DIFFERENTIATION OF WATER USE FOR THREE DOMINANT SPECIES
ON THE EDWARDS PLATEAU

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DIFFERENTIATION OF WATER USE FOR THREE DOMINANT SPECIES

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CHAPTER I: REVIEW OF LITERATURE ON PLANT WATER USE STRATEGIES AND ROOTING PATTERNS

Rooting strategies of woody perennials

Above and below ground, plants experience competition for vital resources both intra- and inter-specifically. To maximize the use of available resources, plant species evolve to partition shared resources, especially when they are limiting. This is usually interpreted as having the effect of reducing competitive interactions and facilitating stable coexistence (Packham et al. 1992, Chesson 2000). In climate zones where water is limiting at least during part of the year, one typically sees a wide range of water use strategies with species diversifying in when, where and how much water is taken up (Walter 1971, Burgess 1995, Casper and Jackson 1997, Meinzer et al. 1999, Williams and Ehleringer 2000). An integral part of the overall water use strategy manifests in the distribution and structure of root biomass below ground.

Rooting strategies involve a number of morphological and anatomical adaptations that include the maximal depth of the root system, which determines how much of the soil can be accessed by a plant (Seyfried and Wilcox 2006), the pattern of vertical distribution of root biomass, which determines the capacity to extract water from a given depth (Gardner 1960, Casper and Jackson 1997), the horizontal extent of the root system, which determines the spatial extent of a plant's "zone of influence" (Casper et al. 2003)

and the structure of the root xylem which controls hydraulic conductivity and cavitation resistance (Tyree and Ewers 1991).

The first generalization that can be made about roots is that most of them are shallow. A global analysis of root distributions found that at least 50% of all roots are located in the top 30 cm of the soil in > 90% of all profiles analyzed (Schenk and Jackson 2002a). This makes sense because, in most systems, soil water replenishes from above, and therefore this is where, on average, most water is available. The strong bias for shallow roots across biomes and climate regions also suggests that deep root growth is associated with significant costs and few advantages (Schenk 2008). Thus, when a species produces deep roots, it is probably necessary to do so within the context of the species' overall water use strategy, which could include drought or competitor avoidance. Rooting depth has limits however, set by the infiltration depth of precipitation since roots cannot grow through dry soil (Walter 1971, Schenk and Jackson 2002b, Collins and Bras 2007).

Woody species are usually deeper rooted than herbaceous species, though this does not mean that plant growth form fully determines rooting depth. Even within woody plant functional types, e.g. shrubs, trees, evergreen and deciduous types, rooting depths vary by species, according to hereditary growth habits (Weaver and Kramer 1932).

Woody species growing in mixed communities in regions where water is limiting typically differentiate in the depth of water uptake, either evolutionarily or phenotypically, consistent with the idea of water source partitioning. For example, in the sagebrush steppe of Utah, sagebrush (*Artemesia tridentata*) is usually deep-rooted, but

was seen to take up water from shallower soil sources when Utah juniper (*Juniperus osteosperma*) was present at high density (Leffler and Caldwell 2005). Differentiation in rooting depth allows species to partition seasonal precipitation (Ehleringer et al. 1991, Flanagan et al. 1992, P. Jackson et al. 1999, Meinzer et al. 1999, Filella and Peñuelas 2003). Species with deeper roots have a greater use of rainy season precipitation that deeply infiltrates, while shallow-rooted species are in a better position to exploit isolated rainfall events that occur during the dry season (Ehleringer et al. 1991, Schwinning and Ehleringer 2001). Some species are both shallow- and deep-rooted and are capable of "switching" water sources based on water availability. For example, a species may take up shallow water during the wet season and deep water during the dry season. This generalist strategy requires a "dimorphic" root system, involving both a deep tap root and an extensive system of shallow lateral roots (Schwinning et al. 2002, Kurz-Besson et al. 2006, Otieno et al. 2006, Duan et al. 2008). Similarly, certain tree species will use groundwater when the water table is high, but switch to shallow soil layers for moisture uptake when the water table drops (*Pinus ponderosa* and *J. virginiana* in Eggemeyer et al. 2009, *P. taeda* in Retzlaff et al. 2001 and *Gutierrezia sarothrae* in Schwinning et al. 2002). However, the apparent most available source of water is not always the one most utilized by surrounding trees. Dawson and Ehleringer (1991) found that mature streamside trees used water from a deeper soil source, not from the stream itself.

Species differences in the timing of water uptake are regulated by physiological drought tolerance and leaf phenology. Evergreens have the capacity to take up water year-round, seasonally deciduous species concentrate water uptake within a specific time of year, typically the warm season, while drought-deciduous species drop leaves in

response to declining water availability. Typically, deciduous species make up for the loss of time for resource uptake by achieving higher rates of resource uptake when they are active (Smith et al. 1997).

