

SPECIAL PAPER

**A GLOBAL ANALYSIS OF XYLEM VESSEL LENGTH IN
 WOODY PLANTS¹**

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- *Premise of the study:* Vessels are the chief conduit for long-distance water transport in the majority of flowering plants. Vessel length is a key trait that determines plant hydraulic efficiency and safety, yet relatively little is known about this xylem feature.
- *Methods:* We used previously published studies to generate a new global data set of vessel length in woody plants. These data were used to examine how evolutionary history, plant habit, environment, and growth ring porosity influenced vessel length. We also examined the relationship between mean vessel length and mean vessel diameter and maximum vessel length.
- *Key results:* Data on mean vessel length were available for stems of 130 species and on maximum vessel length for stems of 91 species. A phylogenetic analysis indicated that vessel length did not exhibit significant phylogenetic signal. Liana species had longer vessel lengths than in tree or shrub species. Vessel diameter was not predictive of mean vessel length, but maximum vessel length strongly predicted mean vessel length. Vessel length did not vary between species that differed in growth ring porosity.
- *Conclusions:* Many traits often assumed to be linked to vessel length, including growth ring porosity and vessel diameter, are not associated with vessel length when compared interspecifically. Sampling for vessel length has been nonrandom, e.g., there are virtually no data available for roots, and sampling for environment has been confounded with sampling for habit. Increased knowledge of vessel length is key to understanding the structure and function of the plant hydraulic pathway.

Key words: cavitation resistance; hydraulic architecture; hydraulic conductivity; vessel diameter; vessel length; water relations.

The structure of xylem vessels is a key determinant of plant hydraulic function. Yet while some traits such as vessel lumen diameter are often measured, other traits such as vessel length are little studied. Limited knowledge of vessel length and its role in plant hydraulic architecture and function has led some to refer to this trait as the “neglected dimension” of vessel structure (Comstock and Sperry, 2000).

Knowledge of vessel length is a necessary component in understanding plant hydraulic structure. For instance, increased vessel length may increase the integration and connectivity of vessel networks, particularly if vessels are both long and tortuous in their pathways (Loepfe et al., 2007; Espino and Schenk, 2009). The distribution of vessel lengths may also be related to the movement of pathogens throughout the plant body (Chatelet et al., 2006).

Vessel length is also a key trait in understanding plant hydraulic function. For instance, longer vessels are less hydraulically limited by pit and end wall resistances, but may have greater pit area that also makes them more susceptible to hydraulic failure via cavitation (Sperry et al., 2005; Wheeler et al., 2005; Sperry et al., 2007). Similarly, increased connectivity in vessel networks composed of longer vessels may make them more efficient and integrated (Espino and Schenk, 2009), but may also increase risk of hydraulic failure (Loepfe et al., 2007).

Knowledge of vessel length is important for studies of plant hydraulics because this trait may be associated with measurement artifacts, including potential inaccuracies in estimates of hydraulic conductance if a large number of conduits are open through a measured sample (Chiu and Ewers, 1993) and potential errors in measures of xylem cavitation resistance (Cochard et al., 2005, 2010; Choat et al., 2010). Many of these methodological concerns have focused on the impact of long vessels in determination of vulnerability to cavitation using air-injection techniques (Martínez-Vilalta et al., 2002; Choat et al., 2010; Limousin et al., 2010; Ennajeh et al., 2011) or centrifuge-based methods (McElrone et al., 2004; Maherali et al., 2006; Sperry et al., 2007; Cochard et al., 2010); however, most hydraulic studies have not included measurements of vessel length distributions.

Concern about vessel length artifacts in plant hydraulic studies has led to the use of other traits to make assumptions about vessel length in specific species or organs. Proxies that have been assumed to be related to vessel length include growth ring

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porosity, plant organ, and vessel diameter. Furthermore, conclusions about vessel length based on these proxies have been used to differentially alter methods based on the species or organ being studied (Martinez-Vilalta et al., 2002; McElrone et al., 2004; Maherali et al., 2006). Additionally, proxies have been used to make broad conclusions about the potential applicability of results to large groups of woody plants, including conclusions that assume that all roots have long vessels (Choat et al., 2010; McElrone et al., 2012) or that ring-porous and vine species have long vessels (Cochard et al., 2010). Importantly, to date, the validity of many of these assumptions has not been evaluated.

Plants have evolved a broad range of vessel lengths (Sperry et al., 2007). Vessel length thus represents a potentially informative trait for understanding the evolution of plant hydraulic systems. Vessel traits have been used to understand paleontological data and to reconstruct past climates (Gilbert, 1940; Herendeen et al., 1999; Wheeler and Baas, 1993). Additionally, vessel traits have been used to inform phylogenetic relationships and to identify species based on familial wood traits (Baas and Miller, 1985; Wheeler et al., 1989). Finally, vessel traits have been examined to understand the evolution of plant hydraulic pathways (Sperry et al., 2007). Vessel length has not been included in many of these studies (however, see Sperry et al., 2007), and it remains to be determined whether vessel length is evolutionarily conserved and thus useful in inferring plant phylogenetic relationships and affinities or is evolutionarily labile and thus represents an important trait for hydraulic ecological adaptation.

We used previously published studies to generate a new global data set of mean and maximum vessel length in woody plants. Using these data, we assessed whether vessel length was phylogenetically conserved. We examined whether vessel length was divergent among plants that differed in ecological traits including habit, environment, and growth ring porosity, and we evaluated several traits that are commonly used to predict vessel length. Finally, we explored the relationship between vessel length and vessel diameter to investigate the role of vessel length in determining plant hydraulic function.

MATERIALS AND METHODS

Data on mean and maximum vessel length were collected from previously published studies. Vessel lengths were included only for woody, vessel-bearing, flowering plants. Most reported maximum vessel lengths were determined using air-injection with methods similar to those described by Greenidge (1952).

For mean vessel lengths, many studies originally reported vessel length data graphically as the percentage of vessels in different length classes calculated using the equations of Zimmermann and Jeje (1981). Most studies did not report means. For these papers, the reported vessel length distribution was converted to the percentage of vessels filled as a function of distance from the injection point (Fig. 1A). The distribution of vessel lengths and the mean vessel length were then calculated using the equations reported of Wheeler et al. (2005) (Fig. 1B). Mean vessel lengths calculated in the present analysis were not different from means calculated using the equations of Zimmermann and Jeje (1981) and reported in previous studies such as Ewers and Fisher (1989a, b) (slope = 1.005, $P < 0.001$, $r^2 = 0.97$, $N = 33$ for newly calculated means compared to reported means).

