation is still elusive. Lumen fraction is constrained to values of somewhat more than 0 and somewhat less than 1 (the “packing limit”), with limitation at the upper end by the need for sufficient mechanical support and at the lower end by the need for at least some conductivity (Preston et al., 2006; Sperry et al., 2008). Different types of stem construction have different levels of F , indicating the influence of the mechanical-support requirement (McCulloh et al., 2004; McCulloh and Sperry, 2005). Within woody angiosperms, F is usually less than 0.5 but more often values are below 0.2 (Jacobsen et al., 2007). However, lianas, which are freed from large investments in mechanical support, typically have higher values of F than do freestanding species (Baas et al., 2004). We were not able to reliably assign growth forms to species in our data set, so were unable to quantify this component. Strong differences in F also occur between gymnosperms and woody angiosperms (McCulloh et al., 2004; McCulloh and Sperry, 2005). Angiosperms separate out transport (mainly via vessels but also in some species via tracheids) from mechanical support (mainly via fibers), while gymnosperms use tracheids for both transport and mechanical support. The bulk of gymnosperm sapwood is tracheids (90–95%) (McCulloh et al., 2004; McCulloh and Sperry, 2005; Chave et al., 2009; Cornwell et al., 2009). Different anatomical designs or different mechanical strength requirements can then lead to different ranges of lumen fraction.

In examining the advantage of variation in F , several patterns emerge. Certainly, increasing F causes a disproportionate increase in conductivity (Fig. 2; online Appendix S1). Also, when a given conductivity is achieved via higher F rather than via

higher S , there is more water volume in vessels at a point in time relative to the flow. This greater water volume can potentially enhance any stem hydraulic capacitance mediated via vessels. On the other hand, higher F means (all else being equal) that there is less space in the xylem tissues outside vessels for water storage (as well as, storage of other resources). A greater gas, rather than water, fraction in the stem though may give plants a cheap way to add volume allowing them to achieve greater size at low cost (Gartner et al., 2004; Poorter, 2008). Additionally, increases in total amount of vessel lumens should lead to greater intervessel connectivity (Pratt et al., 2007). Greater connectivity should increase overall conductivity and also movement of resources between different parts of the plant’s body, although hydraulic safety of the vascular network is also likely to be reduced (Zanne et al., 2006; Loepfe et al., 2007).

One presumed disadvantage of having high F is reduced mechanical strength. The fact that lianas, which rely on other structures for their mechanical support, have greater lumen fractions than freestanding woody angiosperms has been used as an illustration of this principle (Baas et al., 2004). But, most values of F are in the range below 0.2, and mechanical strength should scale with $1 - F$ rather than with F , meaning that a change in F from 0.08 to 0.04 would decrease K_s by one third but would only increase mechanical strength 4–5%. So in the operating range of most freestanding woody angiosperms, the influence of varying F on mechanical strength seems small compared to influences due to properties of the non-lumen tissue.

Non-lumen tissue density, D_N —In our data set, density of tissue outside the lumen was inferred to be the principal determinant of wood density. Even if variation in wood density and non-lumen fraction were strongly correlated, based on variation in $1 - F$ found here, it could only explain at most 15% of variation in D . These results are similar to what has been found when wood density and lumen fraction are measured on the same stems from the same sites (Jacobsen et al., 2005, 2007; Preston et al., 2006; Pratt et al., 2007; Martínez-Cabrera et al., 2009). A study of 50 chaparral species in California found one of the stronger reported relationships between D and F ($r^2 = 0.312$) (Preston et al., 2006). Nevertheless, 69% of the variation in wood density remained unexplained by lumen fraction. Non-lumen xylem tissue likely varies in density because of variation in fiber, vessel walls, and parenchyma (Hacke and Sperry, 2001; Hacke et al., 2001; Jacobsen et al., 2007; Pratt et al., 2007; Chave et al., 2009). In fact, in a recent study of 61 shrub species across diverse rainfall environments, wood density was best explained by variation in fiber traits and was unrelated to vessel traits (Martínez-Cabrera et al., 2009). Interestingly in that study, wood density increased with percentage axial but decreased with percentage ray parenchyma, although parenchyma traits were less strongly related to wood density than were fiber traits.

Our findings also indicate that wood density is a property almost entirely disconnected from traits related to conductivity (and only accounts for 2% of the variation in conductivity). The possibility of a direct connection between density and conductivity is ruled out in part by the weak relationship between F and D . Density could also be linked to conductivity through coordination with S . However, in our data set D was unrelated to S ($r^2 = 0.006$, $N = 584$, $P = 0.054$). This point is important to emphasize, given that many recent papers have suggested that low-density wood will also tend to be wood with high conductivity (Stratton et al., 2000; Meinzer, 2003; Bucci et al., 2004; Santiago et al., 2004; Swenson and Enquist, 2007), but see

(Roderick and Berry, 2001). However, a *Leptospermum* species in New Zealand has dense wood with widely scattered, large vessels (Meylan and Butterfield, 1978), suggesting that indeed wood density and conductivity can be decoupled.

