

Hydraulic responses to extreme drought conditions in three co-dominant tree species in shallow soil over bedrock

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Abstract An important component of the hydrological niche involves the partitioning of water sources, but in landscapes characterized by shallow soils over fractured bedrock, root growth is highly constrained. We conducted a study to determine how physical constraints in the root zone affected the water use of three tree species that commonly coexist on the Edwards Plateau of central Texas; cedar elm (*Ulmus crassifolia*), live oak (*Quercus fusiformis*), and Ashe juniper (*Juniperus ashei*). The year of the study was unusually dry; minimum predawn water potentials measured in August were -8 MPa in juniper, less than -8 MPa in elm, and -5 MPa in oak. All year long, species used nearly identical water sources, based on stable isotope analysis of stem water. Sap flow velocities began to decline simultaneously in May, but the rate of decline was fastest for oak and slowest for juniper. Thus, species partitioned water by time when they could not partition water by source. Juniper lost 15–30 % of its stem hydraulic conductivity, while percent loss for oak was 70–75 %, and 90 % for elm. There was no tree mortality in the year of the study, but 2 years later, after an even more severe drought in 2011, we recorded 34, 14, 6, and 1 % mortality among oak, elm, juniper, and Texas persimmon (*Diospyros texana*), respectively. Among the study species, mortality rates ranked in the same order as the rate of sap flow decline in 2009. Among the angiosperms, mortality rates correlated with wood density, lending further support to the hypothesis that species with more cavitation-resistant

xylem are more susceptible to catastrophic hydraulic failure under acute drought.

Keywords Edwards Plateau · Hydraulic conductivity · Karst · Stable isotopes · Tree mortality · Wood density

Introduction

Tree species differentiate in root distributions, xylem vulnerability to embolism, leaf phenology, and other traits that collectively characterize a species' hydrological niche (Araya et al. 2011; Penuelas et al. 2011; Schwinning and Ehleringer 2001). Hydrological niches are thought to determine where species can persist (Kattge et al. 2011; Reu et al. 2011), which species can coexist (Chesson et al. 2004), and how species respond to extreme hydrologic events such as flooding and drought (Dietze and Moorcroft 2011; Lopez and Kursar 2003; McDowell et al. 2011). Models of vegetation distribution and coexistence usually assume that functional trait differences between species can always be expressed, but there are some environments that limit the expression of important hydrological traits. One example are habitats composed of rocky, shallow soils where tree roots are constrained to grow through cracks in the bedrock or other hardpan layers (Duniway et al. 2007; Schenk 2008). In deep, homogeneous soils, plant roots have maximal control over root development and can attain a great diversity of root structures (Fitter 1987; Hodge et al. 2009). In rock substrates, this ability is highly constrained by the availability, geometry, and distribution of fractures and soil pockets within the bedrock. Since a diversity of root system sizes and shapes is a nearly universal characteristic of plant communities, from the moist tropics (Lopez et al. 2005) to hyper-arid deserts (Schulze et al. 1996),

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we may ask: what happens to hydraulic niches when opportunities for the development of different spatial patterns of root distribution are highly constrained?

To address this question, we conducted a study in a limestone karst region, the Edwards Plateau of central Texas, USA, at a site where the soil was 30 cm deep and rocky. Vegetation consisted of partially thinned woodland, dominated by three tree species: Ashe juniper (*Juniperus ashei*), live oak (*Quercus fusiformis*), and cedar elm (*Ulmus crassifolia*). The hydrological niches of these species are distinct; juniper and oak are evergreen, while elm is winter-deciduous. Two species are moderately (elm) to highly (juniper) drought tolerant (Fonteyn et al. 1985; Willson and Jackson 2006; Willson et al. 2008; Wrede 2005), while live oak is less tolerant (McElrone et al. 2004) and keeps closer control on leaf transpiration (Bendevis et al. 2010).

The rooting depths of these species in rock substrates have been examined in a study involving root samples taken in caves, in which roots protruding from cave ceilings were identified to species by DNA fingerprinting (Jackson et al. 1999). Live oak roots were found in caves as deep as 22 m, while roots of juniper and elm were found in caves no deeper than 9 m. The deeper roots of oak allow this species to tap into deeper perennial water sources, where they are present, for example, into subterranean streams (McElrone et al. 2004). However, the existence of such perennial water sources at depth is by no means certain in karst regions.

Under severe drought, live oak will shed leaves to reduce transpiration demand and protect its xylem from embolism. By contrast, juniper and elm have greater capacity to assimilate carbon during relatively dry periods, which may free them from the cost of growing deep roots (Schenk 2008), but would add a lost opportunity cost in the form of reduced gas exchange potential during wet periods (Bendevis et al. 2010; Hacke and Sperry 2001; Pittermann et al. 2006). Elm, like oak, sheds leaves under more intense water stress, but juniper has little capacity for shedding its scaly leaves. Thus, juniper, by necessity, has greater need for investment in embolism-resistant xylem. However, as a conifer, it achieves higher cavitation resistance with less investment in wood density (Hacke and Sperry 2001).

In comparison to the sites where Jackson et al. (1999) conducted their study, our study site is more constraining to root development. Its shallow soils are underlain by only moderately fractured limestone. While our site also features a shallow cave 5–10 m below the surface, no roots were found protruding from the cave walls or in the soils (except near the entrance), suggesting that most roots are restricted to soil and the upper 5 m of the fractured rock matrix. The site of Jackson et al. (1999) had relatively shallow groundwater, in one case, 18 m below the surface and, based on stem water isotope ratios, live oak trees were tapping into it. At our site,

the groundwater table lies between 50 and 60 m below the surface, which is more typical for the Edwards Plateau, and indicates that at a landscape scale trees are unable to access a more stable water table during times of drought.