For several recent papers, the distribution of vessel lengths were not reported and instead mean vessel lengths from the log-transformed vessel length distribution were reported (cf. Sperry et al., 2005; Wheeler et al., 2005; Hacke et al., 2006, 2009). For most of the species examined in these studies, we recalculated mean vessel lengths from raw data using the equations reported by Christman et al. (2009). This procedure allowed us to recalculate mean values for all but four species for which log means were originally reported. We chose to use means rather than log means because of the much larger number of studies that originally

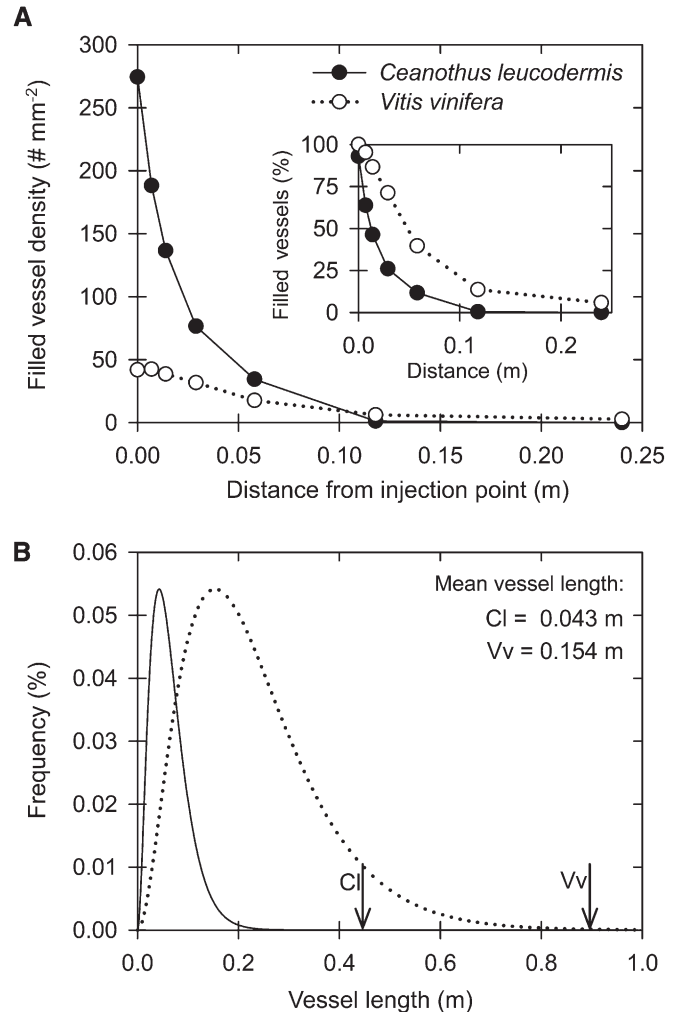


Fig. 1. Vessel length distribution for a single stem sample of a short-vesselled shrub, *Ceanothus leucodermis* (Cl), and a long-vesselled liana, *Vitis vinifera* (Vv) (previously unpublished data of the authors). Samples were injected with silicon using the methods of Wheeler et al. (2005), and the density of filled vessels was determined at many distances from the injection point (A). These data are also shown as the decline in the percentage of filled vessels with distance from the injection point (A inset). The equations published in Wheeler et al. (2005) were used to determine the frequency of vessel length classes (B). The length of the longest vessels (i.e., the maximum vessel length) as determined using air-injection are indicated in panel B by arrows.

reported means but did not include distributions, thus precluding conversion to log means (~30 species) (see Appendix S1 of the Supplemental Data with the online version of this article for a list of which species means were recalculated and which were not). For the four species for which we only had log mean data and could not recalculate the means, we did not include these data in analyses because log means are shorter than mean vessel lengths from nontransformed distributions and are therefore not directly comparable (Lens et al., 2011).

Multiple injection techniques were used to generate the mean vessel length data included in the present paper. Included studies used paint, air, or silicon injection to measure the distribution of vessel lengths within a sample. Previous studies have compared some of these techniques and found general agreement between techniques (air and paint injection, Ewers and Fisher, 1989a; but see Sperry et al., 2005). In the present paper, these different techniques were found to produce similar vessel lengths, although there were only eight species for which data were reported for samples of similar stem diameter using multiple techniques. These were all comparisons of air vs. paint injection and mean vessel lengths were consistent between techniques

(slope = 1.070, $P = 0.008$, $r^2 = 0.72$, $N = 8$). Data from all techniques were pooled for analyses of vessel length.

When available, data on mean vessel diameter and site and species characteristics (such as habit, environment, and site) were extracted from papers that also reported mean or maximum vessel length. We included only vessel diameters reported in the same papers as vessel length data to standardize sample site and material.

Data on growth ring porosity (i.e., ring, semiring, or diffuse porous) were compiled from published references (Panshin and de Zeeuw, 1980; Carlquist and Hoekman, 1985) and an online database (InsideWood, <http://insidewood.lib.ncsu.edu/search>, accessed 23 January 2012). Porosity data were included in the present study only when reported for the exact species included in the study (i.e., porosity was not inferred from congeners), and we reported them exactly as they were originally reported. This resulted in six categories for porosity: diffuse porous, semiring porous, ring porous, diffuse to semiring porous, semiring to ring porous, and diffuse to ring porous.

Linear regression models were used to examine whether two traits that are commonly used to infer mean vessel length, maximum vessel length and mean vessel diameter, were predictive of mean vessel length. Linear regressions were used instead of SMA because regression is more appropriate than SMA when the goal of the fit is prediction, even when both the x and y variables contain error (see Warton et al., 2006). Mean vessel length was compared between differing plant habits and between species differing in growth ring porosity using ANOVA followed by a Fisher's post hoc analysis. Only data from similar sized samples and from stems were included in these analyses, and cultivated varieties were excluded (see Results section for a more detailed explanation of which samples were excluded). Data were transformed as necessary to meet the assumptions of statistical models and alpha was set at 0.05 for all comparisons. Statistical analyses were performed using the program Minitab (release 16.1.0, Minitab, State College, Pennsylvania, USA).

To examine how vessel length may have been influenced by phylogeny, we constructed a phylogeny using the program Phylomatic (<http://www.phylodiversity.net/phyloomatic/index.html>, accessed 2 January 2012). We constructed a family-level tree because the majority of families were represented by only a single species within our data set. Additionally, when more than one species was present within a family, data were not available to resolve the phylogenetic relationships among these species. Where more than one species from a family were included in our data set, mean vessel length was averaged within family. Phylogenetic conservatism in vessel length was then analyzed using Blomberg's K statistic (Blomberg et al., 2003). The phylogenetic signal of a trait is calculated as a K . A K of <1 means that the trait values close relatives are less similar to one another and a K of >1 implies that trait values of close relatives are more similar to one another compared to expectations from a Brownian motion model of evolution (Blomberg et al., 2003). Phylogenetic analyses were performed using the program R version 2.8.1 (R Development Core Team, 2011) including packages APE (Paradis et al., 2004) and Picante (Kembel et al., 2010).

RESULTS

Although there were 320 reported vessel length values, many species were measured and reported multiple times in the literature (some as many as 14 times). When averaged by species, mean vessel length data were available for stems of 130 species and maximum vessel length data were available for stems of 91 species (see online Appendix S1). Both mean and maximum vessel length values were available for 65 species.

