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Hydraulic properties and freezing-induced cavitation in sympatric evergreen and deciduous oaks with contrasting habitats

J. CAVENDER-BARES & N. M. HOLBROOK

Harvard University, Department of Organismic and Evolutionary Biology 16 Divinity Avenue, Cambridge, MA 02138, USA

ABSTRACT

We investigated the hydraulic properties in relation to soil moisture, leaf habit, and phylogenetic lineage of 17 species of oaks (*Quercus*) that occur sympatrically in northern central Florida (USA). Leaf area per shoot increased and Huber values (ratio of sapwood area to leaf area) decreased with increasing soil moisture of species' habitats. As a result, maximum hydraulic conductance and maximum transpiration were positively correlated with mean soil moisture when calculated on a sapwood area basis, but not when calculated on a leaf area basis. This reveals the important role that changes in allometry among closely related species can play in co-ordinating water transport capacity with soil water availability. There were significant differences in specific conductivity between species, but these differences were not explained by leaf habit or by evolutionary lineage. However, white oaks had significantly smaller average vessel diameters than red oaks or live oaks. Due to their lower Huber values, maximum leaf specific conductivity (K_L) was higher in evergreen species than in deciduous species and higher in live oaks than in red oaks or white oaks. There were large differences between species and between evolutionary lineages in freeze–thaw-induced embolism. Deciduous species, on average, showed greater vulnerability to freezing than evergreen species. This result is strongly influenced by evolutionary lineage. Specifically, white oaks, which are all deciduous, had significantly higher vulnerability to freezing than live oaks (all evergreen) and red oaks, which include both evergreen and deciduous species. These results highlight the importance of taking evolutionary lineage into account in comparative physiological studies.

Key-words: Hydraulic conductance; freezing-induced embolism; soil moisture; vulnerability to cavitation; vessel diameters.

INTRODUCTION

Water availability plays a critical role in determining the ecological distribution of plants (see for example Bahari, Pallardy & Parker 1985; Cowell 1993; Morano & Walker 1995; Alder, Sperry & Pockman 1996; Long & Jones 1996; Yoke & Rennie 1996). Hydraulic properties, or the capabilities of plants to transport water from soil to leaves, are important both in determining how plants respond to water availability and in setting maximum rates of gas exchange (Sperry & Tyree 1988; 1990; Brodribb & Feild 2000). Previous studies have shown that xylem structure and hydraulic architecture are correlated to water availability, suggesting that environmental factors were important selective forces in moulding hydraulic properties (Tyree, Alexander & Machado 1992; Shumway, Steiner & Kolb 1993; Woodcock & Ignas 1994; Villar-Salvador *et al.* 1997). Oaks have been characterized as differing greatly in distribution relative to the availability of water but as being well-adapted, in general, to drought (Bahari *et al.* 1985; Abrams 1990). Several species of deciduous oaks in North America, including *Quercus gambelii* Nutall, *Quercus rubra* Linnaeus and *Quercus alba* Linnaeus, have been shown to differ from species in other genera by having higher water transport capacities and extensive cavitation during freezing episodes (Cochard & Tyree 1990; Sperry & Sullivan 1992; Tyree *et al.* 1992; Sperry *et al.* 1994). Studies of oak species that differ in leaf habit (evergreen versus deciduous) (Tognetti *et al.* 1996; Villar-Salvador *et al.* 1997) or in rooting depth (Goulden 1996) have found significant intraspecific differences in hydraulic properties, which were thought to be important in determining ecological distribution.

In the present study, we compare the hydraulic properties and water relations in closely related evergreen and deciduous oaks that occur sympatrically in northern central Florida (USA) but occupy contrasting local habitats. We test hypotheses about the hydraulic properties of the 17 oak species within this system in relation to three major axes that could explain their variation: average soil moisture, leaf habit (evergreen/deciduous), and species' phylogenetic lineage.

Soil moisture

Despite their close geographic proximity, the 17 oak species in this study occur in starkly contrasting habitats. The Karst topography in northern central Florida creates a landscape where small changes in elevation lead to dramatic changes in water availability (Brown, Stone & Carlisle 1990). These

Correspondence: J. Cavender-Bares. Present address: Smithsonian Environmental Research Center, PO Box 28, Edgewater, MD 21037, USA. Fax: +1 301 261 7954; e-mail: Cavender@serc.si.edu

oaks occur across an ecological gradient ranging from sandhill, where the water table is far below deep sands, to river edges and ravine bottoms where the water table is at or near the surface. Previous studies have shown increased transport capacity but greater vulnerability to cavitation in species which have greater access to water (Tyree *et al.* 1992; Machado & Tyree 1994), and smaller vessel sizes accompanied by reduced hydraulic conductance in climates or soils with lower water availability (Baas 1983; Tyree & Ewers 1991). In the present study, we tested the hypothesis that within this system of closely related and co-occurring species, oak species from xeric habitats have lower water transport capacities, lower vulnerability to tension-induced cavitation and lower transpiration rates than species from mesic or hydric habitats.

Leaf habit

The phenologies and leaf longevities of these south-eastern US oak species are quite variable with six evergreen, seven deciduous and four intermediate species, and leaf longevities ranging from 6 to 12 months (Cavender-Bares 2000). Although evergreen species maintain foliage year-round, they do not necessarily have longer leaf lifespans than deciduous species as several evergreen species flush multiple times per year. Sobrado (1993) found a trade-off between hydraulic conductance and foliage duration of tree canopies in coexisting evergreen and drought deciduous species in a tropical dry forest. Drought deciduous species were found to maximize hydraulic conductivity in the short term at the expense of seasonal occurrence of embolism. Evergreen species had reduced water transport capacity but maintained relatively constant hydraulic conductivity during the wet and dry seasons (Sobrado 1993). We tested the hypothesis that among the oaks there is a trade-off between water transport capacity and the ability to maintain foliage year-round such that evergreen species have lower maximum hydraulic conductivities than deciduous species.

Evergreen species have also been shown to be more resistant to freeze–thaw-induced cavitation than deciduous species, a pattern which has been linked to vessel diameter (Cochard & Tyree 1990; Sperry & Sullivan 1992; LoGullo & Salleo 1993; Sperry *et al.* 1994; Davis, Sperry & Hacke 1999). During freezing events, dissolved gases in the xylem sap are forced out of solution to form bubbles in the ice. Upon thawing, these bubbles can lead to the formation of emboli. The probability of a bubble being of sufficient size that it will expand when the vessel thaws, and tensions again develop, is thought to be related to vessel diameter (Ewers 1985; Sperry 1995; Davis *et al.* 1999). Davis *et al.* (1999) showed that coniferous evergreen species are more resistant to freeze–thaw cycles than deciduous species and that diffuse porous species are more resistant than ring porous species. They attributed this increased resistance to smaller conduit diameters. Freeze–thaw events occur multiple times throughout the winter months in northern central Florida with temperatures dropping below –3 °C two to three times per year (Fig. 1). Deciduous oak species drop their leaves and cease water transport during this period, whereas evergreen oaks maintain their ability to transport water. We tested the hypothesis that evergreen oak species within this system are less vulnerable to freezing-induced cavitation than deciduous species.