Non-lumen tissue density is likely better related to hydraulic safety, with greater density increasing the ability to avoid vessel implosion and thus indirectly linked to the ability to avoid drought-induced embolisms (Hacke and Sperry, 2001; Hacke et al., 2001). For angiosperms, however, this argument makes most sense if fiber and lumen sizes are coordinated, which was not found in one study (Martínez-Cabrera et al., 2009). Additionally, low-density tissue can store more water than high-density tissue (Stratton et al., 2000; Bucci et al., 2004; Santiago et al., 2004; Pratt et al., 2007; Scholz et al., 2007), and this water storage is likely occurring outside the vessels in the fiber lumen (Pratt et al., 2007) and perhaps parenchyma. The result of low D_N should be higher capacitance, that is, greater release of water into the xylem stream as water potential of the stem declines. High capacitance can buffer leaf water potentials against temporary water shortage, allowing gas exchange to be maintained at higher levels or for more prolonged periods (Stratton et al., 2000; Meinzer et al., 2003; Scholz et al., 2007). In this case, species with low wood density should have a relatively large percentage of water-holding space outside of vessels (Jacobsen et al., 2007).

Variation in wood density is also thought to relate to variation in life-history strategy. For instance, an important implication of low-density wood is that it requires less resources to construct, so that a given volume extension of stem is built at a lower cost (Poorter, 2008). Such a stem is also weaker mechanically (Niklas, 1997; Hacke et al., 2001; Jacobsen et al., 2005; van Gelder et al., 2006; Jacobsen et al., 2007; Osunkoya et al., 2007; Chave et al., 2009). Species with low wood density typically have high growth rates but also incur high mortality rates, potentially from greater susceptibility to stem breakage or pathogens (Augsburger and Kelly, 1984; Roderick, 2000; Chao et al., 2008; Poorter, 2008; Chave et al., 2009). Connected with this trade-off, low wood density has been associated with shade-intolerant, early-successional, rapidly growing species (Sterck et al., 2006; Poorter, 2008). In fact, in a recent study across 42 rainforest species in Bolivia, species with faster growth rates had lighter wood and wider vessels at lower numbers, but survival was only connected (positively) to wood density not vessel anatomy (Poorter et al., 2010; see also Zanne and Falster, 2010 for further analyses incorporating S and F), confirming that vessel anatomy and wood density can differentially influence plant performance.

Phylogenetic influences—Relationships among traits were similar whether considered across present-day taxa or as phylogenetic divergences (i.e., independent contrasts). These results indicate that the observed relationships have arisen repeatedly and widely throughout the evolutionary history of angiosperms, rather than arising from divergences between a few major clades.

Conclusions—We show three orthogonal axes of sapwood variation relating to (1) vessel composition S , (2) vessel lumen fraction F , and (3) non-lumen tissue density D_N . Due to availability of data, we examined these relationships using mean vessel size per stem and included vessel anatomy and wood density data, at times collected from different parts of the plant. It will be valuable to gather further information across many

species on vessel size distributions (Ackerly, 2004; Hacke et al., 2006) and on variation in vessel anatomy (Weitz et al., 2006; Fan et al., 2009) and wood density (Swenson and Enquist, 2008) consistently collected at different locations in the plant. These data will help to evaluate whether the orthogonal nature of the three axes holds across changes in ontogeny and with different life forms, as well as measure hydraulic conductivity and lumen fraction more accurately from vessel anatomy. Some angiosperms possess tracheids, which are conducting cells with much smaller values of A . A database including tracheids, as well as vessels, would be useful as they may influence relationships among our three orthogonal axes. Additionally, a global compilation of the amount of sapwood carried for a unit leaf area would allow us to assess the third way in which plants can adjust their rates of water supply.

In our explorations of sapwood anatomy, we have decoupled influences of amount of lumen vs. vessel composition vs. density of non-lumen tissue, but we have been unable to explore other important influences on conductivity in any great detail. Our derivations relating conductivity to S and F (see online Appendix S1) make several assumptions, including that variation in mean vessel size is a stronger driver of conductivity than variation in vessel size and that the contribution to hydraulic resistivity is approximately equal from vessel lumens and end walls (including perforation plates). These assumptions seem reasonable, but data to test them are currently limited. It is important to have better quantification of how widely coefficient of variation in vessel size varies across angiosperm species, and whether it is coordinated with S or F . Hydraulically weighted measures of vessel size do not link to the important dimension of how much of the stem is in vessel lumens, whereas A and the coefficient of variation in vessel size do. If future studies of vascular anatomy reported both mean vessel size and coefficient of variation in vessel size, rather than (or in addition to) just hydraulically weighted vessel size, we could begin to explore these separate influences. Similarly, it is important to increase our sampling of K_S vs. conductivity through end walls (and perforation plates) to determine if and how they are coordinated with S or F . To date, findings suggest that variation in end-wall conductivity is relatively low (Sperry et al., 2005, 2006; Wheeler et al., 2005; Choat et al., 2006, 2008; Hacke et al., 2006). Finally, an understanding of the selective pressures leading to variation in F is of great interest. While this trait varied less than S , it did vary 11-fold. And, while we assume it is constrained to a narrow range of variation due to constraints on mechanical strength and diminishing returns on investment, it is important to test these assumptions.

Understanding the importance of construction costs, hydraulic safety and efficiency, mechanical strength, and hydraulic capacitance in driving variation in wood density and vessel anatomy will give us a better sense of the selective pressures leading to relative amounts of different tissue types and the density of those tissues. Our decoupling of stem construction into three independent axes of vessel composition, vessel lumen fraction, and non-lumen wood density is a first step toward this goal. Global compilations of these trait data have thus been useful in gaining insight into the functional significance and evolutionary coordination in stem design. Additionally, wood makes up a large component of stored carbon pools (Harmon et al., 1990) and can influence hydrological patterns via influences on evapotranspiration (Denman et al., 2007). Variation in these traits likely have ecosystem- to global-scale consequences as well (e.g., Cornwell et al., 2009).

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