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Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure

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Abstract Wood density (D_t), an excellent predictor of mechanical properties, is typically viewed in relation to support against gravity, wind, snow, and other environmental forces. In contrast, we show the surprising extent to which variation in D_t and wood structure is linked to support against implosion by negative pressure in the xylem pipeline. The more drought-tolerant the plant, the more negative the xylem pressure can become without cavitation, and the greater the internal load on the xylem conduit walls. Accordingly, D_t was correlated with cavitation resistance. This trend was consistent with the maintenance of a safety factor from implosion by negative pressure: conduit wall span (b) and thickness (t) scaled so that $(t/b)^2$ was proportional to cavitation resistance as required to avoid wall collapse. Unexpectedly, trends in D_t may be as much or more related to support of the xylem pipeline as to support of the plant.

Keywords Wood density · Xylem cavitation · Water transport · Ecological wood anatomy · Hydraulic architecture

Introduction

Wood density (D_t) varies from below 0.1 to above 1.0 g cm,$^{-3}$ and correlates with breaking strength (Niklas 1992). It is natural to assume that denser and stronger wood is needed to support and protect the plant against gravity, wind, snow load, and other external forces. However, there is no relationship between D_t and maximum plant height, either from theory or observation (McMahon 1973). Furthermore, denser branches can be a mechanical liability because they are also less flexible under a wind or snow load which increases the likelihood of breakage (Vogel 1988). Here, we examine the significance of D_t from a counter-intuitive perspective: not in terms of plant support, but with regard to supporting the xylem pipeline against implosion by negative pressure. Although the avoidance of implosion is thought to be the original function of thickened and lignified cell walls as they evolved in the first vascular plants (Raven 1987), the implications for wood structure have not been quantitatively evaluated.

Negative water pressure causes two kinds of stresses in the xylem conduit wall (Fig. 1A). Compressive hoop

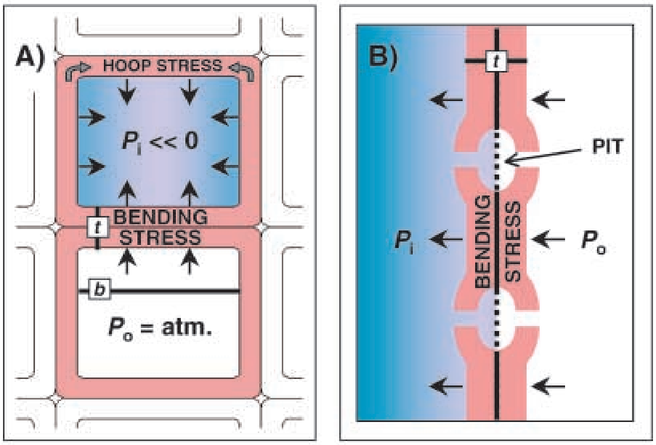

Fig. 1 **A** Stresses in the conduit wall from negative pressure (P_i) in a water-filled conduit (*shaded*). *Hoop stresses* are relatively small. Larger *bending stresses* occur in the common wall between an embolized and water-filled conduit. Bending stresses are related to the thickness of the double wall (t), its span (b), and the pressure difference P_i-P_o where P_o is the gas pressure (near atmospheric) in the embolized conduit (Eq. 1). **B** Longitudinal view of double wall between water-filled (*shaded*) and embolized conduits showing the thickened region bearing the *bending stress*, and the porous *pits* through which air-seeding nucleates cavitation

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Table 1 List of study species and attributes, alphabetic by family. *Wood types* are conifer (*C*), diffuse-porous (*DP*), and ring-porous (*RP*). *Habitats* are Sonoran desert (*SD*), Wasatch mountains of northern Utah (*WM*), University of Utah campus (*UU*), greenhouse seedlings (*GH*), Great Basin of central Utah (*GB*), California Chaparral (*CC*), and Piedmont of central North Carolina (*PD*). *Source* indicates where cavitation data were obtained if not measured for this paper