Previous studies have reported that vessel length increased with increasing stem diameter and/or age intraspecifically in many species (Zimmermann and Jeje, 1981; Zimmermann and Potter, 1982; Ewers et al., 1990; Ewers and Fisher, 1989b), and we also found support for this pattern. Both mean and maximum vessel length increased with sample diameter for most of the nine species for which vessel lengths were available from samples of three or more different sample diameters (see Fig. 2A for data on mean vessel length; data on maximum vessel length not shown). For these same species, mean vessel diameter also increased with sample diameter (Fig. 2B). The relationship between the diameter of measured samples (i.e., small twigs vs.

larger branches) and vessel length and diameter was variable and species specific.

Interspecifically, the vast majority of samples were from stems of relatively small diameter (less than 0.015 m). Samples larger than this were excluded from additional analyses to standardize the material for comparison across species and due to the relationship described above (see Fig. 2). This was a natural break in the data and samples larger than 0.015 m tended to be quite large and had an average diameter of $0.107 \text{ m} \pm 0.012$. Most species with data from large sample diameters also had data reported from smaller sample diameters, so excluding these samples lead to the exclusion of 25 of 320 reported values, but only 9 of 157 species.

We focused predominantly on mean vessel length rather than maximum vessel length in our analyses, because this represented the majority of reported vessel length data (mean vessel lengths were available for 123 species and maximum vessel lengths were available for 83 species after excluding values to standardize for sample diameter). Additionally, for the 64 species for which both mean and maximum vessel length were available, maximum vessel length was highly correlated with mean vessel length (Fig. 3A).

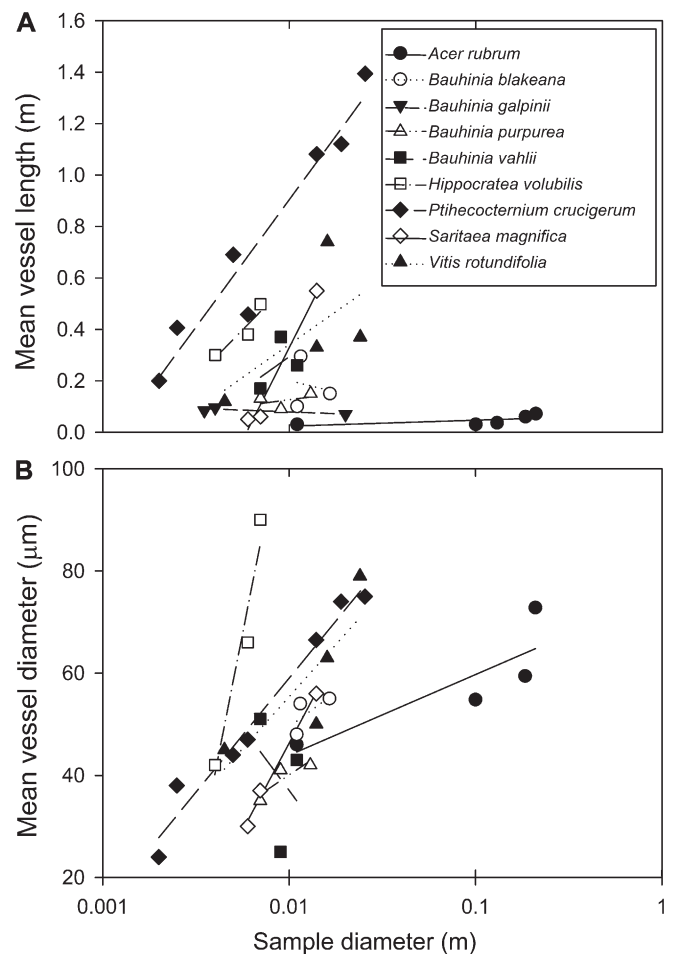


Fig. 2. Vessel size increases with increases in sample diameter and vessels tends to increase in (A) length and (B) diameter with increasing age and width of samples. Different species are marked with different symbols.

Maximum vessel length was significantly correlated with mean vessel length in lianas (filled circles, solid line; $F_{1,19} = 37.88$, $P < 0.001$, $r^2 = 0.67$), shrubs (open circles, dotted line; $F_{1,14} = 53.75$, $P < 0.001$, $r^2 = 0.79$), and trees (gray triangles, dashed line; $F_{1,15} = 57.13$, $P < 0.001$, $r^2 = 0.61$). Additionally, maximum vessel length was correlated with mean vessel length across all species when different habits were pooled ($F_{1,51} = 140.05$, $P < 0.001$, $r^2 = 0.73$).

While maximum vessel length predicted mean vessel length, maximum vessel lengths were much longer than the length of most vessels (see Fig. 1). Overall, maximum vessel length was 5.6 ± 0.4 times the mean vessel length (mean ± 1 SE), but the relationship between mean and maximum vessel length varied with plant habit. Maximum vessel length was 4.8 ± 0.5 times the mean in lianas, 7.1 ± 0.8 times the mean in shrubs, and 5.2 ± 0.5 times the mean vessel length in trees.

In contrast, mean vessel diameter was not a strong predictor of vessel length (Fig. 3B). Mean vessel diameter was not correlated with mean vessel length in lianas ($F_{1,19} = 1.12$, $P = 0.303$) or trees ($F_{1,22} = 2.66$, $P = 0.117$), but was correlated with vessel length in shrubs ($F_{1,42} = 28.62$, $P < 0.001$, $r^2 = 0.41$) (Fig. 4B). When all species were pooled, mean vessel diameter was weakly correlated with mean vessel length ($F_{1,87} = 14.09$, $P < 0.001$, $r^2 = 0.14$).

Mean vessel length varied significantly with plant habit (Fig. 3; $F_{2,112} = 45.12$, $P < 0.001$). Mean vessel lengths of lianas were significantly longer than those of shrubs and trees (Fig. 4 inset panel; $P < 0.001$ for lianas compared to both trees and shrubs), but shrubs and trees did not differ in their mean vessel length (Fig. 4 inset panel; $P > 0.05$). Mean vessel length (± 1 SE) for lianas was $0.335 \text{ m} \pm 0.045$ with some lianas having mean vessel lengths as short as 0.05 m. Shrub species had the shortest mean vessel lengths ($0.061 \text{ m} \pm 0.005$), and tree species had slightly longer mean vessel lengths than shrubs ($0.096 \text{ m} \pm 0.016$).

The majority of samples from the present data set (51.6%) were measured from plants grown in irrigated gardens or irrigated potted plants. Site and source material for an additional 8.4% of samples were not reported. Mean annual precipitation data (MAP) were available for the remaining species (either

reported in the source study or available from the research station or preserve from which they were originally collected). For this limited subset of species, MAP was not correlated with either mean or maximum vessel length, but was correlated with mean vessel diameter (see online Appendix S2). When species were lumped into general environmental categories based on what was reported in source studies (tropical/subtropical, temperate, or arid/semiarid environments) and irrespective of whether they were irrigated, environment did not appear to impact vessel length within different plant habits. However, even this larger data set of 115 species was not able to be fully analyzed because different environments were not replicated among the different plant habits (Table 1). Mean vessel lengths were generally similar within a habit (liana, shrub, or tree), regardless of environment (Table 1). For instance, shrubs had short vessels regardless of whether the species sampled were tropical, arid, or temperate species. Similarly, lianas generally had longer vessels, although there was considerable variability among different liana species.