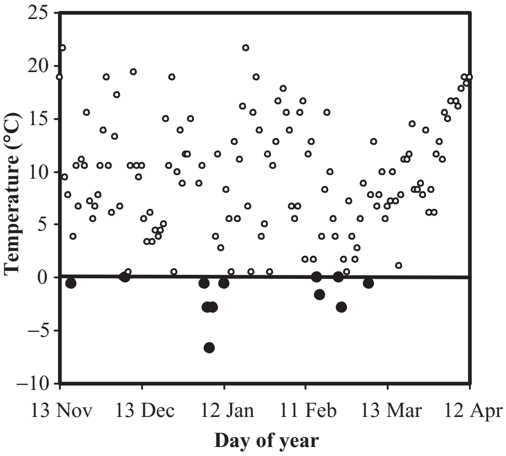

Figure 1. Minimum daily temperatures in Gainesville FL during the winter months of 1998–99. Filled circles represent days for which temperatures were less than or equal to 0 °C.

Phylogenetic lineage

There are three distinct clades of *Quercus* that occur in Florida, including section *Lobatae* Loudon, the red oaks; section *Quercus sensu stricto* Nixon and Muller, the white oaks; and section *Quercus* subsection *Virentes* Nixon, the live oaks. The red oaks are widely distributed throughout North and Central America; the white oaks have a largely temperate distribution in North America and Asia, whereas the live oaks have a warm temperate to subtropical distribution in North and Central America (Nixon 1989; Manos, Doyle & Nixon 1999). Differences in functional traits are likely to exist among clades due to differences in their geographic distributions and the different climatic influences that were present throughout their evolutionary histories. We tested the hypothesis that hydraulic properties are more similar among species within a phylogenetic clade than across species in different clades.

MATERIALS AND METHODS

Hydraulic conductivity

Branches were collected in the morning (between 0800 and 1030 h) from 17 species of oaks that occur sympatrically in northern central Florida. Ten individual trees were measured per day. All collections were made at the San Felasco Hammock State Preserve, a 2650 ha park north-west of Gainesville in Alachua County, with the exception of *Quercus myrtifolia* Wildenow and *Quercus chapmanii* Sargent. These two species were collected at Payne's Prairie State

Preserve, south-east of Gainesville. Branches exposed to direct sunlight were sampled from the top of the canopy and were collected with a pruning pole, with the aid of an aerial lift (JLG, 4WD, 20 m boom; JLG Industries Inc., McConnellsburg, PA, USA), or from scaffolding towers (20–25 m). Branch segments of approximately 1·5 m were cut and recut immediately under water, removing approximately 0·5 m from the cut end of the branch. With the cut end in water, the branches were transported back to the laboratory facilities at the University of Florida in Gainesville. There they were cut again under water, removing approximately an additional 0·5 m.

Native hydraulic conductivity, maximum hydraulic conductivity and percentage loss of conductivity (PLC) were determined by measuring the flow rate of water under a known pressure gradient (Sperry, Donnelly & Tyree 1988). We sampled predominantly second-year growth, although in some species only first-year growth could be sampled and occasionally third-year growth was sampled in order to get a long enough segment. Stem segments (approximately 10 cm in length) were cut under water in the laboratory and the ends recut with a fresh razor blade. Segments were immediately installed in a tubing apparatus for conductivity measurements. Conductivity was determined gravimetrically by measuring the flow rate of distilled and ultra-filtered (particle size <0·2 μm) water through a stem segment under a known pressure gradient. All measured branch segments had diameters <0·4 cm. Flow rate was determined by an electronic balance (±0·1 mg) connected to a computer. A thin film of mineral oil was used to minimize evaporation from the water reservoir located on the balance. Pressure differences across the stem segment were determined by measuring the vertical distance between the water levels in the supply reservoir and the balance (Fig. 2). The hydraulic pressure head was maintained at approximately 2 kPa so as not to flush naturally formed emboli from the stem segments. Before each measurement was taken we waited until the zero-pressure (background) flow was zero. The tubing was bleached periodically to prevent fungal or algal growth.

Measurements were taken after steady-state flow was reached, requiring approximately 5–10 min. Following initial conductivity measurements, branches were flushed with water at 50–60 kPa pressure for 45 min using a captive air tank attached to the tubing apparatus. The conductivity was then re-measured and PLC calculated. Eight to 15 stem segments were measured per species. Sapwood area, calculated as cross-sectional area (without bark) minus the pith area, was used in the denominator for specific conductivity measurements, and leaf area was used for calculations of leaf-specific conductivity. Leaf area was measured using a portable leaf area machine (Li-1000; Licor Inc., Lincoln, NB, USA). We were careful to measure a range of species on any given day and to sample individuals from the same species at multiple locations; the trade-off was that collec-

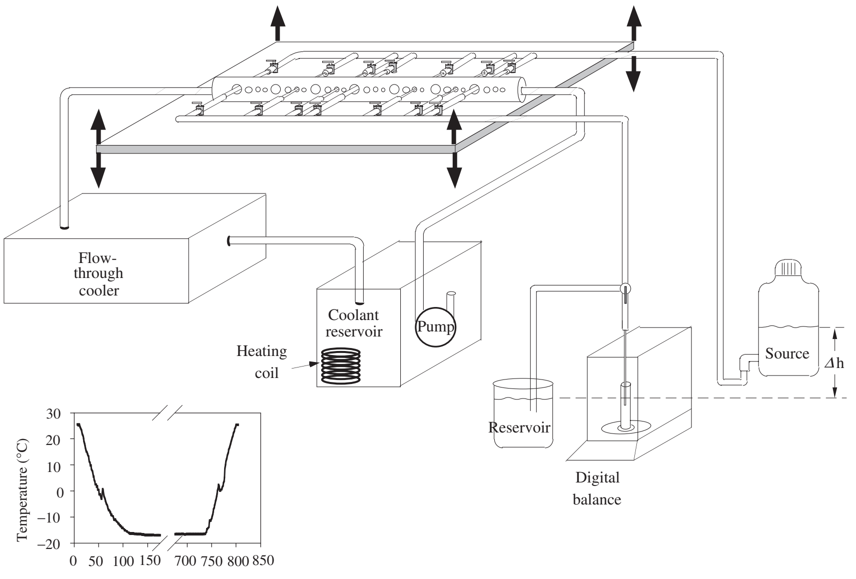

Figure 2. Apparatus for measuring stem conductivity and for freezing stems. For each stem, either end was inserted in plastic tubing. Valves in the plastic tubing were used on both ends of the stem in order to control the flow of water through the stem; flow could be directed through a single stem. When the manifold was assembled, water flowed from the source reservoir through the stems inserted in the manifold and exited underwater in a graduated cylinder placed on a digital balance. Stems were inserted into 8 cm long copper tubes, which were soldered into a 8-cm diameter copper tube that contained flowing ethylene glycol (coolant). The height of the large copper tube could be adjusted via a pulley system, which is omitted for clarity. The coolant reservoir had a programmable temperature controller that could modulate the temperature of the coolant. Inset: A representative temperature regime during freezing of stems. Temperature was measured using a thermocouple attached to the stem. Stems were frozen at a rate of ~0·4 °C per min, lowered to −16 °C and held overnight and returned the next morning to 25 °C at ~0·6 °C per min.

tion times were lengthy. From the sapwood area and leaf area measurements, we calculated the Huber value (the ratio of sapwood area to leaf area) for each stem segment.