The primary goal of this study was to determine (1) whether the three species were able to differentiate in terms of rooting depth or access to water despite the physical constraint, and (2) how the species regulated water uptake over time, especially going into a summer drought period. Unable to excavate roots, we inferred differences in root locations between species by analyzing the stable isotope ratios of stem water, on the assumption that different water sources are subjected to different rates of evaporative enrichment. Usually, deeper water sources, being further from the sites of evaporation, have less evaporative enrichment (Barnes and Walker 1989; Mathieu and Bariac 1996). Water availability in the thin soil was measured directly, but integrated water availability throughout the root zone was estimated from the predawn water potentials of the study species in monthly intervals. The relative impact of water deficit on whole-plant transpiration was determined by continuous measurement of sap flow velocities. The degree of water stress experienced by the three species was evaluated by determining the relative loss of stem hydraulic conductivity at the end of summer.

The study took place in 2009, a year of record drought in central Texas. However, this event was soon overshadowed by the drought of 2011, which caused widespread tree mortality, including at our study site. Thus, we were able to examine not only species differences in hydraulic control, as originally planned but also the consequences of differences in hydraulic control on rates of mortality.

Materials and methods

Study site

The study site is located in central Texas on 2.3 ha (5 acres) of private property on the eastern Edwards Plateau just outside the city limits of San Marcos. The soil is shallow and rocky, about 30 cm deep, over epikarst derived from Edwards limestone (Abbott 1975). On site, a cave entrance leads to a network of passageways 5–10 m beneath the surface.

The climate is semi-arid to humid sub-tropical (Dixon 2000) with a mean August maximum of 35 °C and a mean January minimum of 4 °C. Mean annual precipitation is 864 mm (30 years, San Marcos Municipal Airport).

In 2009, the dominant tree and shrub species, in order of frequency, were: *Ulmus crassifolia* Nutt. (cedar elm), *Quercus fusiformis* Small (escarpment live oak), *Juniperus ashei* Buchholz (Ashe juniper), *Diospyros texana* Scheele

(Texas persimmon), *Celtis laevigata* var. *reticulata* (Torr.) L. Benson (netleaf hackberry), and *Berberis trifoliolata* Moric. (agarita). Except for the relative low abundance of Ashe juniper, which had been selectively thinned, this community was representative of Edwards Plateau oak–juniper woodlands (Van Auken et al. 1980; Wills 2005).

Study design: overview

Six mature trees (>3 m height) of each of the three study species, cedar elm, Ashe juniper, and live oak (from now on referred to as elm, juniper, and oak), were randomly selected from an area of approximately 800 m² directly above the underlying cave system. The 18 trees were instrumented with Granier sap flow sensors (Granier 1985) and measured continuously between May and mid-September 2009, when instrument malfunction terminated further data collection. Predawn xylem water potentials (Ψ_{pre}) and stem samples for stable isotope analysis were taken at monthly intervals from February to November. Stem samples for the determination of stem hydraulic conductivity were taken in September and October, immediately following the summer drought period, to determine the degree of native xylem embolism. Additional stem samples were taken in the following spring.

Weather, soil moisture and cave drip

A weather station was installed on 8 January 2009 to record precipitation, wind speed and direction, solar radiation, temperature, and relative humidity (Onset Computer, Bourne, MA, USA). Measurements were logged at 10-min intervals.

Precipitation samples for stable isotope analysis were collected continuously, stored under exclusion of evaporation, and sampled weekly to monthly, depending on precipitation frequency.

Volumetric water content at 25 cm depth was measured with four EC-5 sensors (Decagon Devices, Pullman, WA, USA) from May to September. All sensors were damaged on 6 July and replaced on 5 August, resulting in data loss during this period.

In the cave 5 m below the site, drip rate from a group of speleothems was determined by collecting drip water on a tarp and routing it into a tipping bucket rain gauge connected to an Onset Computer Micro-station data logger (Onset Computer). Cave drip samples were also collected periodically for stable isotope analysis.

Sap flow data collection and analysis

Single 10 mm Granier sap flow sensors (Granier 1985) were installed at breast height on the north facing side of the tree trunks and wrapped in sheets of reflective bubble

insulation. The thermocouples were positioned 5 mm deep into the sapwood. Sensors were connected to an AM 16/32B relay multiplexer controlled by a CR1000 datalogger (Campbell Scientific, Logan, UT, USA). Sensors were queried every 60 s and 15-min averages were logged. The datalogger, multiplexer and the Granier sensors were powered by three 125-W solar panels. Sensor installation and testing was completed by 2 May 2009. After 10 September, at the beginning of a rain-intensive period, the system experienced intermittent instrument failure, which made the calculation of sap flow values impossible.

Sap flow velocity (u , m s⁻¹) was estimated from the temperature difference between heated and reference sensors using the empirical relationship developed by Granier (1985):

$$u = 119 * 10^{-6} K^{1.231} \quad (1)$$

where

$$K = \frac{\Delta T_M - \Delta T}{\Delta T} \quad (2)$$

The term ΔT_M is the maximal temperature difference measured when sap flow is zero, and ΔT is the temperature difference for $u > 0$, i.e. at any other time. Sap flow results in accelerated heat dissipation in the heated probe and a reduction in the temperature differential ΔT . Thus, under wet conditions, ΔT is maximal and flat at night and drops during the day when trees are transpiring.

Temperature artifacts, due to uneven temperature distribution of the xylem sap, tend to have the opposite diurnal trend than the sap flow effect, increasing ΔT during the day and decreasing ΔT at night. This sets a limit to measuring flow rates during summer drought, as temperature artifacts cancel out or even overwhelm the sap flow effect. We set sap flow categorically to zero whenever the diurnal trend in ΔT was opposite from the expected trend.

When the diurnal trend of ΔT was high at night and low during the day, we determined ΔT_M from among all 96 data points collected between 1200 and 2345 hours to calculate flow velocity. In a second pass through the data, we eliminated flow velocity spikes and filled the data gaps by extrapolation between adjacent data points. One oak tree was removed from the analysis, since we had difficulties finding the active part of the sap wood, even after several trials. However, this tree remained included for the measurement of predawn water potential and water isotope analysis and exhibited no anomalies with respect to these variables.