Surprisingly, mean vessel length did not differ among growth ring porosity types. Across all species, vessel length did not differ among species that were diffuse-, ring-, or differing categories of semiring porous (Table 2; $F_{5,58} = 0.51$, $P = 0.770$). Within habits, porosity types did not differ in vessel length among shrub species (Table 2; $F_{4,28} = 0.41$, $P = 0.779$); however, among trees, vessel length differed significantly among different growth ring porosity types ($F_{2,22} = 6.53$, $P = 0.006$). Ring porous trees had longer vessels than diffuse porous tree species, but there was no difference in vessel length between semiring porous trees and either ring porous or diffuse porous trees ($P > 0.05$ for semiring porous compared to ring or diffuse porous vessel length; Table 2). We caution that this analysis was heavily influenced by limited available data for ring porous trees. Additionally, all ring-porous trees were from temperate environments, whereas diffuse porous trees occurred across different environments. Xylem porosity was not analyzed among lianas because of limited sample sizes for differing porosity categories (Table 2).

Xylem vessel length did not appear to be evolutionarily constrained. Across all species, phylogenetic signal was low

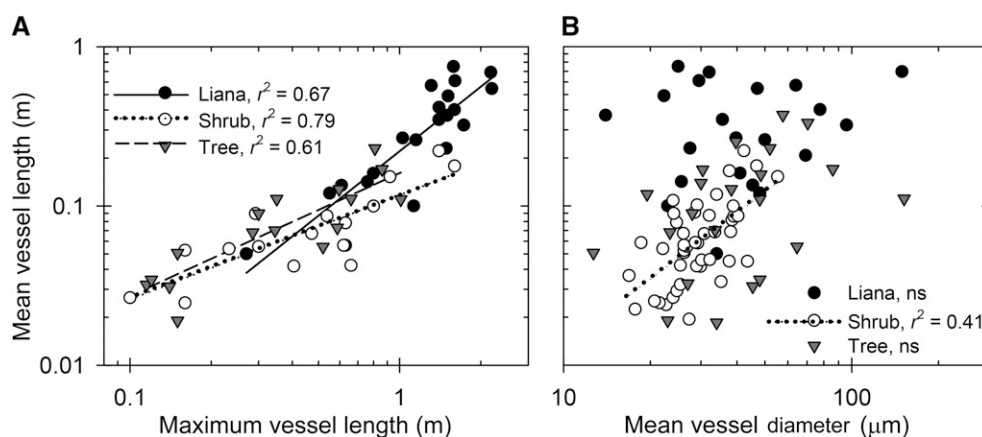


Fig. 3. (A) Maximum vessel length and (B) mean vessel diameter as predictors for mean vessel length. Maximum vessel length was a significant predictor of mean vessel length in lianas (filled circles, solid line; $P < 0.001$; mean vessel length = $-0.0862 + 0.335 \times$ maximum vessel length), shrubs (open circles, dotted line; $P < 0.001$; mean vessel length = $0.0160 + 0.115 \times$ maximum vessel length), and trees (gray triangles, dashed line; $P < 0.001$; mean vessel length = $0.0202 + 0.151 \times$ maximum vessel length). Mean vessel diameter did not predict mean vessel length in lianas ($P = 0.303$) or trees ($P = 0.117$), but vessel diameter was correlated with vessel length in shrubs ($P < 0.001$; mean vessel length = $-0.0349 + 0.00343 \times$ diameter).

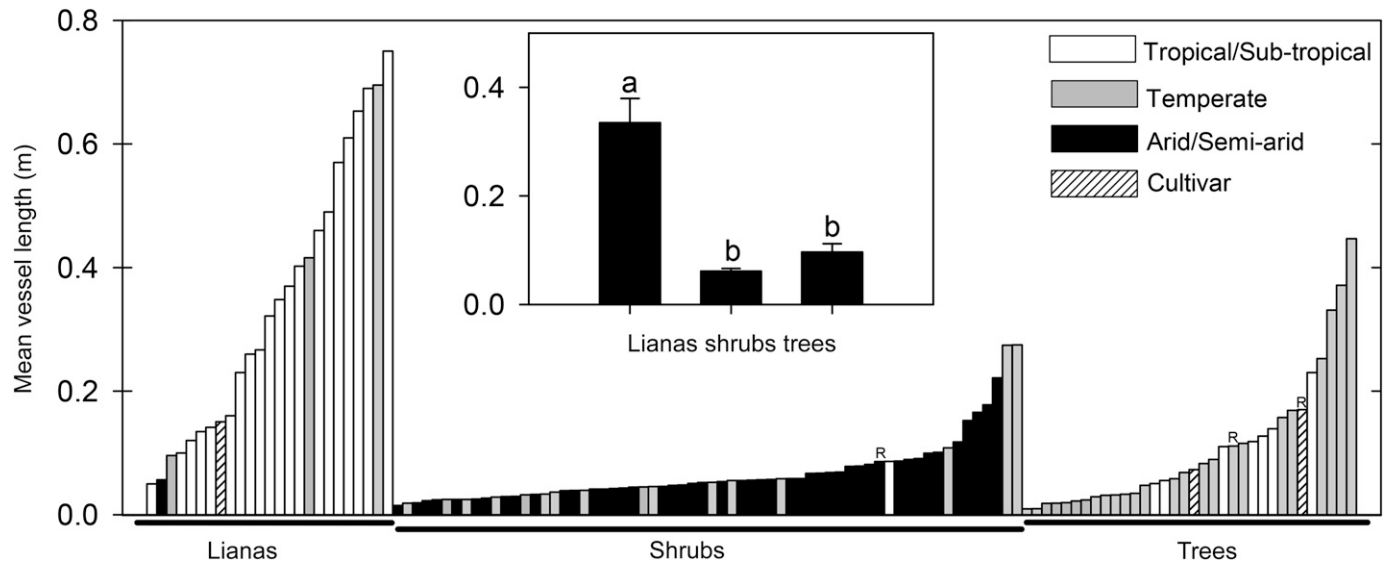


Fig. 4. Mean vessel length for 121 woody angiosperm species (123 values are shown because of the inclusion of both root and stem data for some species). Each bar represents a species mean for stems (the majority of the data) or roots (indicated with an “R” above the bar). Data are divided between species that differ in habit (lianas, shrubs, or trees) and environment (tropical/subtropical, white bars; temperate, gray bars; arid/semi-arid, black bars; and, cultivated varieties, hashed bars). Lianas significantly differed from shrubs and trees in their mean vessel length (inset; $P < 0.001$; different letters indicate significant difference).

($K = 0.278$), which indicated that vessel length tended to diverge even among closely related species and families. Indeed, vessel length was highly variable both within and between closely related species and families (Fig. 5).

Data on root vessel length were available for only three species. For the three cases in which root vessel lengths have been reported, only two were conducted concurrently with stem measures. In a desert shrub, root vessels were longer than in shoots (Kolb and Sperry, 1999); however, in a temperate tree maximum vessel lengths were similar between similarly sized root and stem samples (Zimmermann and Potter, 1982).