Xylem vessel measurements

After conductivity measurements were completed, stems were removed from the conductivity apparatus and fixed in 70% alcohol. Cross-sections (30 or 40 μm thick) were made with a sliding microtome and prepared with glycerine. Images were obtained from a digital video camera (Prog-Res 3012; Kontron Elektronik, GmbH, Eching, Germany) attached to a light microscope (Leica DMRB; Leica Mikroskopie & Systeme GmbH, Wetzlar, Germany) at 5× and 10× magnification and captured with Adobe Photoshop software version 5·0 (Adobe Systems Inc., San Jose, CA, USA). Images were calibrated using a stage micrometer. Each image was imported into the freeware package Object Image for analysis. Vessel radii were measured from all vessels in three radial sectors within each cross-section (15–20% of total area). Sectors were located randomly around the circumference. Vessels were measured by tracing the inner perimeter of the vessel lumen and calculating the radius for a circle of the same area. Measurements for each years' growth were counted separately and then totalled. Means for each stem segment ($n > 300$ conduits) and a grand mean for each species was calculated ($n = 7$ segment means). A hydraulically weighted mean diameter was calculated as $2(\Sigma r^5/\Sigma r^4)$, where r is the radius of a conduit (Sperry *et al.* 1994). In multiple stems of 12 species, we supplied safranin dye (0·1%) to transpiring cut branches to determine whether first-year vessels were reused during the second year.

Leaf-level transpiration

Maximum leaf-level transpiration on a leaf-area basis was measured using a Licor 6400 portable gas exchange system (Licor Inc.) in June 1988 on leaves of sunlit canopy branches of 6–10 individuals of each species. Light level was maintained at 2000 μmol m^{-2} s^{-1} using the attachable red–blue light emitting device (Quantum Devices Inc., Barneveld, WI, USA), and leaf temperature was maintained at 28 °C using the built-in temperature control system. Three to five leaves were measured per individual. In June 1999, a subset of these species were again measured ($n = 13$). Transpiration measurements were not necessarily made on the same individual trees on which hydraulic conductance measurements were made. We also calculated transpiration on a sapwood area basis by dividing species means for transpiration by the mean Huber value per species.

Freezing protocol

A freezing apparatus was made from an 8 cm diameter copper tube with a series of small diameter tubes running through the diameter of the large copper tube, cut to fit and soldered to the outer edges of the large tube (Fig. 2). Using a programmable temperature controller with a circulating pump (Cole-Parmer, Vernon Hills, IL, USA) in conjunction with a flow-through cooler (Neslab Instruments Inc., Newington, NH, USA), we decreased the temperature of ethylene glycol, which was pumped through the large copper tube, at a rate of approximately 0·4 °C per minute. Stem segments were inserted through the small-diameter tubes and heat-sink paste was injected into the copper tubing around the stem to ensure thermal contact between the stems and the copper tubing. The temperature of the stems dropped to approximately –16 °C (Fig. 2 inset). Stems were left frozen overnight and were thawed in the morning at a rate of approximately 0·6 °C per min. Copper–constantin thermocouples (Omega Engineering Inc., Stamford, CT, USA) were attached to the outside of the stems with a small strip of parafilm, and temperatures were recorded at 1 min intervals throughout the chilling period using a 21X Campbell data logger (Campbell Scientific Inc., Logan, UT, USA). Prior to making these measurements, we established that freezing occurred throughout the stem sections by monitoring temperatures during the freeze–thaw cycle with thermocouples inserted inside and attached to the surface along the length of the segment. Freezing could be verified by exotherms as the temperature dropped (Fig. 2 inset). Additionally, during freezing, conductivity fell to zero.

Stems were raised approximately 2 m above the water supply reservoir and the balance using a pulley system to create a small amount of tension (approximately 0·02 kPa) in the stems during chilling. The pressure gradient between the water supply reservoir and the balance was maintained at approximately 2 kPa. Conductivity was measured before and after raising the stems to determine whether raising the stems affected the conductivity measurements. After thawing, conductivity was again measured while the stems were raised. There was no significant difference in the measurements before and after raising the stems, however, we always report PLC after freezing from measurements with the stems raised both before and after freezing. Field PLC measurements were calculated from flushed values obtained before raising the stem segments.

Vulnerability curves

Vulnerability to tension-induced cavitation was compared in two species, *Q. myrtifolia*, a xeric evergreen species found in scrub habitats (Myers 1990; Long & Jones 1996; Menges & Hawkes 1998) and *Quercus stellata* Wangenheim, a mesic deciduous species often found in bottomlands (McKnight *et al.* 1981; Long & Jones 1996). Tension was generated in the sap within xylem conduits by rotating the stem around its midpoint at increasing angular velocities in a centrifuge (Sorvall Model RC-5B; Ivan Sorvall Inc., Norwalk CT, USA) fitted with a modified rotor (Pockman, Sperry & O'Leary 1995; Alder *et al.* 1997). Stem segments, approximately 30 cm in length with no side branches, were placed inside the tube and spun in a horizontal plane with the centre of the stem located on the axis of rotation. Each end of the segment was inserted into a water-filled cap with a small hole facing upwards that allowed water to be extruded during rotation (Melcher 1999; Cochard *et al.* 2000). This created a constant meniscus such that 2 cm of the stem at each end remained immersed in water during rotation. Tensions were created in a gradient from atmospheric at the meniscus holes at the distal ends of the stem to a maximum tension in the centre at the axis of rotation. The radius was measured from the centre of the stem to the meniscus of the water caps at the distal ends of the stem.

Four (*Q. myrtifolia*) or six (*Q. stellata*) stems were used to create the two vulnerability curves. Stem segments were recut from branches under water and flushed to remove emboli as described earlier. Stems were spun for 6 min, and the conductivity of the stems was measured approximately 10 min after spinning stopped. Alder *et al.* (1997) showed that neither the spinning time nor the amount of time before measurement significantly affected the percentage loss of conductivity. The same stem segment was spun at increasing angular velocities and measured after each spinning period. Stems were not reflushed after spinning.

Stem and leaf water potential

Stem and leaf water potential (Ψ) was measured before dawn (0400–0500 h) and at midday (1200–1400 h) using a pressure chamber (PMS Instruments, Corvallis, OR, USA). Two hours prior to midday measurements, intact leaves were wrapped with aluminium foil and sealed in plastic bags. A small piece of moist tissue was kept in the bag without touching the leaf to increase humidity and reduce transpiration to near zero. This procedure allowed the water potential of the leaf to equilibrate with that of the stem. Bagged leaves were used for measurement of stem water potential whereas unbagged leaves were used for measurement of leaf water potential. For pre-dawn measurements, we assumed that leaf and stem water potentials were equal. Three to five individuals of 14 species were measured in the summer of 1998. In the summer of 1999, six to 10 individuals were measured for only two species, *Q. myrtifolia* and *Q. stellata*. Measurements were carried out on sunlit canopy leaves.