Species	Family	Wood	Habitat	Life form	Source
Conifers					
Juniperus monosperma	Cupressaceae	C	SD	Tree	Pockman and Sperry (2000)
J. osteosperma	Cupressaceae	C	WM	Tree	Linton et al. (1998)
J. scopulorum	Cupressaceae	C	WM	Tree	
Abies lasiocarpa	Pinaceae	C	WM	Tree	
Picea engelmannii	Pinaceae	C	WM	Tree	
Pinus edulis	Pinaceae	C	WM	Tree	
P. flexilis	Pinaceae	C	WM	Tree	
P. monophylla	Pinaceae	C	WM	Tree	
P. nigra	Pinaceae	C	GH	Seedling	
P. ponderosa	Pinaceae	C	GH	Seedling	Hubbard et al. (2001)
P. taeda	Pinaceae	C	PD	Tree	Hacke et al. (2000b)
Pseudotsuga menziesii	Pinaceae	C	WM	Tree	Sperry and Ikeda (1997)
Angiosperms:					
Acer grandidentatum	Aceraceae	DP	WM	Tree	Alder et al. (1996)
A. negundo	Aceraceae	DP	WM	Tree	Hacke et al. (in press)
A. rubrum	Aceraceae	DP	PD	Tree	
Rhus laurina	Anacardiaceae	RP	CC	Shrub	Jarbeau et al. (1995)
Artemisia tridentata ssp. *tridentata*	Asteraceae	DP	GB	Shrub	Kolb and Sperry (1999)
A. tridentata ssp. *vaseyana*	Asteraceae	DP	GB	Shrub	Kolb and Sperry (1999)
A. tridentata ssp. *wyomingensis*	Asteraceae	DP	GB	Shrub	Kolb and Sperry (1999)
Baccharis salicifolia	Asteraceae	DP	SD	Shrub	Pockman and Sperry (2000)
B. sarothroides	Asteraceae	DP	SD	Shrub	Pockman and Sperry (2000)
Chrysothamnus nauseosus	Asteraceae	DP	GB	Shrub	Hacke et al. (2000a)
C. viscidiflorus	Asteraceae	DP	GB	Shrub	Hacke et al. (2000a)
Alnus incana	Betulaceae	DP	WM	Tree	Hacke et al. (in press)
Betula nigra	Betulaceae	DP	PD	Tree	
B. occidentalis	Betulaceae	DP	WM	Tree	Davis et al. (1999b)
Acacia constricta	Fabaceae	RP	SD	Tree	Pockman and Sperry (2000)
A. greggii	Fabaceae	RP	SD	Tree	Pockman and Sperry (2000)
Cercidium microphyllum	Fabaceae	RP	SD	Tree	Pockman and Sperry (2000)
Prosopis velutina	Fabaceae	RP	SD	Tree	Pockman and Sperry (2000)
Quercus gambelii	Fagaceae	RP	WM	Tree	Sperry and Sullivan (1992)
Fouquievia splendens	Fouquieriaceae	DP	SD	Tree	Pockman and Sperry (2000)
Aesculus hippocastanum	Hippocastanaceae	DP	UU	Tree	
Fraxinus velutinus	Oleaceae	RP	SD	Tree	Pockman and Sperry (2000)
Ceanothus crassifolius	Rhamnaceae	DP	CC	Shrub	Davis et al. (1999a)
C. cuneatus	Rhamnaceae	DP	CC	Shrub	Davis et al. (1999a)
C. leucodermis	Rhamnaceae	DP	CC	Shrub	Davis et al. (1999a)
C. megacarpus	Rhamnaceae	DP	CC	Shrub	Langan et al. (1997)
C. oliganthus	Rhamnaceae	DP	CC	Shrub	Davis et al. (1999a)
C. spinosus	Rhamnaceae	DP	CC	Shrub	Davis et al. (1999a)
Adenostoma fasciculatum	Rosaceae	DP	CC	Shrub	Davis et al. (1999a)
Prunus virginiana	Rosaceae	DP	WM	Tree	
Populus angustifolia	Salicaceae	DP	WM	Tree	Hacke et al. (in press)
P. fremontii	Salicaceae	DP	SD	Tree	Pockman and Sperry (2000)
P. tremuloides	Salicaceae	DP	WM	Tree	Hacke et al. (in press)
Salix goodingii	Salicaceae	DP	SD	Tree	Pockman and Sperry (2000)
Tamarix ramosissima	Tamaricaceae	DP	SD	Tree	Pockman and Sperry (2000)
Larrea tridentata	Zygophyllaceae	DP	SD	Shrub	Pockman and Sperry (2000)