DISCUSSION

Mean and maximum vessel length varied greatly within and among species. Interspecifically, both mean and maximum vessel length varied more than 200-fold. Intraspecific, mean vessel length exhibited a 40-fold range of variation among differing sample diameters, which contrasted markedly with mean vessel diameter, which had only a 4-fold range between high and low values (see Fig. 2). Mean vessel length was also highly variable both within and between families and was not phylogenetically conserved.

Mean vessel length differed among species that differed in habit. Lianas had longer vessels than tree and shrub species. This is consistent with previously published data on vessel length that suggested that lianas and woody vines have longer

mean and maximum vessels than self-supporting shrubs and trees (Zimmermann and Jeje, 1981). Among co-occurring species and even among vine and shrub forms of the same species, woody vines have also been consistently reported to have wider vessel diameters and greater hydraulic efficiency compared to shrubs or trees (Ewers, 1985; Gartner et al., 1990; Gartner, 1991; Chiu and Ewers, 1993). We were unable to fully evaluate the impact of environment on vessel length; however, the available data suggest that vessel length is not heavily impacted by environment (i.e., shrubs generally have short vessels no matter where they occur and lianas generally have longer vessels).

Although lianas generally have longer vessels, most species, including lianas, have predominantly short vessels (less than a few centimeters; Zimmermann and Jeje, 1981; Ewers et al., 1990). Even in widely divergent species, such as a short-vesselled shrub and a long-vesselled liana, most vessels are quite short and do not extend far into a sample. Thus, in general, the number of open vessels declines rapidly with increasing sample length, even for species identified as having “long” vessels. Indeed, we found that maximum vessel lengths were typically 5.6 times longer than mean vessel lengths. Importantly, all species exhibited very similar vessel length distributions (i.e., the shape of the vessel length distribution curve) consistent with Nijssen (2004), with the predominant difference between species occurring in shifts in the lengths associated with the peak and tail of the distribution (i.e., in the mean vessel length and maximum vessel length) (see Fig. 1).

TABLE 1. Stem vessel lengths (m) standardized to samples less than 0.015 m in diameter of liana, shrub, and tree species from different environments including tropical/subtropical, temperate, and arid/semi-arid (mean \pm 1 SE; number of species in each category in parentheses).

Environment	Lianas (N)	Shrubs (N)	Trees (N)
Tropical/subtropical	0.3452 \pm 0.0488 (19)	0.0641 (2)	0.1150 \pm 0.0200(8)
Temperate	0.4025 \pm 0.1732 (3)	0.0445 \pm 0.0063 (13)	0.0868 \pm 0.0216 (23)
Arid/Semi-arid	0.0565 (1)	0.0651 \pm 0.0064 (46)	— (0)

TABLE 2. Stem vessel lengths (m) for similar diameter samples (standardized to samples less than 0.015 m in diameter) of differing growth ring porosities (mean \pm 1 SE) for all species in the data set and as divided by plant habit (liana, tree, shrub; number of species in each category in parentheses). Within each column, different letters indicate a significant difference in vessel length between different porosity types.

Porosity	All species (N)	Lianas (N)	Trees (N)	Shrubs (N)
Diffuse	0.0080 \pm 0.0237a (25)	0.4460 (2)	0.0534 \pm 0.0130a (16)	0.0649 \pm 0.0171a (7)
Ring	0.1314 \pm 0.0384a (15)	0.3006 (2)	0.1857 \pm 0.0585b (5)	0.0552 \pm 0.0086a (8)
Semi	0.0810 \pm 0.0225a (15)	(0)	(0)	0.0810 \pm 0.0225a (6)
Diffuse to ring	0.0959 (1)	0.0959 (1)	(0)	(0)
Diffuse to semi	0.0645 \pm 0.0124a (10)	(0)	0.0690 \pm 0.0203ab (4)	0.0616 \pm 0.0710a (6)
Semi to ring	0.1046 \pm 0.0379a (7)	(0)	0.331169 (1)	0.0668 \pm 0.0044a (6)

There was no difference in vessel length between species that differed in their growth ring porosity. The lack of a clear relationship between vessel length and ring vs. diffuse porosity is particularly notable because porosity is often discussed as

being indicative of vessel length. Ring porous species, in particular, are often assumed to be long vesselled (Frost, 1930; Cochard et al., 2005, 2010; Choat et al., 2010). However, globally and across habits, there are many ring porous species that