Predawn water potentials

Predawn xylem water potentials (Ψ_{pre}) were taken with a Scholander pressure bomb (Model 1000 Pressure Chamber

Instrument; PMS Instruments, Albany, OR, USA), provided they had green leaves at the time of measurement. According to theory, the predawn water potential is a soil-to-root conductance weighted average water potential across the rhizosphere, based on the assumption of zero transpiration and equilibrium between xylem and rhizosphere water. Where direct measurements of rhizosphere water content are unavailable, it is often used as a proxy of plant-available water, although this is not without complication due to the fact that predawn water potentials tend to be heavily weighted towards the wettest source in the rhizosphere, since this is where hydraulic conductances are maximal. This tends to overestimate plant-available water. Another complication is that, at very low water potentials, xylem water may not fully equilibrate with rhizosphere water, which would underestimate plant-available water (Donovan et al. 2003). However, for the purpose of this study, the predawn water potential provided an adequate measure of drought progression.

Since elm is winter-deciduous, samples for this species were taken from April to November, when trees had foliage ($n = 4$ for November). In September, two oak trees had only brown leaves and were also not sampled, since this would have violated the assumption of soil-to-leaf flow continuum. One oak tree did not leaf out after the onset of rain and was not measured again for the rest of the year. In August, three elm trees had Ψ_{pre} values that exceeded tank pressure (8 MPa), thus we could only conclude that their average Ψ_{pre} values were less than -8 MPa.

Stable isotope analysis

Stem samples for stem water stable isotope analysis were collected between 0900 and 1100 hours on the same days Ψ_{pre} were measured (February to November), following the sampling procedure described in Schwinning (2008). We omitted sampling from trees without green leaves at the time, since these samples were not expected to reflect the isotope composition of rhizosphere water.

Stem samples were stored frozen in capped and parafilm vials until cryogenic vacuum extraction (Ehleringer et al. 2000). Stem water extracts, as well as precipitation and cave drip samples were analyzed at Texas State University-San Marcos on a LGR DLT-100 Liquid Water Stable Isotope Analyzer (Los Gatos Research, Mountain View, CA, USA) along with internal standards created using the LGR certified standards. Values are expressed in delta notation as parts per thousand (‰) relative to the V-SMOW standard (Gonfiantini 1978):

$$\delta D \text{ or } \delta^{18}O = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) * 1,000 \quad (3)$$

Precision was estimated at 0.5 per mil for δD and 0.3 per mil for $\delta^{18}O$.

Native embolism and hydraulic conductivity

Stem samples were taken either from the experimental trees or nearby trees of equivalent size, for a total of 6–8 samples per species. At least 30-cm-long branches were cut between 2 and 3 m height from inside the canopies of trees (usually incorporating both shade- and sun-exposed leaves) and placed in a dark, humidified container for transport to the laboratory. Branches were then reduced to unbranched stem segments of 15 cm length and uniform thickness (~ 0.5 cm in diameter) by cutting away all other parts underwater. Just before measurement, thin slices of wood were shaved off both ends with a sharp razor blade to remove potentially crushed xylem elements.

Native hydraulic conductivity was determined following the method described by Sperry et al. (1988). Hydraulic conductivities (k_h , $\text{kg s}^{-1} \text{ m MPa}^{-1}$) were calculated using Darcy's Law (Sperry et al. 1988):

$$k_h = \frac{v}{\left(\frac{dP}{dl} \right)} \quad (4)$$

with flow rate v (kg s^{-1}) and the pressure differential dP (MPa) across the length of the stem dl (m).

The percent loss of hydraulic conductivity due to embolism was calculated using the formula:

$$\text{Loss (\%)} = \left(1 - \frac{k}{k_{\text{max}}} \right) * 100 \quad (5)$$

where k is the conductivity measured on stems collected in the field or after air injection and k_{max} is the hydraulic conductivity of the stem segment after “flushing.” Stems were flushed with micron-filtered water for 20–30 min under comparatively high pressure (0.03–0.7 MPa) to push air out of embolized vessels and tracheids thus restoring maximal hydraulic conductivity.

In 2009, we had difficulty producing meaningful values for juniper, as hydraulic conductivities often decreased rather than increased after flushing, a problem specific to gymnosperms as mentioned by Sperry and Tyree (1990). We did not solve this problem in 2009, and instead report laboratory values obtained in 2010 with stems pressurized to 8 and 9 MPa, using the air injection method (Sperry and Saliendra 1994) to simulate the pressure gradient across the xylem wall experienced in the previous year's drought (8 MPa to simulate predawn values, and 9 MPa to simulate hypothetical daytime values). Stems were pressurized inside a pressure sleeve attachment to the pressure chamber (PMS Instruments). For comparison, elm and oak were also included in this analysis, using pressures equivalent to their

respective minimal Ψ_{pre} values, as well as $\Psi_{\text{pre}} - 1$ MPa values, measured the previous year; 4 and 5 MPa for oak, and 8 and 9 MPa for elm.

Tree mortality

In November 2011, we censused an area directly over the cave, containing 657 mature trees of stem diameters >3 cm at the base, including a fourth species, Texas persimmon, the next most common woody plant species after Ashe juniper. We measured basal stem circumference and registered a tree as either alive or recently dead, ignoring trees that had been dead for more than 1 year. We recognized trees that had been dead for over a year by the amount of terminal branch snag. We assumed that a tree was recently dead if it had only brown leaves or scales attached and terminal branches were desiccated. Elm trees had generally lost their spring leaves by November, but live trees had grown a second leaf flush in October that allowed us to distinguish dead and live elm trees. Live trees were further characterized by the approximate percentage of the canopy composed of recently dead branches.

Wood density

We estimated the wood density from cuttings of larger branches (>2 cm diameter) collected at the study site. We cut a cylindrical section of branch, removed bark and phloem, and measured the volume of the cylinder by the water displacement method. We then weighed the wood section after drying at 70 °C for several days.