stresses encircle the wall, but are probably relatively small and can be propagated to adjacent walls across the middle lamella. Furthermore, they may be absent altogether if the adjacent cells are conduits at the same pressure. Larger bending stresses arise in the double wall between water- and gas-filled (embolized) conduits. The thicker the double wall (t in Fig. 1A) relative to its maximum span (b), the greater the reinforcement against collapse from bending (Young 1989). We might expect conduit reinforcement (t/b) to scale with the most negative pressure the conduit must hold so as to prevent conduit collapse on the one hand, while minimizing construction cost on the other.

The negative pressure range for a conduit is limited by cavitation, or vaporization, of the xylem water. Cavitation is caused by air seeding at the porous connections (pits) between embolized and water-filled conduits (Fig. 1B; Jarbeau et al. 1995). The xylem pressure causing 50% loss of hydraulic conductivity by cavitation (P_{50}) varies widely among species, and reflects the range of pressure experienced by the plant in its habitat (Sperry 1995; Davis et al. 1999a; Hacke et al. 2000a).

We propose that there is a link between P_{50}, conduit wall reinforcement (t/b), and D_t. Our two-part hypothesis is: (1) increasing D_t will correspond with increasingly negative P_{50}, and (2) this trend is consistent with the scaling of (t/b) with P_{50} required to maintain a safety factor from conduit collapse by negative pressure. This hypothesis does not necessarily imply a direct causal link between the collapsing stresses and the air seeding of cavitation, and in fact the two phenomena are localized to different wall regions (Fig. 1B). We tested the hypothesis in 48 species from 16 families, three wood types (coniferous, diffuse- and ring-porous), shrub and tree growth forms, and several habitats including the Wasatch Mountains of northern Utah, Californian Chaparral, Great Basin and Sonoran deserts, and Piedmont of North Carolina (Table 1).

Materials and methods

P_{50} and D_t

The P_{50} for 37 of the species was obtained from previous work (see Table 1). The P_{50} for the remaining species was measured using the centrifuge method (Alder et al. 1997) with $n>5$ branch segments per species. Branches were 6–13 mm in diameter.

The D_t (dry weight per fresh volume) was measured for all 48 species on the same or similar branches (same study site, and often same individuals) used for measuring P_{50}, using the method of Hacke et al. (2000a). Density was averaged for $n=6$ to 10 samples per species.

Wall stress analysis and anatomy

Bending stress (σ, force per cross-sectional wall area, MPa) at the center of the double wall (Fig. 1) was estimated assuming the wall was a rectangular plate fixed between the two conduits (Young 1989):

$$\sigma=(P_o-P_i)\ \beta\ (b/t)^2 \tag{1}$$

where (P_o–P_i) is the pressure difference (MPa) between gas- and water-filled conduits, respectively. The dimensionless coefficient β depends on the ratio of b and length of the plate, and approximates 0.25 for a ratio of 0.5 or less (as for the double wall). Using $P_i=P_{50}$ to represent the "operating" range of P_i, the corresponding maximum $\sigma=\sigma_{P50}$. If conduits maintain a safety factor from stress causing cell wall failure (σ_c), the following relationship is expected:

$$P_{50}=-(\sigma_c/k)\ \beta^{-1}(t/b)_h^2+P_o \tag{2}$$

where k is the safety factor from failure of the double-wall, $k=\sigma_c/\sigma_{P50}$. The $(t/b)_h^2=(t/b)^2$ for conduits of hydraulic mean diameter for the sample (d_h; Kolb and Sperry 1999). Conduits of this diameter will cavitate at P_{50} if cavitation progresses from large to small conduits with pressure, as observed within a sample (e.g., Hargrave et al. 1994). This is consistent with an observed inverse relationship between $(t/b)^2$ and diameter within a sample.