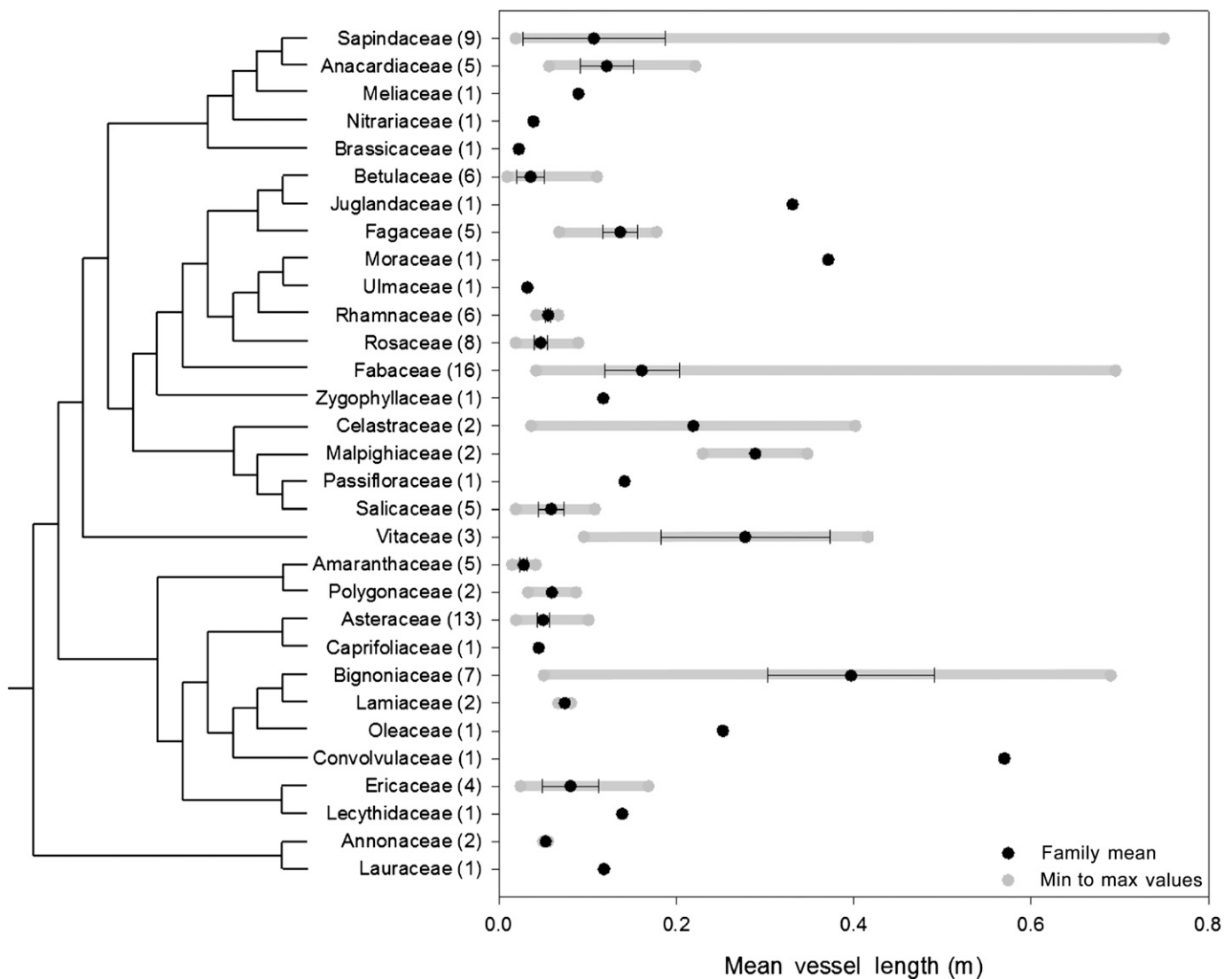


Fig. 5. Mean vessel length shown by family. Phylogenetic relationships are shown for the families for which vessel length data were available. For most families, there was only one species for which vessel length data were available (black circles). For other families, species values were averaged (black circles, mean \pm 1 SE), and the range of species mean vessel lengths are indicated by gray bars. Parentheses after family names indicate the number of species within that family for which mean vessel length data were available. Mean vessel length was highly variable both within families and between closely related families.

have very short vessels. Additionally, porosity is not a fixed character and can change with organ, age, or wounding (Gilbert, 1940). This variability in porosity may partially explain the categorization of species into intermediate or variable categories (Table 2) and highlights the potential difficulties of relying on porosity as an indicator of vessel length.

Vessel diameter was not strongly predictive of mean vessel length, as in previous studies that have found inconsistent agreement between these traits. Some studies have reported that there was no relationship between vessel diameter and length (Ewers et al., 1990; Wheeler et al., 2005), while other studies have found that these traits are linked (Lens et al., 2011; with log means, Hacke et al., 2006; Sperry et al., 2007). Additionally, previous studies have reported that vessel diameter can vary greatly along the length of a single vessel, further complicating the potential relationship between diameter and length (Akachuku, 1987; Ewers and Fisher, 1989b). The lack of a link between these traits is apparent within species and not just between them. For instance, in *Acer rubrum* vessel diameter increased with increasing sample diameter, but vessel length did not change (see Fig. 2). Freezing temperatures could affect the relationship between vessel length and diameter. Freezing-induced embolism has been shown to be linked to conduit diameter (Davis et al., 1999; Pittermann and Sperry, 2003), but not to conduit volume (Pittermann and Sperry, 2003). Thus, freezing may select for reduced conduit diameter but length would not necessarily be impacted.

The decoupling of vessel diameter and length has potentially important implications for plant hydraulic function. While the diameter of vessels is strongly correlated with hydraulic flow, functional measures of the hydraulic efficiency of the xylem tissue of plants rarely achieve the efficiency predicted by the Hagen–Poiseuille equation (Tyree and Ewers, 1991) because pit membranes and perforation plates add additional resistance to hydraulic flow (Ellerby and Ennos, 1998; Zwieniecki et al., 2001; Sperry et al., 2005; Choat et al., 2006; Hacke et al., 2006). While some studies have found that these resistances are balanced (i.e., wider vessels are longer so that end walls do not limit hydraulic flow) (Sperry et al., 2005; Hacke et al., 2006), our data suggests that this appears not to be the case globally, which could result in nonhydraulically optimized suites of vessel traits (Hacke et al., 2009).

In spite of its functional and structural importance, vessel length has been measured in relatively few species. Compared to other vessel traits, such as vessel lumen area, which is known for thousands of species (Zanne et al., 2010), data on vessel length is surprisingly limited, especially for roots. Vessel length data are also limited over the course of woody plant development, and few studies have examined developmental changes in woody plant xylem structure and function (Panshin and de Zeeuw, 1980; Tyree et al., 1991; Hacke and Sauter, 1996; Domec and Gartner, 2002, 2003; Domec et al., 2009). We found evidence that both vessel length and vessel diameter increased as the diameter of sampled stems increased. This is consistent with what has been reported in previous studies that found that vessel length (Zimmermann and Jeje, 1981; Zimmermann and Potter, 1982; Ewers et al., 1990; Ewers and Fisher, 1989b) and vessel diameter (Zimmermann and Potter, 1982; Ewers and Fisher, 1989b; Ewers et al., 1990; Sperry and Ikeda, 1997; López-Portillo et al., 2000; McCulloh et al., 2010) increased with plant age and/or stem size.

Many of the proxies that have been assumed to be indicative of vessel length in plant hydraulic studies, such as the assumption of vessel length based on porosity, plant organ, or vessel

diameter, are not well supported by the available data. Particular concern has been expressed about hydraulic methods appropriate for use in roots, with the common assumption that roots will contain long vessels. Although roots have consistently been reported as having wider diameter vessels (Zimmermann and Potter, 1982; Ewers et al., 1992; Hacke et al., 2000; Pratt et al., 2007), wider vessels do not necessarily correlate with having longer vessels (see Fig. 4). It is difficult to justify assumptions of root vessel length in any direction given the very limited data available for roots. For other commonly used proxies such as porosity and vessel diameter, there are more data available, and these suggest that neither porosity nor vessel diameter are particularly useful in estimating vessel length. Finally, it should be noted that vessel length does not appear to pose a methodological issue for some hydraulic methods and techniques. Recent papers have not found evidence supporting the proposed “long vessel artifact” when certain hydraulic methods are used (Li et al., 2008; Christman et al., 2012; Jacobsen and Pratt, 2012; Sperry et al., 2012).

Conclusion—Mean and maximum vessel length vary greatly intra- and interspecifically. Assumptions of vessel length that are based on organ, porosity, environment, or vessel diameter are potentially problematic, either because these vessel and plant traits are not generally predictive of vessel length or because there are only limited data available, as in the case of root vessel lengths. Increased knowledge of xylem vessel length is key to understanding the structure and function of the plant hydraulic pathway, and more research is needed to identify the methodological, structural, and physiological basis for differences in vessel length among species that vary in habit and the changes in these traits that occur during woody plant development.