Soil moisture measurements

Weighted mean soil moisture values of species' habitats were determined following methods of Jongman, TerBraak & Van Tongeren *et al.* (1995). A total of 74 random plots (20 m × 50 m) were established in three state parks in northern central Florida where these 17 species of oaks co-occur (Cavender-Bares 2000). In all plots, basal area of each species was recorded. Soil water content was measured to 1 m depth within four subplots of each plot using time domain reflectometry following previously established methods (see for example: Holbrook, Burns & Sinclair 1992; Gray & Spies 1995; Gregory *et al.* 1995; Cuenca, Stangel & Kelly 1997; Fredeen *et al.* 1997; Frueh & Hopmans 1997; Schaap, Bouten & Verstraten 1997). A pair of 1 m stainless steel probes was inserted 5 cm apart, creating a wave-guide at each measurement location. One centimetre of the probes remained above ground and was connected via a coaxial cable to a Tektronix 1502B cable tester (Tektronix Inc., Beaverton, OR, USA). Measurements were calibrated for two soil types: sandy soil (2% organic matter) and sandy soil with organic matter (5% organic matter). Regression lines were fitted to the data and used to convert the flight time of an electromagnetic pulse down the wave-guide to soil moisture content (Fig. 3). For plots with average organic matter content <5%, the equation for sandy soil were used; for plots with >5% organic matter, the equation for sandy soil with organic matter were used. Five sets of measurements were taken during all seasons over a 14 month period between June 1998 and August 1999 and were averaged for each plot. These soil moisture values were weighted by basal area of species within plots, providing a weighted mean value of soil moisture for each species. Weighted minimum and maximum soil moisture values were also calculated.

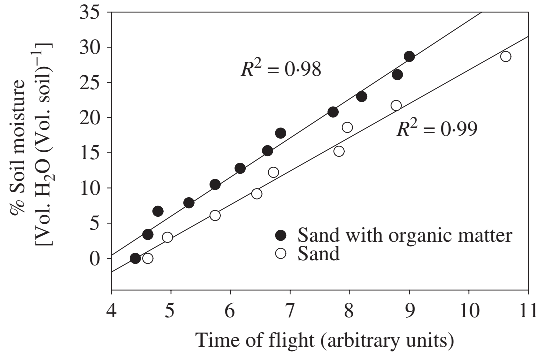

Figure 3. Regression lines for calibration of time domain reflectometry measurements with volumetric soil moisture content (Vol. H_2O/Vol. soil) for sandy soil (open circles) and soil with organic matter (closed circles) using 1 m probes. The x-axis is the time (in arbitrary units) required for an electromagnetic pulse to travel twice the distance of the probes.

Statistical analyses

Analysis of variance was calculated with the main effect of species nested within either of the fixed factors of phylogenetic clade or leaf habit. Dependent variables were Huber value, native specific conductivity, maximum specific conductivity, native leaf specific conductivity, maximum leaf specific conductivity, transpiration rate, average vessel diameter, PLC field and PLC after freezing. Differences between group means were determined by Scheffe's *post hoc* tests.

Pearson product moment correlation coefficients and P-values were determined for relationships between pairs of traits. Eight different traits were tested for correlation with soil moisture of species' habitats. To account for these multiple correlations, sequential Bonferroni correction was used (Sokal & Rohlf 1995). In the case of Huber value, where slopes differed between clades, analysis of covariance (ANCOVA) was calculated with clade as a main fixed effect and soil moisture as a covariate. All analysis were carried out using Data Desk version 5·0 (Velleman 1995).

RESULTS

Xylem anatomy

Although oaks are generally described as ring porous, it is difficult to apply the ring porous and diffuse porous terminology to 2-year-old stems (Fig. 4). In many species, both evergreen and deciduous, there was a range of vessel sizes in the early wood with a decrease in vessel size in the late wood. Yet in some species, notably the three live oaks, similar-sized vessels occurred in radial files extending from the pith outward (Fig. 4). These species, however, did not have smaller maximum vessel sizes than species with the first pattern.

Average vessel diameters of second year growth ranged from 25·2 μm in *Q. chapmanii* to 39·0 μm in *Quercus nigra* Linnaeus. First year vessels were small relative to vessels of second year growth (Table 1). Among species that were not runner oaks, mean first year vessel diameters ranged from 13·7 μm in *Quercus margaretta* Ashe to 18·4 μm in *Quercus shumardii* Buckley. *Quercus minima* Small and *Quercus pumila* Walter, the 'runner oaks', had exceptionally large first-year vessel diameters of 25·3 and 23·5 μm, respectively. Both of these species have large underground stems and are adapted to recover after fire. During the summer when their hydraulic conductivities were measured, they were in their first year of rapid growth following a fire. The white oak clade had smaller vessel diameters, on average, than the other two clades (Table 2).

By incorporating safranin dye in the transpiration stream, we determined that almost all species showed some persistent use of first-year vessels, particularly late wood vessels, although it was generally less than 10% of the total first-year vessels. In all of the stem sections we measured, first-year vessels were significantly smaller than second-

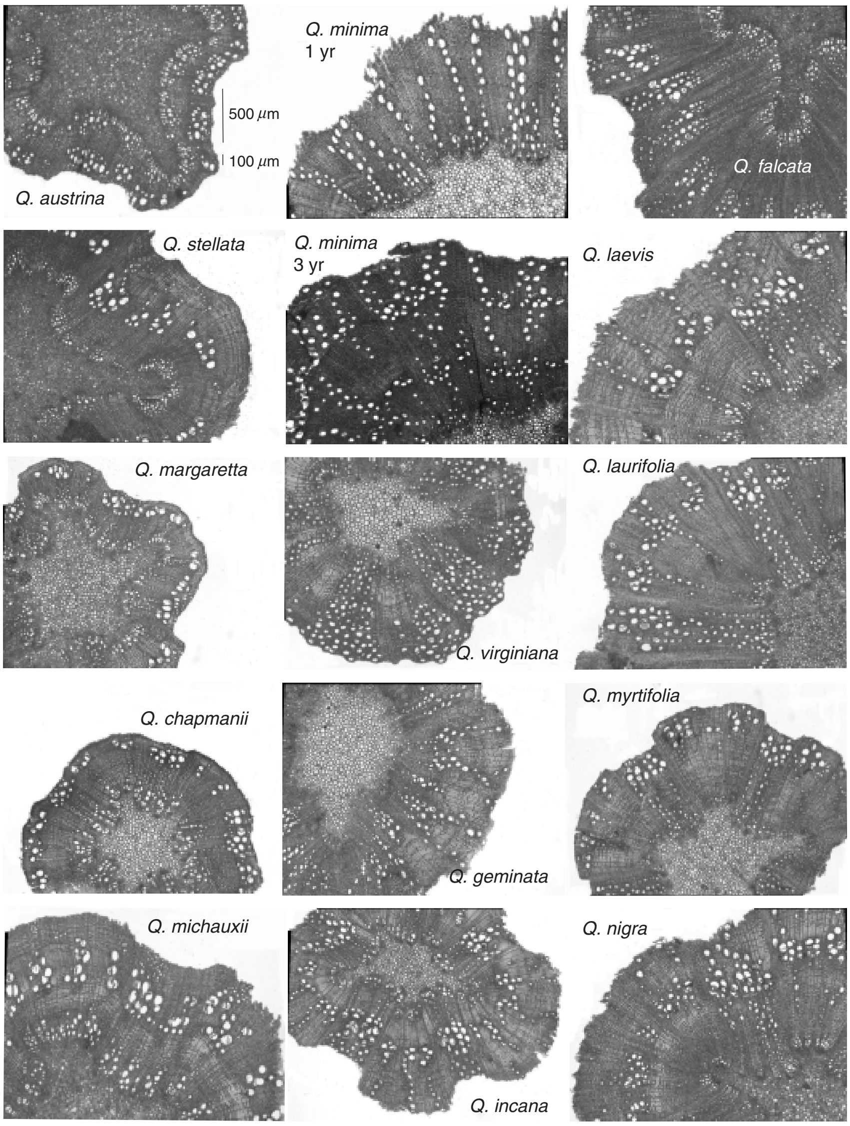

Figure 4. Cross-sections of stems for 14 oak species. Scale bars representing 100 μm and 500 μm are included. White oaks are shown in the first column; Live oaks are shown in the second column as well as *Q. incana*, a red oak, in the bottom panel. *Quercus minima* is shown both for a 3-year-old stem and a 1-year-old stem. Red oaks are shown in the third column.