Data analysis

Univariate ANOVA was used to test for species effects on Ψ_{pre} , stable isotope ratios and hydraulic conductivities, using Fisher's LSD for post hoc comparisons. We used SPSS software (v.10; SPSS, Chicago, IL, USA).

Results

Total precipitation in 2009 recorded at the field site was 750 mm, only 13 % below the local 30-year average. However, precipitation in the previous year was lower at 485 mm (44 % below average; Ameriflux site US/FR-2, data courtesy of James Heilman, Texas A&M University). NOAA's National Climate Data Center classified central Texas as progressing from moderate to extreme drought between mid-May and mid-September 2009, based on the Palmer Drought Index. Growing season conditions were therefore very dry in 2009.

Values of Ψ_{pre} steadily declined between May and August, reaching minima of -8.0 MPa in juniper, less than -8 MPa in elm, and -5.2 MPa in oak (Fig. 1). Stem water stable isotope ratios were consistently more enriched than meteoric water. During the drought episode, the stem water isotope ratios of all three species became successively more enriched along an evaporitic trend between May and August, and dropped back to values closer to meteoric water in September, following the first substantial rainfall events (Fig. 2). Linear regressions of stem water δD on $\delta^{18}\text{O}$ for the months of May to August were non-significantly different between species and had a point of intersection with the local meteoric water line (LMWL) at approximately $\delta\text{D} = -40$ ‰ and $\delta^{18}\text{O} = -7$ ‰, which is below groundwater values for the region (Fahlquist and Ardis 2004), and below samples collected from a private well on site from January 2009 to November 2011 ($\delta\text{D} = -24.6$ ‰ ± 1.9 , and $\delta^{18}\text{O} = -4.5$ ‰ ± 0.66 , $n = 67$; ranges express ± 1 standard deviation). Drip water isotopes from samples collected 5 m beneath the surface between May and September were also different from stem water isotope ratios at all times. Average drip water isotope ratios from January 2009 to October 2011 were: $\delta\text{D} = -19.9$ ‰ ± 4.8 , and $\delta^{18}\text{O} = -4.3$ ‰ ± 0.55 ($n = 69$). Only one precipitation sample, collected on 10 December 2008, was more negative than the intersection of the stem water isotope ratios with the LMWL and it came from a small sleet storm of <10 mm precipitation and isotope ratios of $\delta\text{D} = -67.5$ ‰ and $\delta^{18}\text{O} = -10.6$ ‰.

From February to December 2009, the three species' stem water remained largely similar in isotopic composition, but stem water isotope ratios did separate during the peak of the summer drought (Fig. 3). In August, juniper had the least enriched and oak the most enriched stem water isotope ratios.

Sap flow velocities of the three tree species declined steeply beginning in mid-May, and there were clear species differences in the patterns of decline (Fig. 4). Oak was the first species to reach sap flow velocities below the detection limit in early June. Elm reached baseline flow rates about 3 weeks later, although flow rates remained above the detection limit for most days. In juniper, sap flow velocities declined more gradually through August and remained above the flow velocities of the other two species.

The species also differed in their abilities to respond to isolated rainfall events during the summer drought. Elm responded strongly to two events in July (9 mm on 7 July and 8.4 mm on 18 July), while juniper responded strongly to the first event and less so to the second. Oak showed no response to the first event and a minimal response to the second. Two mid-summer rain events on 26 and 27 August (12.6 mm combined) elicited a response only from juniper.

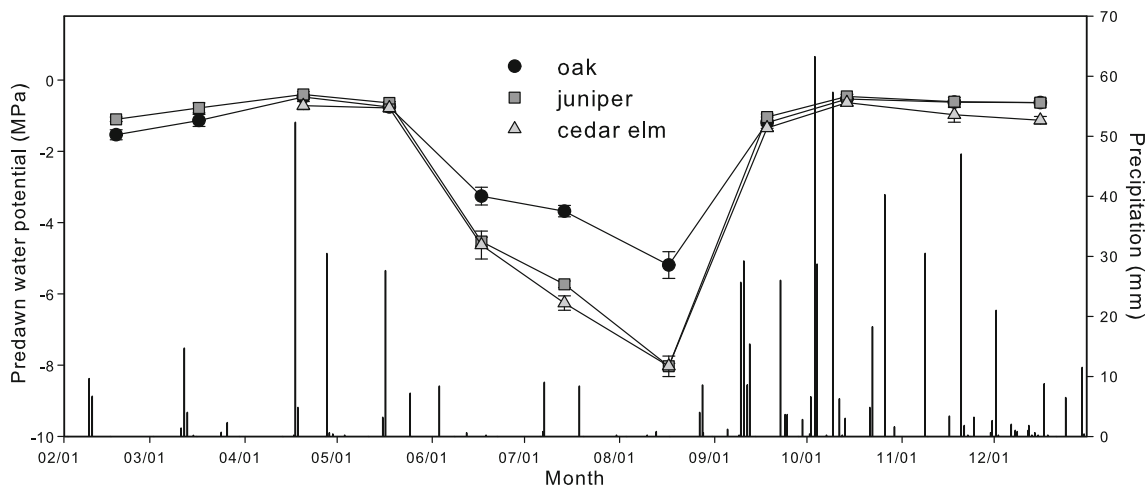


Fig. 1 Precipitation (columns, mm) and average predawn water potentials (Ψ_{pre} , MPa) between February and December 2009. Error bars standard errors. The August Ψ_{pre} measurement for elm was

composed of only 3 trees that had water potentials at or above -8 MPa, the measurement limit set by the tank pressure on that day. Across all samples, the Ψ_{pre} of elm was therefore less than -8 MPa