LITERATURE CITED

- AKACHUKU, A. E. 1987. A study of lumen diameter variation along the longitudinal axis of wood vessels in *Quercus rubra* using cinematography. *International Association of Wood Anatomists Bulletin* 8: 41–45.
- BAAS, P., AND R. B. MILLER. 1985. Functional and ecological wood anatomy: Proceedings of the Martin H. Zimmermann memorial symposium, 1985. International Association of Wood Anatomists, Leiden, Netherlands.
- BLOMBERG, S. P., T. GARLAND JR., AND A. R. IVES. 2003. Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution* 57: 717–745.
- CARLQUIST, S., AND D. A. HOEKMAN. 1985. Ecological wood anatomy of the woody southern Californian flora. *International Association of Wood Anatomists Bulletin* 6: 319–347.
- CHATELET, D. S., M. A. MATTHEWS, AND T. L. ROST. 2006. Xylem structure and connectivity in grapevine (*Vitis vinifera*) shoots provides a passive mechanism for the spread of bacteria in grape plants. *Annals of Botany* 98: 483–494.
- CHIU, S.-T., AND F. W. EWERS. 1993. The effect of segment length on conductance measurements in *Lonicera fragrantissima*. *Journal of Experimental Botany* 44: 175–181.
- CHOAT, B., T. W. BRODIE, A. R. COBB, M. A. ZWIENIECKI, AND N. M. HOLBROOK. 2006. Direct measurements of intervessel pit membrane hydraulic resistance in two angiosperm tree species. *American Journal of Botany* 93: 993–1000.
- CHOAT, B., W. M. DRAYTON, C. BRODERSEN, M. A. MATTHEWS, K. A. SHACKEL, H. WADA, AND A. J. McELRONE. 2010. Measurement of vulnerability to water stress-induced cavitation in grapevine: A comparison of four techniques applied to long-vesseled species. *Plant, Cell & Environment* 33: 1502–1512.
- CHRISTMAN, M. A., J. S. SPERRY, AND F. R. ADLER. 2009. Testing the ‘rare pit’ hypothesis for xylem cavitation resistance in three species of *Acer*. *New Phytologist* 182: 664–674.