The d_h and $(t/b)_h^2$ were estimated for each species using the same $n\geq5$ branches measured for D_t. The area of each conduit lumen was measured in complete radial sectors of growth rings encompassing both early- and late-wood. The d_h was estimated from these areas as described in Pockman and Sperry (2000). The $(t/b)_h^2$ was measured on digital images using standard image analysis software. The t and b were measured on conduit pairs that averaged within ±3 μm of d_h (±2 μm in conifers). The t was measured directly, and b was estimated as the side of a square with an area equal to the average conduit lumen.

The σ_c (=modulus of rupture, Niklas 1992) was estimated from a regression between σ_c and D_t for air dried (12% moisture content) stem wood in 11 conifer and 29 angiosperm trees given by Niklas (1992, $r^2=0.79$). We corrected σ_c for the higher moisture content of green wood (above fiber saturation at 27% moisture content) using the formula of Panshin and de Zeeuw (1970). The σ_c was converted from a xylem-area- to wall-area basis by dividing by the fraction of cross-sectional xylem area occupied by cell walls (F_w, dimensionless). The F_w was measured on complete radial growth ring sectors using darkness thresholds in the image analysis software.

To estimate the dependence of D_t on $(t/b)_h^2$, we derived the relationship:

$$P_{50}\approx-(\sigma_c/k)\ \beta^{-1}\ (x\ \{[1-(D_t\ m)/D_w]^{-0.5}-1\}^2)+P_o \tag{3}$$

where the expression in parentheses is substituted for $(t/b)_h^2$ in Eq. 2. To obtain the expression in parentheses we first related $(t/b)_h^2$ to the fraction of the conduit cross sectional area occupied by lumen (F_l): $(t/b)_h^2\approx x[(F_l)^{-0.5}-1]^2$, where x (dimensionless) depends on whether conduits are assumed square ($x=4$) or circular ($x=1.6$). The approximation is because the area-averaged t/b will only approximate $(t/b)_h$. The approximation is within 10% for typical conduit size distributions. The F_l of the conduit system is a function of its density (D_c) because the density of the wall (D_w) is approximately constant, and F_l does not vary systematically with length. Under these conditions, $F_l=1-D_c/D_w$. If we assume that D_c is proportional to D_t, with m being the dimensionless proportionality factor ($D_c=D_t\ m$), we obtain the expression in parentheses for $(t/b)_h^2$. The D_w was calculated as D_t/F_w.

Results

Consistent with the first part of our hypothesis, greater D_t was associated with more negative P_{50} (Fig. 2A). Conifers and angiosperms showed a similar curvilinear relationship, but conifers achieved a given P_{50} with considerably lower D_t than angiosperms. Variation in D_t was a function of the amount of wall material per stem volume rather than variation in D_w which was not different between conifers (0.94±0.08 g cm^{-3}) and angiosperms (1.00±0.12 g cm^{-3}, t-test, $P>0.05$, all means are±1 SD).

The second part of our hypothesis, made explicit by Eq. 2, predicts that P_{50} will be directly proportional to $(t/b)_h^2$ if σ_c, k, and P_o are constant. The expected proportionality was seen in two strong relationships (Fig. 2B), one for the 12 conifers in our sample ($r^2=0.78$), and one for the 36 angiosperms ($r^2=0.81$). Neither intercept differed from zero ($P>0.05$, t-test) indicating a P_o of ambient as expected for embolized conduits. There was no difference between the relationship shown and relationships within diffuse- or ring-porous wood types, or if one random species per family was sampled.