Table 1. Average vessel diameters (d, μm) of shoots for the first (current) and second year of growth, respectively; mean pre-dawn (PD) and midday (MD) water potential (Ψ, MPa) for leaves and stems during midsummer of 1998; ± 1 SE shown in parentheses. Species are grouped by clade

Species	Year 1 vessel d	Year 2 vessel d	PDΨ	MD leaf Ψ	MD stem Ψ
White oaks					
Q. austrina	15·0 (0·64)	26·5 (0·52)	–0·27 (0·05)	–2·60 (0·06)	–1·98 (0·17)
Q. chapmanii	13·9 (0·76)	25·2 (1·03)	–0·21 (0·01)	–2·33 (0·29)	–2·26 (0·18)
Q. margaretta	13·7 (0·53)	28·7 (0·59)	–0·24 (0·02)	–3·34 (0·24)	–2·68 (0·19)
Q. michauxii	17·4 (1·35)	30·3 (0·98)	–0·24 (0·03)	–2·91 (0·10)	–2·01 (0·21)
Q. stellata	14·9 (0·53)	27·2 (0·54)			
Red oaks					
Q. falcata	16·5 (0·95)	33·0 (0·64)	–0·22 (0·02)	–2·99 (0·24)	–2·67 (0·21)
Q. hemispherica	16·5 (0·66)	33·3 (0·51)	–0·20 (0·03)	–2·13 (0·07)	–1·75 (0·13)
Q. incana	16·3 (0·91)	30·0 (0·99)	–0·27 (0·04)	–2·86 (0·30)	–2·02 (0·50)
Q. laurifolia	17·9 (1·68)	40·5 (2·31)	–0·20 (0·00)	–2·70 (0·25)	–2·38 (0·37)
Q. laevis	16·6 (0·88)	32·7 (0·03)	–0·21 (0·01)	–2·72 (0·25)	–2·80 (0·37)
Q. myrtifolia	14·3 (0·72)	25·5 (0·04)	–0·28 (0·02)	–2·46 (0·29)	–2·31 (0·24)
Q. nigra	15·4 (0·75)	39·0 (0·48)	–0·24 (0·07)	–2·35 (0·17)	–2·21 (0·20)
Q. pumila	23·5 (0·94)	[a]			
Q. shumardii	18·4 (1·25)	33·9 (0·68)	–0·59 (0·09)	–2·40 (0·10)	–2·25 (0·09)
Live oaks					
Q. geminata	15·7 (1·21)	31·0 (0·57)	–0·23 (0·02)	–3·23 (0·27)	–2·31 (0·24)
Q. minima	25·3 (1·66)	38·2[b]			
Q. virginiana	15·5 (0·57)	31·9 (0·47)	–0·25 (0·05)	–2·17 (0·22)	–1·76 (0·12)

[a] All individuals had only one year of growth.

[b] Only one individual of this species had a second year of growth.

year vessels and consequently had a much lower contribution to conductivity than second-year vessels. We calculated the contribution of first-year vessels as a percentage of total theoretical hydraulic conductance ($\Sigma r^4_{\mathrm{year1}} [\Sigma r^4_{\mathrm{year1+year2}}]^{-1}$). We found that first-year vessels contributed less than 15% to theoretical conductance in all species (with the exception of the two species that only had 1 year of growth), and first-year vessels had an overall average contribution of approximately 10%.

Hydraulic conductivity

Native specific conductivity (K_{L}) ranged from 0·32 kg m^{-1} MPa^{-1} s^{-1} in *Quercus austrina* Small to 1·7 in *Q. nigra* (Fig. 5a). Maximum specific conductivity values ranged from 1·7 kg m^{-1}MPa^{-1} s^{-1} in *Q. margaretta* and *Quercus geminata* Small to 5·2 in *Quercus laurifolia* Michaux (Fig. 5b). Native specific conductivities were roughly 35% of the maximum values, indicating PLCs ranging between 41 and 78%. Native conductivity (K_{S}) measurements were more variable than the measurements of maximum conductivity (Fig. 5c & d). There is a significant relation between both measurements but a low R^2 (0·31), which is explained, in part, by high PLC and high variability of PLC measurements.

Previous work has suggested that it is not appropriate to flush oak stems for measurements of maximum specific conductivities because of the danger of refilling early wood vessels from previous years (Sperry & Sullivan 1992; Sperry *et al.* 1994; Davis *et al.* 1999). Due to the small contribution of first-year vessels to total hydraulic conductance, the maximum error in PLC arising from refilling first-year vessels that were no longer functional is likely to be quite small. In addition, PLC values for *Q. minima* and *Q. pumila* were measured only on current year (first year) wood but were just as high as the other species (75 and 52%, respectively). We also measured several current year stems from other species and found similarly high PLC values (e.g. *Quercus michauxii*, 83%).

Weighted mean soil moisture values for each species are given in Table 3. Native or maximum values of leaf specific conductivity, the hydraulic capacity scaled to supported leaf area, were not correlated with mean soil moistures of species' habitats (Fig. 5a & b). Maximum hydraulic conductivity, normalized by sapwood area, showed a significant positive correlation with soil moisture regime (Fig. 5d). A trend of increasing PLC with soil moisture of habitat was also observed ($P < 0·01$), such that species from wetter habitats had higher losses of conductivity, in general, than species from more xeric habitats (Fig. 5e). This trend was still significant with a P cut-off of 0·05 after Bonferroni correction. The range of observed PLCs was greater in dry habitats.

Within all three clades, the ratio of sapwood area to supported leaf area, the Huber value, decreased with increasing soil moisture of habitat (Fig. 5f). The live oaks (*Virentes*) had higher Huber values and a steeper slope relative to that of the red (*Lobatae*) or white oaks (*Quercus s.s.*). Therefore, we tested the relationship between Huber value and soil moisture using an ANCOVA F-test (16 d.f.) in which differences in slopes between clades was factored

Table 2. Group means of traits important in water relations of oaks are shown for three different leaf habits (left) – evergreen, deciduous and intermediate – and for three phylogenetic clades (right) – red oaks, white oaks and live oaks. Species were nested within leaf habit and within phylogenetic clade; differences between means, determined by Scheffe's *post hoc* tests, are shown with letters (P cut-off <0·05). PLC values were arcsin transformed for analysis of variance. Specific conductivity is abbreviated as K_S, leaf specific conductivity as K_L and percentage loss of conductivity as PLC