- CHRISTMAN, M. A., J. S. SPERRY, AND D. D. SMITH. 2012. Rare pits, large vessels and extreme vulnerability to cavitation in a ring-porous species. *New Phytologist* 193: 713–720.
- COCHARD, H., G. DAMOUR, C. BODET, I. THARWAT, M. POIRIER, AND T. AMÉGLIO. 2005. Evaluation of a new centrifuge technique for rapid generation of xylem vulnerability curves. *Physiologia Plantarum* 124: 410–418.
- COCHARD, H., S. HERBETTE, T. BARIGAH, E. BADEL, M. ENNAJEH, AND A. VILAGROSA. 2010. Does sample length influence the shape of xylem embolism vulnerability curves? A test with the Cavitron spinning technique. *Plant, Cell & Environment* 33: 1543–1552.
- COMSTOCK, J. P., AND J. S. SPERRY. 2000. Theoretical considerations of optimal conduit length for water transport in vascular plants. *New Phytologist* 148: 195–218.
- DAVIS, S. D., F. W. EWERS, J. WOOD, J. J. REEVES, AND K. J. KOLB. 1999. Differential susceptibility to xylem cavitation among three pairs of *Ceanothus* species in the Transverse Mountain Ranges of southern California. *Ecoscience* 6: 180–186.
- DOMEC, J. C., AND B. L. GARTNER. 2002. Age- and position-related changes in hydraulic versus mechanical dysfunction of xylem: Inferring the design criteria for Douglas-fir wood structure. *Tree Physiology* 22: 91–104.
- DOMEC, J. C., AND B. L. GARTNER. 2003. Relationship between growth rates and xylem hydraulic characteristics in young, mature and old-growth ponderosa pine trees. *Plant, Cell & Environment* 26: 471–483.
- DOMEC, J. C., J. M. WARREN, F. C. MEINZER, AND B. LACHENBRUCH. 2009. Safety factors for xylem failure by implosion and air-seeding within roots, trunks and branches of young and old conifer trees. *International Association of Wood Anatomists Journal* 30: 100–120.
- ELLERBY, D. J., AND A. R. ENNOS. 1998. Resistances to fluid flow of model xylem vessels with simple and scalariform perforation plates. *Journal of Experimental Botany* 49: 979–985.
- ENNAJEH, M., F. SIMÕES, H. KHEMIRA, AND H. COCHARD. 2011. How reliable is the double-ended pressure sleeve technique for assessing vulnerability to cavitation in woody angiosperms? *Physiologia Plantarum* 142: 205–210.
- ESPINO, S., AND H. J. SCHENK. 2009. Hydraulically integrated or modular? Comparing whole-plant-level hydraulic systems between two desert shrub species with different growth forms. *New Phytologist* 183: 142–152.
- EWERS, F. W. 1985. Xylem structure and water conduction in conifer trees, dicot trees, and lianas. *International Association of Wood Anatomist Bulletin* 6: 309–317.
- EWERS, F. W., AND J. B. FISHER. 1989a. Techniques for measuring vessel lengths and diameters in stems of woody plants. *American Journal of Botany* 76: 645–656.
- EWERS, F. W., AND J. B. FISHER. 1989b. Variation in vessel length and diameter in stems of six tropical and subtropical lianas. *American Journal of Botany* 76: 1452–1459.
- EWERS, F. W., J. B. FISHER, AND S.-T. CHIU. 1990. A survey of vessel dimensions in stems of tropical lianas and other growth forms. *Oecologia* 84: 544–552.
- EWERS, F. W., G. B. NORTH, AND P. S. NOBEL. 1992. Root–stem junctions of a desert monocotyledon and a dicotyledon: Hydraulic consequences under wet conditions during drought. *New Phytologist* 121: 377–385.
- FROST, F. H. 1930. Specialization in secondary xylem of dicotyledons. I. Origin of vessel. *Botanical Gazette* 89: 67–94.
- GARTNER, B. L. 1991. Stem hydraulic properties of vines vs. shrubs of western poison oak, *Toxicodendron diversilobium*. *Oecologia* 87: 180–189.
- 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.
- GILBERT, S. G. 1940. Evolutionary significance of ring porosity in woody angiosperms. *Botanical Gazette* 102: 105–120.
- GREENIDGE, K. N. H. 1952. An approach to the study of vessel length in hardwood species. *American Journal of Botany* 39: 570–574.
- HACKE, U. G., A. L. JACOBSEN, AND R. B. PRATT. 2009. Xylem function of arid-land shrubs from California, USA: An ecological and evolutionary analysis. *Plant, Cell & Environment* 32: 1324–1333.
- HACKE, U. G., AND J. J. SAUTER. 1996. Drought-induced xylem dysfunction in petioles, branches, and roots of *Populus balsamifera* L. and *Alnus glutinosa* (L.) Gaertn. *Plant Physiology* 111: 413–417.
- HACKE, U. G., J. S. SPERRY, AND J. PITTMANN. 2000. Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. *Basic and Applied Ecology* 1: 31–41.
- HACKE, U. G., J. S. SPERRY, J. K. WHEELER, AND L. CASTRO. 2006. Scaling of angiosperm xylem structure with safety and efficiency. *Tree Physiology* 26: 689–701.
- HERENDEEN, P. S., E. A. WHEELER, AND P. BAAS. 1999. Angiosperm wood evolution and the potential contribution of paleontological data. *Botanical Review* 65: 278–300.
- JACOBSEN, A. L., AND R. B. PRATT. 2012. No evidence for an open vessel effect in centrifuge-based vulnerability curves of a long vesselled liana (*Vitis vinifera*). *New Phytologist* 194: 982–990.
- KEMBEL, S. W., P. D. COWAN, M. R. HELMUS, W. K. CORNWELL, H. MORLON, D. D. ACKERLY, S. P. BLOMBERG, AND C. O. WEBB. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26: 1463–1464.
- KOLB, K. J., AND J. S. SPERRY. 1999. Transport constraints on water use by the Great Basin shrub, *Artemisia tridentata*. *Plant, Cell & Environment* 22: 925–935.
- LENS, F., J. S. SPERRY, M. A. CHRISTMAN, B. CHOAT, D. RABAAY, AND S. JANSEN. 2011. Testing the hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus *Acer*. *New Phytologist* 190: 709–723.
- LI, Y., J. S. SPERRY, H. TANEDA, S. E. BUSH, AND U. G. HACKE. 2008. Evaluation of centrifugal methods for measuring xylem cavitation in conifers, diffuse- and ring-porous angiosperms. *New Phytologist* 177: 558–568.
- LIMOUSIN, J.-M., D. LONGEPIERRE, R. HUC, AND S. RAMBAL. 2010. Change in hydraulic traits of Mediterranean *Quercus ilex* subjected to long-term throughfall exclusion. *Tree Physiology* 30: 1026–1036.
- LOEPFE, L., J. MARTINEZ-VILALTA, J. PIÑOL, AND M. MENCUCINI. 2007. The relevance of xylem network structure for plant hydraulic safety and efficiency. *Journal of Theoretical Biology* 247: 788–803.
- LÓPEZ-PORTILLO, J., F. W. EWERS, G. ANGELES, AND J. B. FISHER. 2000. Hydraulic architecture of *Monstera acuminata*: Evolutionary consequences of the hemiepiphytic growth form. *New Phytologist* 145: 289–299.
- MAHERALI, H., C. F. MOURA, M. C. CALDEIRA, C. J. WILLSON, AND R. B. JACKSON. 2006. Functional coordination between leaf gas exchange and vulnerability to xylem cavitation in temperate forest trees. *Plant, Cell & Environment* 29: 571–583.
- MARTÍNEZ-VILALTA, J., E. PRAT, I. OLIVERAS, AND J. PIÑOL. 2002. Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. *Oecologia* 133: 19–29.
- MCCULLOH, K., J. S. SPERRY, B. LACHENBRUCH, F. C. MEINZER, P. B. REICH, AND S. VOELKER. 2010. Moving water well: Comparing hydraulic efficiency in twigs and trunks of coniferous, ring-porous, and diffuse-porous saplings from temperate and tropical forests. *New Phytologist* 186: 439–450.
- MCÉLRONE, A. J., C. R. BRODERSON, M. M. ALSINA, W. M. DRAYTON, M. A. MATTHEWS, K. A. SHACKEL, H. WADA, V. ZUFFEREY, AND B. CHOAT. 2012. Centrifuge technique consistently overestimates vulnerability to water-stress induced cavitation in grapevines as confirmed with high resolution computed tomography. *New Phytologist*. DOI: 10.1111/j.1469-8137.2012.04244.x
- MCÉLRONE, A. J., W. T. POCKMAN, J. MARTÍNEZ-VILALTA, AND R. B. JACKSON. 2004. Variation in xylem structure and function in stems and roots of trees to 20 m depth. *New Phytologist* 163: 507–517.
- NIJSE, J. 2004. On the mechanism of xylem vessel length regulation. *Plant Physiology* 134: 32–34.
- PANSHIN, A. J., AND C. DE ZEEUW. 1980. Textbook of wood technology, 4th ed. McGraw-Hill, New York, New York, USA.
- PARADIS, E., J. CLAUDE, AND K. STRIMMER. 2004. APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics* 20: 289–290.
- PITTMANN, J., AND J. SPERRY. 2003. Tracheid diameter is the key trait determining the extent of freezing-induced embolism in conifers. *Tree Physiology* 23: 907–914.
- 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.
- R DEVELOPMENT CORE TEAM. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- SPERRY, J. S., M. A. CHRISTMAN, J. M. TORREZ-RUIZ, H. TANEDA, AND D. D. SMITH. 2012. Vulnerability curves by centrifugation: Is there an open vessel artifact, and are “r” shaped curves necessarily invalid? *Plant, Cell & Environment* 35: 601–610.
- SPERRY, J. S., U. G. HACKE, T. S. FIELD, Y. SANO, AND E. H. SIKKEMA. 2007. Hydraulic consequences of vessel evolution in angiosperms. *International Journal of Plant Sciences* 168: 1127–1139.
- SPERRY, J. S., U. G. HACKE, AND J. K. WHEELER. 2005. Comparative analysis of end wall resistivity in xylem conduits. *Plant, Cell & Environment* 28: 456–465.
- SPERRY, J. S., AND T. IKEDA. 1997. Xylem cavitation in roots and stems of Douglas-fir and white fir. *Tree Physiology* 17: 275–280.
- TYREE, M. T., AND F. W. EWERS. 1991. The hydraulic architecture of trees and other woody plants. *New Phytologist* 119: 345–360.
- TYREE, M. T., D. A. SNYDERMAN, T. R. WILMOT, AND J.-L. MACHADO. 1991. Water relations and hydraulic architecture of a tropical tree (*Schefflera morototoni*). *Plant Physiology* 96: 1105–1113.
- WARTON, D. I., I. J. WRIGHT, D. S. FALSTER, AND M. WESTOBY. 2006. Bivariate line-fitting methods for allometry. *Biological Reviews of the Cambridge Philosophical Society* 81: 259–291.
- WHEELER, E. A., AND P. BAAS. 1993. The potentials and limitations of dicotyledonous wood anatomy for climate reconstructions. *Paleobiology* 19: 487–498.
- WHEELER, E. A., P. BAAS, AND P. E. GASSON. 1989. IAWA list of microscopic features for hardwood identification. International Association of Wood Anatomists, Leiden, Netherlands.
- WHEELER, J. K., J. S. SPERRY, U. G. HACKE, AND N. HOANG. 2005. Intervessel pitting and cavitation in woody Rosaceae and other vesselled plants: A basis for a safety versus efficiency trade-off in xylem transport. *Plant, Cell & Environment* 28: 800–812.
- ZANNE, A. E., M. WESTOBY, D. S. FALSTER, D. D. ACKERLY, S. R. LOARIE, S. E. J. ARNOLD, AND D. A. COOMES. 2010. Angiosperm wood structure: Global patterns in vessel anatomy and their relation to wood density and potential conductivity. *American Journal of Botany* 97: 207–215.
- ZIMMERMANN, M. H., AND A. A. JEJE. 1981. Vessel-length distribution in stems of some American woody plants. *Canadian Journal of Botany* 59: 1882–1892.
- ZIMMERMANN, M. H., AND D. POTTER. 1982. Vessel-length distribution in branches, stem and roots of *Acer rubrum* L. *International Association of Wood Anatomists Bulletin* 3: 103–109.
- ZWIENIECKI, M. A., P. J. MELCHER, AND N. M. HOLBROOK. 2001. Hydraulic properties of individual xylem vessels of *Fraxinus americana*. *Journal of Experimental Botany* 52: 257–264.