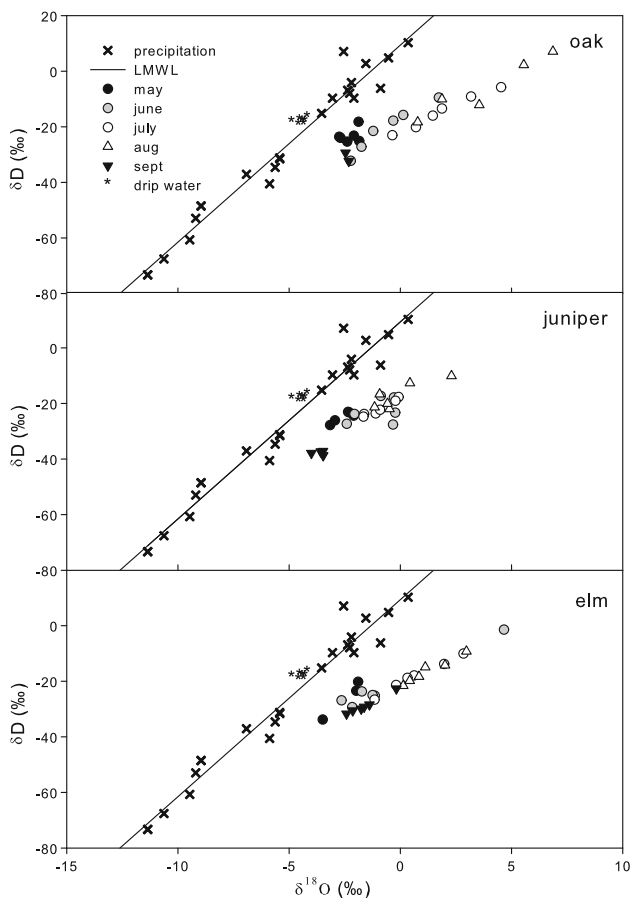


Fig. 2 Stable isotope ratios of oxygen ($\delta^{18}O$) and hydrogen (δD) in rain water (January–December 2009), drip water (April–September 2009) and stem water for selected measurement dates. The local meteoric water line (LMWL) was generated by linear regression from 2009 precipitation

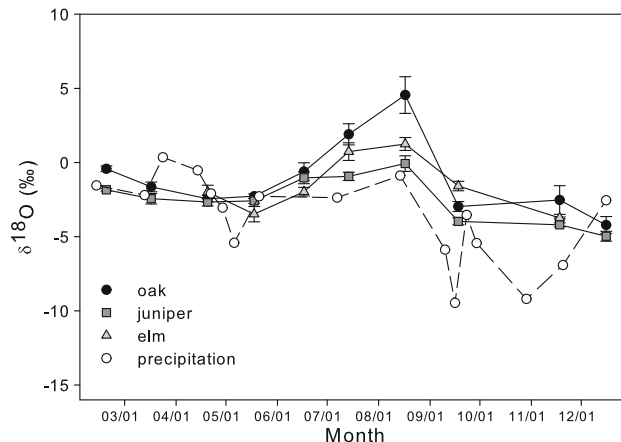


Fig. 3 Average $\delta^{18}O$ values for stem water across all measurement dates, along with values for precipitation. Error bars standard errors

Examples of diurnal variation in sap flow estimates are shown in Fig. 5 for three successively severe drought conditions and a pre-drought day in early May for comparison. In May, the diurnal patterns of sap flow are very similar for the three species, but by June, sap flow velocities were already below the detection limit for oak and highly reduced in elm. For the next two measurement dates, sap flow rates were below detection in oak, just detectable in elm, and successively reduced but well within the measurable range for juniper.

The three species demonstrated differential sensitivity of sap flow velocity to declines in Ψ_{pre} (Fig. 6). Oak had lost detectable sap flow by mid-June at a Ψ_{pre} of -3.7 MPa. By the same date, elm had lost about 70 % of sap flow velocity compared to mid-May at a Ψ_{pre} of -4.6 MPa, while

Fig. 4 Top panel average daily sap flow velocities (m d^{-1}) from May to September 2009 ($n = 6$ for elm and juniper, $n = 5$ for oak). Bottom panel precipitation (columns) and average volumetric water content at 10 cm (solid line) and 25 cm (broken line) depth ($n = 2$). The data gaps are due to instrument error

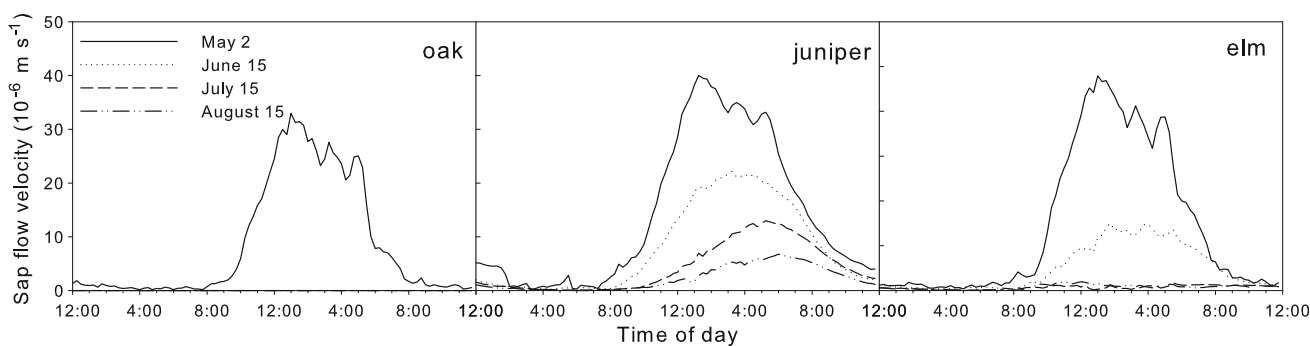
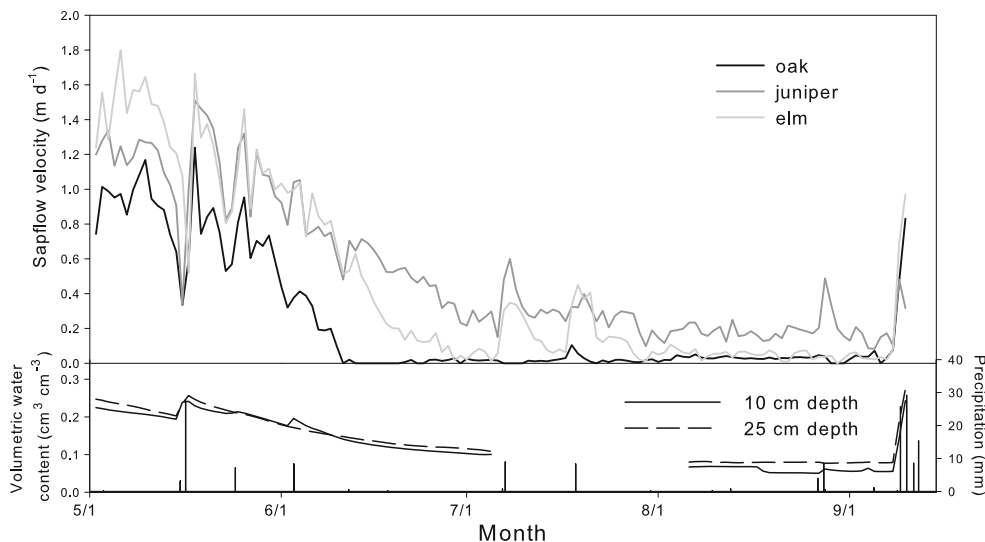