	Deciduous	Evergreen	Intermediate	Red oaks	White oaks	Live oaks
Huber value ($\times 10^4$)	1·65	3·11	1·61	1·84	1·49	4·01
	0·15	0·22	0·07	0·14	0·09	0·30
	a	a	a	a	a	b
Native K_S (kg s^{-1} m^{-1} MPa^{-1})	1·10	0·90	1·61	1·30	1·11	0·73
	0·10	0·09	0·20	0·11	0·13	0·10
	a	a	b	a	a	a
Maximum K_S (kg s^{-1} m^{-1} MPa^{-1})	3·14	2·84	3·30	3·36	2·84	2·67
	0·16	0·18	0·22	0·16	0·17	0·28
	a	a	a	a	a	a
Native K_L ($\times 10^{-4}$) (kg s^{-1} m^{-1} MPa^{-1})	1·57	2·39	2·44	2·03	1·59	2·74
	0·24	0·38	0·54	0·20	0·18	0·59
	a	a	a	a	a	a
Maximum K_L ($\times 10^{-4}$) (kg s^{-1} m^{-1} MPa^{-1})	4·21	7·80	5·54	5·29	3·71	9·40
	0·20	0·51	0·43	0·02	0·03	0·07
	a	b	ab	a	a	b
Transpiration (mmol H_2O m^{-2} s^{-1})	4·77	6·50	5·92	4·84	4·88	8·32
	0·17	0·36	0·39	0·21	0·25	0·27
	a	a	a	a	a	b
Average vessel diameter (μm)	21·81	23·68	23·82	24·20	20·03	23·29
	0·47	0·49	0·66	0·38	0·46	0·70
	a	a	a	a	b	a
PLC field (%)	0·66	0·64	0·58	0·61	0·64	0·68
	0·03	0·03	0·05	0·03	0·04	0·04
	a	a	a	a	a	a
PLC after freezing (%)	0·61	0·45	0·48	0·46	0·68	0·46
	0·04	0·05	0·06	0·03	0·04	0·08
	a	b	ab	a	b	a

out. The Huber value was tested as the dependent variable with phylogenetic clade as the main fixed effect (1 d.f., 15·73 F-ratio, $P < 0·0001$) and was found to correlate significantly with soil moisture (2 d.f., 23·169 F-ratio, $P < 0·0016$).

Transpiration

Maximum transpiration rates measured in 1988 ranged from 3·41 mmol H_2O m^{-2} s^{-1} in *Q. chapmanii* to 8·88 mmol H_2O m^{-2} s^{-1} in *Quercus virginiana.* Values were somewhat higher for all species in 1999. Means for individual species measured either in 1998 or 1999 were positively correlated with maximum leaf-specific conductivities measured in 1999 ($n = 17$, $P < 0·03$ and $n = 13$, $P < 0·03$, respectively). These interspecific correlations were significant, despite the fact that transpiration rates were not measured on the same shoots or necessarily on the same trees as the leaf-specific conductivity measurements. There was no overall difference in transpiration rates among evergreen and deciduous species (Table 2). Maximum transpiration rate, a measure of water flow on a leaf area basis, was not correlated with mean soil moisture values (Fig. 6a). Due to the decrease in Huber values with soil moisture, however, when maximum transpiration rates were calculated on a sapwood area basis, they were significantly positively correlated with soil moisture (Fig. 6b).

Vulnerability to tension-induced cavitation

Quercus stellata, a deciduous species from mesic habitats, was more vulnerable to tension-induced cavitation than *Q. myrtifolia*, an evergreen species from xeric, scrub habitats (Fig. 7). *Quercus stellata* showed immediate loss of conductivity, approaching over 90% at 0·5 MPa. *Quercus myrtifolia*, was clearly less vulnerable to cavitation, approaching 90% at 2 MPa. Measurements of mean native and maximum conductivities indicate higher PLCs for *Q. stellata* than *Q. myrtifolia* (Fig. 7 inset table). In both species, levels of PLC predicted from the vulnerability curve based on midday stem water potentials far exceeded those actually measured. In the case of *Q. stellata*, midday water potentials were significantly more negative than those causing 100% loss of conductivity in the laboratory. The source of this major incongruity between the experimentally deter-

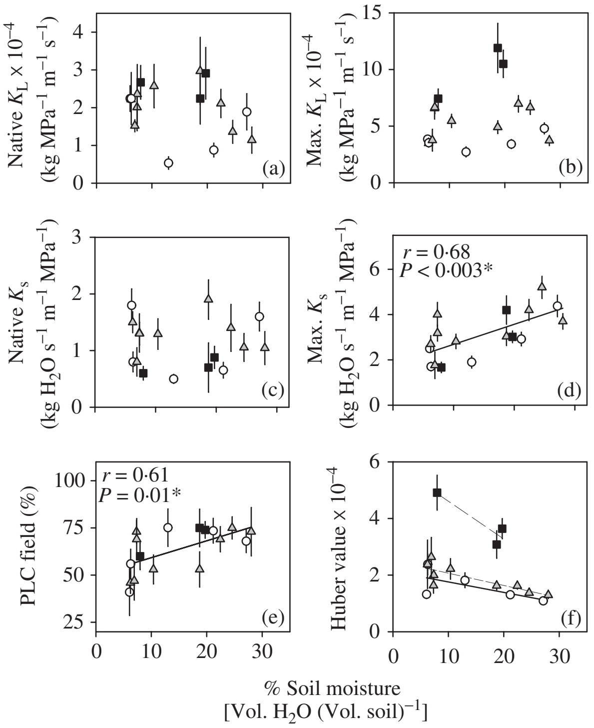

Figure 5. Native (a) and maximum (b) leaf specific conductivity in relation to soil moisture of species' habitats. Native (c) and maximum (d) hydraulic conductivity in relation to soil moisture. (e) Percentage loss of conductivity (PLC) in relation to soil moisture. (f) Huber value (ratio of sapwood area to supported leaf area) in relation to soil moisture. Members of different clades are shown with symbols as follows: white oaks (open circles), red oaks (grey triangles), live oaks (black squares).

mined vulnerability curves and the field measurements may arise from the fact it was necessary to flush the stems with water (to remove emboli) prior to beginning the vulnerability curves due to the high native PLCs in all of these species. A recent study indicates that species differ in the degree to which recently refilled vessels are stable under tension (Hacke *et al.*, 2001). An explanation consistent with these data is that the vessels of these two species (especially *Q. stellata*) become more vulnerable when artificially refilled by flushing. Nevertheless, as relative measures, the water potential measurements and vulnerability curves are consistent across the two species showing that *Q. myrtifolia* is not only less vulnerable to higher xylem tensions, but also experiences higher xylem tensions in the field.

Stem and leaf water potential

Pre-dawn leaf water potentials (Table 1) of all species were relatively high, indicating that trees had access to water. Midday stem and leaf water potential were fairly negative reaching –3 MPa in some cases, consistent with other studies of oaks (Abrams & Menges 1992; Abrams & Kubiske 1994; Bassow & Bazzaz 1998; Cavender-Bares & Bazzaz 2000).

Freeze–thaw induced cavitation

Deciduous species showed significantly higher loss of conductivity after freezing than evergreen species ($P < 0{\cdot}035$; Table 2), with intermediate species falling in between (Fig. 8a). When mean PLC after freezing of each species is plotted against the length of the period for each species in which there is no foliage (and no water transport), there is a significant positive correlation (Fig. 8b). This indicates that species more vulnerable to freezing are those which shed their leaves earlier in the season whereas those that that are more resistant to freezing maintain foliage and water transport capacity year-round. However, there is also a strong effect of phylogenetic lineage on PLC after freezing. White oaks, section *Quercus s.s.*, are significantly more vulnerable to freezing-induced cavitation than live oaks, subsection *Virentes* and red oaks, section *Lobatae* ($P < 0{\cdot}0018$; Table 2, Fig. 8c). There is no relationship between PLC after freezing and hydraulically weighted vessel diameter (Fig. 8d).