The regression slope ($\propto-\sigma_c/k$) was less negative in conifers than angiosperms ($P<0.001$, t-test). This indicates a greater safety factor (k) for conifer xylem, because the estimated σ_c was independent of $(t/b)_h^2$ ($P>0.05$) and was not different between angiosperm (83±10 MPa) and conifer (78±6 MPa) species ($P>0.05$, t-test). The dashed line in Fig. 2B shows the implosion limit obtained by us-

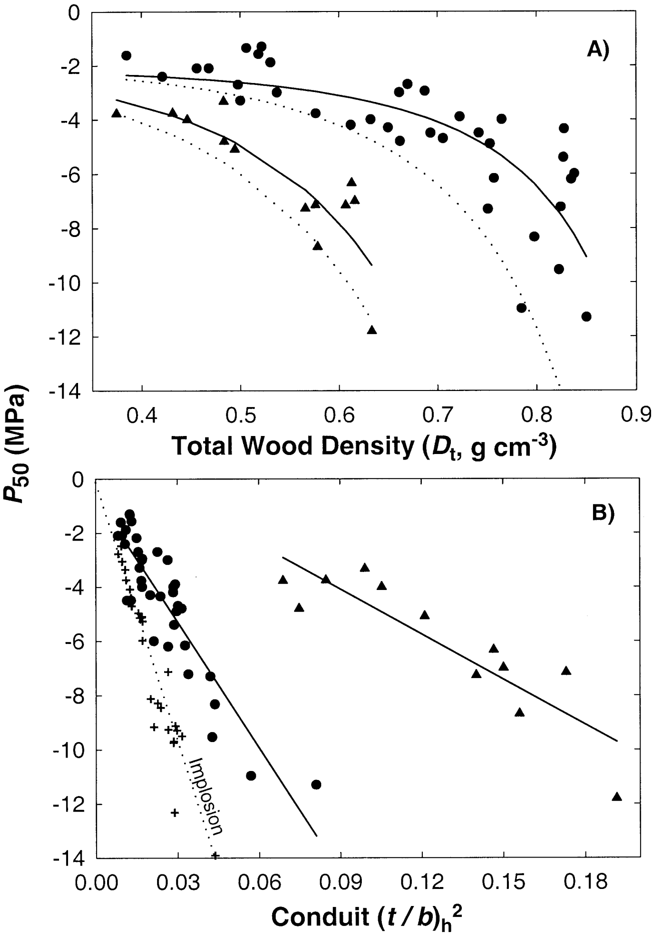

Fig. 2 **A** Cavitation resistance (P_{50}) versus wood density (D_t) for angiosperm (*circles*) and conifer stems (*triangles*). The *curves* are the best fit of Eq. 3 for conifers (r^2=0.73) and angiosperms (r^2=0.62). The *dotted lines* suggest a boundary below which data are excluded because of conduit implosion. **B** P_{50} versus $(t/b)_h^2$ for angiosperm vessels (*circles*) and conifer tracheids (*triangles*). The *regression* represents Eq. 2 applied to conifers (r^2=0.78) and angiosperms (r^2=0.81). *Crosses* and *dashed line* (r^2=0.98) show the implosion limit based on σ_c estimates for angiosperm and conifer species (data extend off scale). Data above the limit indicate a safety factor from implosion. Angiosperm vessels exhibit a lower estimated safety factor (1.9±0.5) than conifer tracheids (6.8±1.5, mean±1 SD)

ing k=1 and the σ_c for each species in Eq. 2. The estimated k averaged 1.9±0.5 in angiosperms and 6.8±1.5 in conifers. These are probably over-estimates because (1) they are based on tensile strength whereas wood generally fails first under compression (Niklas 1992), and (2) they do not account for how the presence of pits might weaken the double wall. Nevertheless, this simplified analysis does show that these conduit dimensions scale with cavitation resistance and the risk of implosion.