Fig. 5 Diurnal courses of sap flow velocities on 4 measurement dates. Lines correspond to average flow velocities across instrumented trees ($n = 6$ for elm and juniper, $n = 5$ for oak)

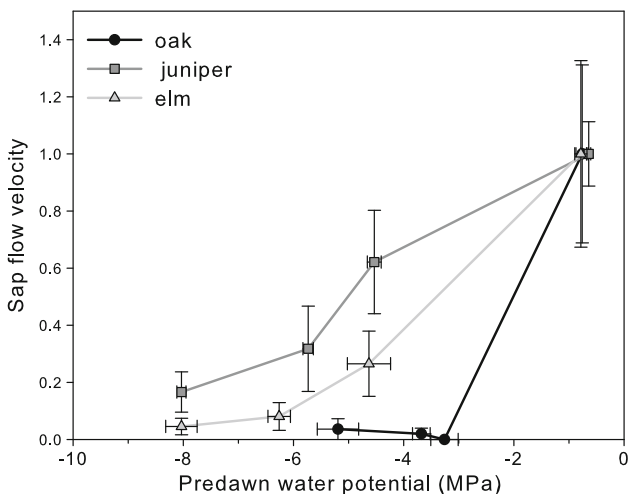


Fig. 6 Average daily sap flow velocities, scaled to velocities measured on May 18, as a function of Ψ_{pre} measured on the same days, from mid-May to mid-August

juniper had lost 80 % by mid-August at a Ψ_{pre} of -8.0 MPa.

Percent loss of hydraulic conductivity measured in late summer 2009 was not significantly different between oak

and elm and averaged 70–75 % for oak and 90 % for elm (Table 1). In the following year, when we induced embolism at the minimal predawn water potentials measured in 2009, oak had the highest loss of conductivity and juniper the least. The same ranking held true for water potentials 1 MPa lower than the minimal predawn potential (to simulate daytime conditions). However, while the loss of conductivity for oak due to natural drought experienced in 2009 was quantitatively similar to that determined in the laboratory in 2010, elm showed greater loss of conductivity under natural conditions than from induced embolism at -9 MPa.

In a census taken in November 2011, 102 of 657 censused mature trees had apparently died the same year (Table 2). Among the three angiosperms (i.e. excluding juniper), mortality rates increased with wood density. Surviving trees also showed partial canopy die-back and substantially more so in elm and juniper than in oak, even though oak had the highest tree mortality. Overall canopy die-back (including partial and 100 % die-back) reduced the differences between the study species, but maintained the same ranking as wood density among angiosperms. There was no significant difference in the

Table 1 Percent mean loss of stem hydraulic conductivity (standard errors in parentheses) for stems collected in the fall of 2009 (corresponding to native embolism), and for stems collected in the fall 2010, which were brought to water potentials corresponding tominimal measured predawn water potentials ($\Psi_{pre,min}$) observed in 2009 (-5 MPa for oak, -8 MPa for juniper and elm), as well as water potentials 1 MPa less than the minimal observed values to reflect potential daytime water potentials

Species	Native	<i>n</i>	Induced at $\Psi_{pre,min}$	<i>n</i>	Induced at $\Psi_{pre,min} - 1$ MPa	<i>n</i>
<i>Quercus fusiformis</i>	76 (9)	6	71 (19)	5	88 (9)	5
<i>Juniperus ashei</i>	–		16 (12)	7	27 (12)	7
<i>Ulmus crassifolia</i>	89 (11)	6	36 (15)	6	55 (13)	6

Table 2 Wood density and results of the 2011 tree census

Species	Wood density (g cm ⁻³) (std err)	Dead/total trees	% dead	Basal circumference of trees (cm) (alive/dead)	% Trees with branch death	% Die-back on trees with branch death	% Overall canopy die-back
<i>Quercus fusiformis</i>	0.84 (0.03)	56/167	33.5	53.9/67.3	5	39	35.5
<i>Ulmus crassifolia</i>	0.76 (0.02)	31/223	13.9	28.0/22.5	23	55	26.5
<i>Juniperus ashei</i>	0.74 (0.01)	9/153	5.9	61.8/66.0	28	29	14.5
<i>Berberis trifoliata</i>	0.67 (0.03)	1/102	1.0	28.0/22.5	0	n/a	1.0

Trees were categorized as dead if 100 % of their branches had either no leaves or only brown leaves or scales

The last column was calculated as the sum of total and partial canopy die-back (column 4 + column 6 × column 7 × 0.01)

average stem circumferences of live trees and those that died in 2011.