DISCUSSION

Soil moisture

Maximum hydraulic conductivity and the ratio of sapwood area to leaf area (Huber value) are related to mean soil moisture in the habitats of each species (Fig. 5d & f). The relationship between transpiration rate and soil moisture appears to be mediated by the ratio of sapwood area to leaf area. When transpiration rates are calculated on a sapwood area, but not on a leaf area basis, they are positively corre-

Table 3. Weighted averages of minimum, mean and maximum soil moisture (Vol. H_2O/Vol. soil) for each species, based on fluctuations in soil moisture throughout the year, across 74 plots. The weighted average (μ^*) is calculated as $\mu^* = \Sigma(y_i\, x_i)/\Sigma(y_i)$, where y_i is the total basal area of the species in plot i and x_i is the value of soil moisture in plot i (after Jongman *et al.* 1995)

	Soil moisture		
	Min	Mean	Max
Q. austrina	10·69	12·99	17·97
Q. chapmanii	5·52	6·06	11·50
Q. falcata	5·39	7·33	10·81
Q. geminata	5·51	7·97	12·45
Q. hemispherica	8·17	10·39	15·50
Q. incana	5·62	7·35	11·51
Q. laurifolia	12·40	24·58	34·54
Q. laevis	4·04	6·23	8·79
Q. margaretta	3·97	6·28	9·30
Q. minima	11·21	18·72	26·97
Q. michauxii	22·72	27·12	39·32
Q. myrtifolia	5·41	6·92	11·54
Q. nigra	17·52	22·44	34·59
Q. pumila	11·21	18·72	26·97
Q. shumardii	23·99	28·03	44·67
Q. stellata	17·49	21·17	27·90
Q. virginiana	14·28	19·72	27·07

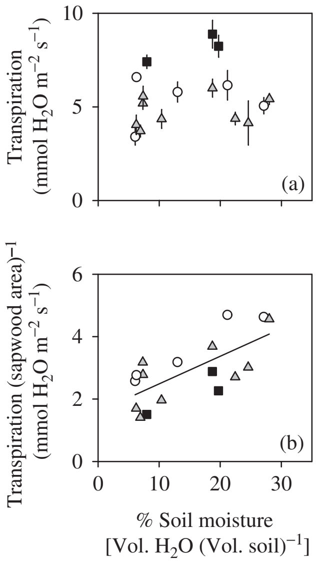

Figure 6. (a) Mean maximum transpiration rate in relation to mean soil moisture of species' habitats. (b) Transpiration divided by sapwood area in relation to soil moisture. Members of different clades are shown with symbols as follows: white oaks (open circles), red oaks (grey triangles), live oaks (black squares).

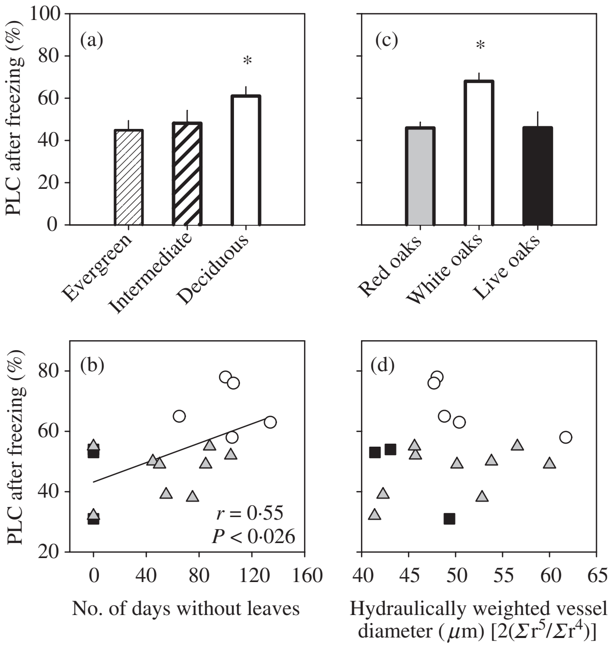

Figure 8. (a) Percent loss of conductivity (PLC) after freezing shown as means for evergreen, intermediate and deciduous species, and (b) in relation to average number of days the trees are without foliage. (c) Species means of percentage loss of conductivity after freezing for white, red and live oaks. (d) PLC as a function of hydraulically weighted vessel diameter, $2(\Sigma r^5/\Sigma r^4)$. Members of different clades are shown with symbols as follows: white oaks (open circles), red oaks (grey triangles), live oaks (black squares).

lated with soil moisture (Fig. 5a & b). This is consistent with the results for hydraulic conductivity in which conductivity is positively correlated with soil moisture when it is normalized by sapwood area but not when it is normalized by leaf area. This indicates that species occurring in wetter habitats are able to transport water faster through a given cross-sectional area of stem than species from drier habitats but the transport capacity per leaf area does not change with soil moisture. This highlights the important role that changes in allometry among closely related species can play in co-ordinating water transport capacity with soil water availability.

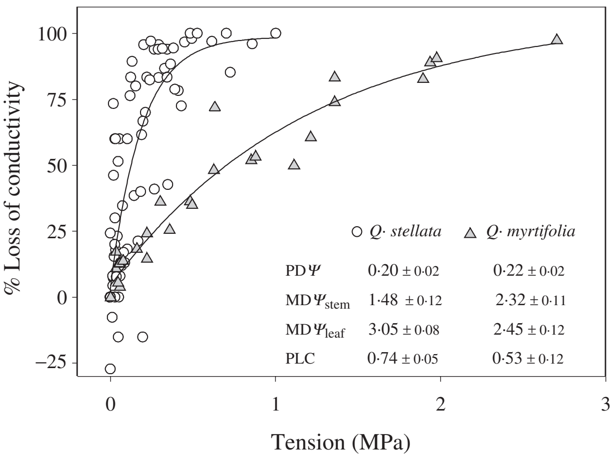

Figure 7. Vulnerability curves of a deciduous species from a mesic habitat (*Q. stellata*) and an evergreen species from a xeric habitat (*Q. myrtifolia*). The percentage loss of conductivity was measured following a protocol for subjecting the stems to tension via spinning in a centrifuge. Stem and leaf water potential (MPa) measured for the same species in the field at pre-dawn and midday, as well as percentage loss of conductivity (PLC) from branches collected in the morning, are shown for comparison to the vulnerability curves. ±1 SE shown to the right of each mean.

Vulnerability curves comparing a xeric species and a mesic species show that the mesic species is more vulnerable to tension-induced cavitation (Fig. 7). *Quercus myrtifolia*, a red oak from a xeric habitat, had low losses of conductivity relative to many other species, low hydraulic conductivity, low transpiration rates and low midday water potentials. *Quercus stellata* had higher hydraulic conductivity, higher losses of conductivity, higher transpiration rates and higher midday water potentials. The greater vulnerability of *Q. stellata* relative to *Q. myrtifolia* is consistent with the general profile of these two species, the former being mesic and the latter xeric. PLC generally increased in species that occur in higher soil moisture regimes, but native K_S was relatively constant among species occurring across the soil moisture gradient. It remains unclear why PLC was so high for these oaks during midsummer. The midday water potentials from Table 1 suggest that these oaks can experience tensions sufficient to cause more than 50% embolism, based on vulnerability curves of northern oak species (Cochard & Tyree 1990; Tyree *et al.* 1992) and other hardwood species (Sperry 1995; Salleo *et al.* 1996). Furthermore, the stems measured in this study were collected from the top of the canopy rather than from lower branches.