Conduit $(t/b)_h^2$ was a much better structural correlate with P_{50} than either b or t alone. Maximum b for a conduit will tend to be correlated with its maximum diameter, and within a species the larger conduits are often more susceptible to cavitation (Hargrave et al. 1994). However, plotting mean conduit diameter against P_{50} *across* our species produced ambiguous results: within conifers, the r^2 was less than half that of the $(t/b)_h^2$ relationship (0.37 vs. 0.78), and angiosperms showed no relationship. Thus, $(t/b)_h^2$ can vary independently of mean conduit diameter, and along with D_t, is a better predictor of P_{50}.

Equation 3 provides the expected linkage between D_t and P_{50} based on the need to avoid conduit collapse. In conifers, D_t and D_c are approximately equal (m≈1), and fitting Eq. 3 yields the curve in Fig. 2A, which explains 73% of the variation in D_t. The application of Eq. 3 to the angiosperm data was not as straightforward, because D_t is influenced by fibers in addition to conduits. Nevertheless, the equation explains 62% of the variation in D_t in angiosperms (curve, Fig. 2A). This suggests that m is approximately constant across angiosperm woods, meaning that the density of the fiber matrix is approximately proportional to that of the conduit system.

Discussion

Our results come to the counter-intuitive conclusion that trends in D_t are strongly linked to resisting internal loads arising from the transport function of wood. At the level of individual conduits, there was a tight proportionality between conduit wall reinforcement $[(t/b)_h^2]$ and cavitation resistance (Fig. 2B). When scaled to the tissue level, this relationship explained over 60% of the variation in D_t (Fig. 2A). These results merit a more detailed analysis of wall stress and structure in relation to water transport than the intentionally simple approach of this initial survey.

The D_t data also describe an inner boundary line with the curvature expected from Eq. 3 (Fig. 2A, dotted lines). A boundary may exist because woods substantially under it are impossible without experiencing conduit implosion. Xylem would cluster just above the boundary if excess D_t is disadvantagous. High D_t is achieved at the cost of reduced growth rate and stem storage capacity (Enquist et al. 1999), and particularly in conifers, a reduction in conduit lumen area for water conduction. Woods far above the boundary may indicate where high D_t is advantageous for reasons other than the support of the xylem pipeline. The somewhat weaker relationship in angiosperms is probably because of the presence of fibers whose structure may be indirectly related to conduit support, and more directly related to plant support and protection.

The contrast between conifers and angiosperms is consistent with their anatomical differences. Conifer wood consists mostly of tracheids, and conduit reinforcement can be achieved with minimum investment at the tissue level. The higher k predicted for tracheids is consistent with their walls having to withstand not only stress from negative pressure, but also from support of the plant. In contrast, angiosperms have vessels which can be more efficient in water conduction than tracheids, and so fewer are required. The space between vessels is often occupied by supporting fibers. A smaller k for vessels is appropriate given that external loads are chiefly born by fibers. However, the correspondence between D_t and P_{50} suggests that the reinforcement of the fiber matrix is correlated with conduit pressure. It is possible that the propagation of conduit stresses into the fibers is significant, and requires their reinforcement as well.

One could question whether conduit implosion is an important determinant of wood structure because it is seldom observed (Baas 1986). Implosion might occasionally occur if a defective wall could not withstand a P_i-P_o that did not first cause cavitation by air entry at pits. However, even in this case, the incipient rupture of the wall could trigger cavitation and stop implosion. Implosion might only happen if the wall is so weak that it crumples under a slightly negative P_i where cavitation is unlikely. Accordingly, conduit collapse has been observed in mutants with major defects in wall development (Piquemal et al. 1998).

The D_t versus P_{50} relationship indicates a cost of cavitation resistance. The advantage of conifers in this respect must compensate to some extent for the lower maximum conducting efficiency of their xylem. When low resource availability prevents high gas exchange and photosynthetic rates across all life forms, the cheaper conifer xylem may provide an advantage. This could contribute to the rapid expansion of drought-resistant *Juniperus* species into arid lands across the western United States (West 1989). It may also contribute to the success of conifers in resource-limited habitats and in achieving massive height growth.

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