Discussion

The initial purpose of this study was to characterize the hydrologic niches of three tree species subjected to a shared constraint of root development in fractured bedrock. However, the year of the experiment turned out to be an unusually dry one, arguably not representative of “average” conditions. Unexpectedly, but fortuitously, the study provided a rare insight into the onset of one of the worst droughts on record, overshadowed only by the most recent drought of 2011.

To set the year of the experiment into context, even though most of 2009 was an exceptionally dry year, it did not lead to widespread tree mortality, and was followed by a wetter than average year (approximately 1,000 mm, 18 % above average). By contrast, the drought of 2011 did trigger regional tree mortality that has yet to be rigorously quantified. How were the two drought events different? In 2009, substantial rainfall occurred in March and April that was missing in 2011, and cumulative rainfall from October to June was 315 mm in 2008/9 and 239 mm in 2010/11 (San Marcos Municipal Airport). Perhaps the most

important difference between the two drought years was that the period from July through September was both drier and warmer in 2011, with July, August, and September being 1.3, 1.6, and 2.9 °C warmer on average than in 2009. While rain in early September ended acute drought conditions in 2009 and dropped temperatures, warm and dry conditions lasted until early October in 2011. Personal observation suggests that trees became critically impaired only during the last month of the drought. Thus, while the drought of 2009 may have brought trees to the brink of mortality, the drought of 2011 exceeded the endurance of many trees simply by lasting a month longer. In this context, our observations in 2009 may provide insights into the species-specific onset and experience of drought conditions that were almost, but not quite, lethal.

The first of our original questions was whether the three tree species used different water sources. This was apparently not the case at our study site. The stable isotope ratios of stem water were usually very similar and changed in concert over time. Maximal enrichment levels were observed in oak stems in the month of August, which could indicate that the water sources of oak were different and more susceptible to evaporative enrichment. However, we think it more likely that oak experienced significant back-diffusion of enriched leaf water into the xylem due to the very low sap flow velocities at that time. The low water

potential and lack of response to mid-summer rainfall events also excludes the alternative hypothesis of hydraulic redistribution from deep water into the shallow soil, where it could have been evaporatively enriched before uptake. Back-diffusion would have been least likely to occur in juniper, which maintained low but consistent sap flow velocities into August.

None of the species exhibited a tendency to “switch” to deeper, less enriched water sources, as is commonly observed in winter-wet, summer-dry systems with unlimited soil water storage capacity (Evans and Ehleringer 1994; Lee et al. 2007; West et al. 2007). Drip rates at speleothems in the cave during the summer of 2009 were very low, further evidence that little water was stored in the rock above the cave by May 2009. Stable isotope ratios in drips were different from the isotope ratios of water extracted from stems, as well as from the extrapolated meteoric sources of stem water, and showed no trend of isotopic enrichment. All this suggests quite strongly that the water sources supplying the speleothems were disconnected from the rhizosphere and possibly deeper. This sets the lower limit of the tree root zone conservatively to 5 m, the depth of cave roof at the sampling site.

The only marked difference in the water source use by species that we observed was the differential utilization of isolated rainfall events in July and August. Over the course of the summer, species gradually lost the ability to use rainfall events in the order of their drought tolerance: first oak, then elm, but not juniper. Contrary to earlier reports (Bendavis et al. 2010; McCole and Stern 2007), juniper clearly responded to summer rain events all the way into late August. Thus, it may be that the longer a plant remains at very low sap flow velocities the lower its capacity to take up water from the shallow soil, perhaps due to the shedding of fine roots. Earlier in the dry-down event, shallow roots may have remained hydrated through hydraulic lift (Bleby et al. 2010), but, as sap flow declined and the shallow soil became extremely dry, fine roots may have desiccated.

Oak had barely detectable levels of sap flow from 8 June to 9 September, i.e. for 90 days. According to our estimates, oak had lost 70–75 % of stem hydraulic conductivity by the end of summer. McElrone et al. (2004) determined the loss of hydraulic conductivity for stems and deep roots of live oak to be about 90 % at -3 MPa, while we recorded average Ψ_{pre} values less than -3 MPa from mid-June to mid-August, with the lowest recorded value of -5.2 MPa. Clearly, the oaks on our study site were acclimated to the drier edaphic conditions.

Sap flow in elm trees never dropped below the detection limits imposed by the temperature artifact, but the baseline flow velocity of about 0.15 mm day^{-1} was reached by the end of July, and was elevated only intermittently following rainfall events until 9 September (Fig. 4). The rate of

decline in sap flow velocity with Ψ_{pre} was intermediate between juniper and oak (Fig. 6), suggesting intermediate levels of drought tolerance. However, the direct measurement of stem hydraulic conductivity was inconclusive. While the native loss of hydraulic conductivity was about 90 %, in the laboratory we obtained a loss of only 55 % at -9 MPa. Part of the incongruity could have been due to differences in early wood characteristics between years in this ring-porous species, in which about 90 % of saturated hydraulic conductivity is accounted for by the youngest, largest vessels (Ellmore and Ewers 1985, 1986; Li et al. 2008). It is also possible that the xylem water potential of elm trees in the summer of 2009 dropped even lower than -9 MPa. In fact, in August, three out of six trees had Ψ_{pre} values below -8 MPa and dry conditions continued for 10 more days, which could have lowered xylem water potentials still further. Overall, it appears that elm trees operated quite close to their hydraulic limits by the end of August 2009. However, the nearly complete loss of hydraulic conductivity is commonplace in ring-porous, deciduous species and swiftly reversed by growing new sapwood in spring (Taneda and Sperry 2008).