Cochard *et al.* (1997) showed that upper canopy branches of *Fraxinus excelsior* were significantly more vulnerable to cavitation than branches from the lower canopy.

In general, our expectation that species from xeric habitats are more conservative in water transport and water use than species from mesic habitats appears to hold, although these relationships are mediated by the allometric relationships between supported leaf area of a shoot and sapwood area. It is also interesting to note the significant differences among species in transpiration rates and hydraulic conductivities showing that the water use of these closely related species can vary considerably. Although it is clear that oaks generally possess drought adaptations (Bahari *et al.* 1985; Abrams 1990; Goulden 1996; Cavender-Bares & Bazzaz 2000), there is a wide range in the water relations and physiological performance of different species of oaks.

We note that soil moisture measured to 1 m and averaged per species over a 14 month period is not correlated with pre-dawn water potential measurements for each species. Pre-dawn Ψ were high for almost all species whereas average surface soil moisture varied markedly. The pre-dawn Ψ measurements represent the wettest part of the soil to which the plants have access; overnight, the whole plant has time to equilibrate to this water potential. During the day, however, tap roots that may have access to deeper water reserves may not be able to keep up with evaporative demand of the leaves. Therefore, higher xylem resistance may be important in mediating water transport in those species occurring in habitats where water availability in the top 1 m may be limiting. Although deep roots may not be able to supply total evaporative demand, they are likely to increase survival during drought.

Leaf habit

Differences in leaf habit appear to explain interspecific variation in vulnerability to freezing and maximum leaf specific conductivity, with evergreen species having higher freezing tolerance and higher maximum K_L. The K_L values were higher in evergreen species, contrary to our expectation, because they had significantly lower Huber values. Evergreen species also have significantly smaller and thicker leaves than deciduous species. Leaf habit did not explain variation in water transport on a sapwood area basis or in transpiration rates.

Differences in leaf habit might be expected to result in contrasting hydraulic properties because evergreen species must supply leaves with water during the winter despite the risk of xylem disruption due to freezing. In addition, evergreen species may capture and allocate resources differently as a result of having sustained access to resources year round (Chabot & Hicks 1982; Sobrado 1986). Deciduous species, in contrast, would be expected to have traits suited to a limited growing season, with higher conductances when water availability is highest, and less conservation necessary, because they drop their leaves and remove the stress of water loss later in the season. Consequently, they might have less conservative water transport strategies. For oaks in northern central Florida, however, this is not the case. In this climatic region, the unfavourable period is only about 4 months, which is significantly shorter than more temperate regions. It is not clear why evergreen species should have higher maximum leaf specific conductivities. It may be that by having a higher water transport capacity on a leaf area basis, a greater degree of embolism can be endured during the unfavourable season. Alternatively, it may merely be a consequence of different allometry from smaller, but thicker leaves, which reduce evaporative surface area and may prevent desiccation during the unfavourable period when water availability is often limited (Chen & Gerber 1990).

With respect to vulnerability to freezing, evergreen species are significantly less vulnerable to freezing than deciduous species overall (Fig. 8a). However, it is difficult to separate leaf habit from phylogeny, as discussed below. There is no relationship between PLC after freezing and the hydraulically weighted vessel radius. This is not necessarily inconsistent with the results of Davis *et al.* (1999), however, because the weighted vessel diameters and the mean vessel diameters were below the critical value (44 μm), above which they found a high probability of cavitation after freezing. In addition, we used a lower tension during freezing than Davis *et al.* (1999), and the results are therefore not strictly comparable. The branches we measured were also smaller and had smaller diameter vessels. These are likely to be the branches that freeze most rapidly as they are small in diameter and are exposed to the canopy surface.

Lineage

Species' differences in maximum specific conductivity, rather than differences at the clade level, are correlated with species distribution along a gradient of soil moisture. There was no difference between phylogenetic clades in the relationship between hydraulic conductivity and habitat. Within each clade, however, species had widely varying conductivities corresponding to their contrasting habitats. Species may be able to adapt to local environments, including soil moisture regime, by changing a few flexible traits, such as leaf size and sapwood area. It is possible that selection may act more at the species level than at the clade level with respect to hydraulic conductivity and factors that increase survival in local habitats.

In contrast, differences between clades were more important in explaining vulnerability to freezing and changes in the sapwood area to leaf area ratio. As discussed previously, differences among clades may be related to leaf habit, particularly because one clade, the live oaks (*Virentes*) is entirely evergreen and one clade, the white oaks (*Quercus s.s.*), is largely deciduous with the exception of *Q. chapmanii*, which has a leaf lifespan of approximately 10 months and is classified as intermediate. The red oaks (*Lobatae*) are the only clade that includes both evergreen and deciduous species. White oaks have higher losses of conductivity after freezing and a greater foliage-free period in the winter. The white oak clade also has a more temperate distribution than the other two clades (Manos *et al.* 1999). Live oaks, in contrast have significantly lower losses of conductivity after freezing than the white oaks (Fig. 8c) and maintain a foliated canopy year-round.

Lineage explains variations in traits for Huber value, transpiration rate, average vessel diameter, maximum leaf specific conductivity and PLC after freezing (Table 2). It may be that traits related to biogeographic distribution and climatic factors, including vulnerability to freezing, and traits important for coping with warm temperatures, such as high transpiration rates and leaf size, are explained better at the clade level than at the species level.

In summary, hydraulic properties tend to vary with soil moisture as expected within this system when they are calculated on a sapwood area basis; species occurring in wetter habitats had higher maximum hydraulic conductance and transpiration rates per unit cross-sectional stem area than those occurring in dry habitats. However, there was no correlation between either transpiration on a leaf area basis or leaf specific conductivity and soil moisture of species' habitats. This indicates that species occurring in wetter habitats are able to transport water faster through a given cross-sectional area of stem than species from drier habitats, but transport capacity per leaf area does not co-vary with soil moisture. Contrary to our expectations, there is not a trade-off between water transport capacity and the ability to maintain foliage year-round as evergreen species actually have higher maximum K_L than deciduous species. As anticipated, evergreen species are more tolerant of freezing-induced cavitation than deciduous species, a result that arises largely from the greater vulnerability of the deciduous white oaks. Finally, although certain hydraulic properties, such as freezing tolerance and Huber value show greater similarity within an evolutionary lineage, properties such as maximum hydraulic conductivity do not, and thus appear to correspond more closely to environmental factors.

Soil moisture, leaf habit and phylogenetic lineage all explain some of the variation in hydraulic properties and water relations in Florida oak species. Hydraulic properties of stems are likely to contribute to the success of individual species in their respective habitats, and they help explain species' ability to partition heterogeneity in the landscape in northern central Florida. Contrasting leaf phenologies in this system of oaks are linked to significant differences in vulnerability to freezing but not to water transport capacity per unit sapwood area. Physiological differences between evergreen and deciduous species also tend to follow evolutionary lineages as leaf habit itself is phylogenetically conserved.

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