The sap flow velocity of juniper decreased gradually from May to August and remained well above the velocities of oak and elm over most of this period. Loss of hydraulic conductivity estimated in the laboratory ranged between 16 and 27 %, roughly equivalent to the estimates of McElrone et al. (2004), who reported the loss of hydraulic conductivity at -9.5 MPa to be 30 % for Ashe juniper stems. Willson et al. (2008) reported a P_{50} (the xylem water potential corresponding to 50 % loss of hydraulic conductivity) for Ashe juniper of -12.5 MPa. Thus, juniper was without doubt the most drought-resilient species at this site and not even near any critical stress level by the end of the 2009 drought.

In conclusion, while spatial restrictions on root development may have narrowed one dimension of the hydrologic niche, the partitioning of water sources, it may have separated the species more strongly in terms of the temporal partitioning of water uptake based on differences in xylem construction and the control of transpiration under drought conditions.

Trying to relate the water status of trees in the summer of 2009 to the mortality patterns observed in 2011 highlights some of the problems associated with inferring drought mortality in extreme years from drought response in moderately dry years. For example, the species that maintained the highest water potential in 2009—oak—suffered the greatest mortality in 2011. The species that probably suffered the greatest loss of hydraulic conductivity in 2009—elm—did not suffer the greatest mortality in 2011. And while for the one conifer in this study—juniper—a cavitation-resistant xylem did afford protection

from drought mortality, among the angiosperm species—oak, elm, and persimmon—cavitation resistance as indicated by wood density correlated positively, instead of negatively, with drought mortality. One pattern that did consistently link the drought response of 2009 with the mortality rates of 2011 was that mortality rates ranked in the same order as the sequence in which species attained baseline sap flow velocities during the dry-down. Assuming that a similar dry-down occurred in 2011, the data suggest, quite reasonably, that mortality risks increase with the amount of time a tree spends in a state of no—or extremely low—flow.

The counter-intuitive relationship between wood density and drought susceptibility was also observed by Hoffmann et al. (2011), in a study involving 22 deciduous tree and shrub species of a temperate forest in the eastern USA. Specifically, trees and shrubs with denser wood, and higher xylem resistance to cavitation, also had higher rates of hydraulic failure (measured as % desiccated leaf area) and a greater tendency to operate at or below the species' P_{50} value.

Explaining species differences in susceptibility to death by desiccation during acute drought conditions has been the subject of many recent review articles (Allen et al. 2010; Hartmann 2011; McDowell et al. 2008; McDowell 2011; Sala et al. 2010). One hypothesis suggests that drought-tolerant species with cavitation-resistant xylem operate closer to their critical water potentials, the one that induces runaway cavitation (McCulloh et al. 2011; McDowell et al. 2008), i.e. they maintain narrower “hydraulic safety margins” (Sperry 2000). This would indeed explain why drought-tolerant, anisohydric species succumb to acute drought more often than isohydric drought-avoiders.

However, categorical differences in hydraulic safety margins do not easily explain differences in drought mortality within a group of drought-adapted, anisohydric species. It would be inefficient to invest in cavitation-resistant xylem without using it to extend periods of gas exchange. Thus, species variation in safety margins should be smaller than variation in critical water potential values, and, consequently, species with more vulnerable xylem should become critically water-stressed sooner during a dry-down event than species with less vulnerable xylem, and one might therefore also expect their mortality rates to be higher.

The concept of the hydraulic safety margin is often discussed as if it were a variable set-point, regulated by stomatal sensitivity and physiological triggers of leaf abscission (e.g., McDowell et al. 2008; Sperry 2000). However, this view is difficult to rationalize evolutionarily, as it is hard to imagine scenarios in which it is adaptive for an established tree that can live for many more decades to risk life rather than accept carbon loss. It may be more

useful to conceptualize the events leading up to the death of all or parts of a tree as a failure of control, not necessarily associated with deterministic trigger points based on the assumption of flow equilibrium (e.g., Sperry et al. 1998), but with insufficient control over matching water demand with capacity for water uptake. Short-term, diurnal imbalances between rates of water uptake and rates of water loss are buffered in part by water stored in the sapwood, but as the water potential of the tree declines, so does the volume of water available for buffering (Sperry et al. 2008). Consequently, as a tree goes into a drought phase, it must respond to day-to-day fluctuations in water demand ever more rapidly to maintain water balance. This would be especially constraining for species with higher wood density, which have less water stored per unit sapwood volume even when fully hydrated.

It is possible that a delay in leaf abscission or continuing water loss through lenticels (Lendzian 2006) even after leaf abscission is enough to cause runaway cavitation from which the tree or branch cannot recover. This “failure of control” hypothesis would explain why acute drought can kill branches and whole trees, even though most trees have the ability to shed all leaves and recover. It would also explain why, as in our study, the length of time spent in a state of minimal sap flow velocity increases the risk of irreversible desiccation of branches or trees, since time spent in a precarious state increases the probability that a fatal accident happens. Further, it would explain why die-off events are typically associated with high temperature (Adams et al. 2009; Allen et al. 2010), since dry heat could amplify water disequilibrium in trees, and why trees with dense wood and hence low water storage capacity have higher mortality rates. Less stored water would shorten the amount of time that trees have to cap transpiration before stem tissues desiccate irreversibly (Hoffmann et al. 2011; Sperry et al. 2008).

Patterns of rising tree mortality during drought-prone centuries and slow recovery during wetter, cooler centuries, have been demonstrated for western Colorado (Shinneman and Baker 2009), and Edwards Plateau woodlands may be equally dependent on centennial climate fluctuations. However, the loss of some species such as live oak may be irreversible regardless of climate, since this species and possibly others do not recruit well under the high rates of deer browsing which today is the norm on the Edwards Plateau (Russell and Fowler 1999). In addition, business-as-usual scenarios of future climate in the southwestern United States project more severe droughts with higher temperatures compared to even the medieval droughts, while the occurrence of wet periods could be reduced (Romm 2011; Shinneman and Baker 2009). This may suggest that we are seeing the beginning of the desertification of the Edwards Plateau.

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