One would expect that patterns of leaf phenology are associated with certain rooting strategies. For example, it would make sense for drought-deciduous species to invest less in deep roots and for evergreens to invest more, since deep roots allow trees to cope with dry periods, but there does not seem to be a clear correlation between phenology and rooting habit (Schenk and Jackson 2002a).

Physiological and anatomical drought tolerance determines how long a species is able to maintain water uptake, as water availability in the root zone, thus water potential, declines. Drought tolerance is costly however and there is a strong tendency for plants to only be as tolerant as is necessary to persist in a given environment (Hacke and Sperry 2001). A necessary requirement for drought tolerance in plants is a cavitation-resistant xylem. Cavitation is the allowance of air into xylem vessels at a certain pressure differential between the xylem and ambient air pressure (Tyree and Zimmermann 2002). Air embolism interrupts water flow through the xylem and decreases the hydraulic conductivity of the sapwood. Larger conduits tend to be more vulnerable to cavitation, but have higher hydraulic conductivity (Sperry et al. 1998). Thus, there is a tradeoff between maximizing water transport under wet conditions and maintaining water transport capacity under dry conditions. Species separate along a continuum of usually fast-growing, drought intolerant trees with low wood density (large vessels) to slow-growing, drought tolerant trees with dense wood (narrow vessels, thick walls; Hacke et al. 2001). Examples of relatively drought intolerant species are riparian trees with access

to shallow groundwater, such as *Populus fremontii* and *Salix gooddingii,* native to southern Arizona. These species are quick to become water stressed when the groundwater table drops (Horton et al. 2001). By contrast, species from upland areas of the same region in Arizona, including *J. monosperma* and *Prosopis velutina* continue to transpire at water potentials that would kill riparian species (Pockman and Sperry 2000).

Evergreen species in seasonally dry environments are typically more cavitation-resistant, while deciduous species are less so (Jacobsen et al. 2007, Chen et al. 2009). Though evergreen species may have lower hydraulic conductivity compared to deciduous species under wet conditions, evergreens are able to keep functioning at water potentials that induce leaf senescence in deciduous species (Sobrado 1993, Brodribb et al. 2002). In a database comparison of 167 species, Maherali et al. (2004) found that evergreen conifers, in particular, have a higher cavitation resistance compared to drought and winter deciduous species.

Differences in rooting depth are correlated with changes in root xylem anatomy, presumably to optimize function. In regions with shallow groundwater levels, conduit diameters of trees generally increase with rooting depth, whether the tree is evergreen or deciduous, conifer or angiosperm (McElrone et al. 2004). Deep roots need wide conduits and higher conductivities, in part, to compensate for the increased distance the water has to travel (McElrone et al. 2004). But even where roots are far from groundwater, as is the case for the semi-shrub broomweed (*G. sarothrae*) growing in the Utah desert, deeper roots tend have higher axial and radial hydraulic conductivities than shallow lateral roots (Wan et al. 1994), presumably because deeper roots are specialized for taking up water when the degree of water saturation is relatively high. By contrast, shallow roots are

frequently exposed to dry conditions between rainfall events and require more cavitation-resistant xylem to maintain function.

Roots in rock

The preceding review of root adaptations and function within the context of an overall plant water use strategy has been based almost entirely on the study of roots in soil. However, there are many landforms where soil cover is quite shallow and roots explore fractured bedrock (Schwinning 2010). In contrast to a rooting medium composed of homogenous soil, where a developing root system can spread freely into all directions, the rooting medium of karst areas is characterized by highly constrained pathways for root growth, raising the question to what degree woody plants growing on such substrates can show genetic or phenotypic differences in root distribution and thus achieve hydrologic niche differentiation.

One landform where plants potentially rely more on the extraction of water from fissures in rock than on soil water is a karst system. Karst is a landscape formed by the chemical solution of bedrock (White 1988). Soluble carbonate rocks, e.g. limestone and dolomite, make up the majority of karst systems, where the slow movement of acidic water over time creates a drainage system through the rock composed of fractures, conduits, and caves (White et al. 1995). Karst systems with underlying aquifers are ecologically highly sensitive areas because of the high degree of connectivity between surface processes and the aquifer below (White et al. 1995, Wilcox et al. 2006, Bonacci et al. 2009). In the karst region of the eastern Edwards Plateau (Texas, USA), the top soil is typically thin (10-50 cm) and extremely rocky (Schwinning 2008). Beneath the soil lies a layer called "epikarst," a transition zone between soil and the bedrock that can

range in thickness from a few meters to 10-15 m (Klimchouk 2004). Water can easily

infiltrate into the top of the epikarst due to high porosity and permeability, however

permeability declines with depth and bedrock structures sometimes facilitate the

formation of perched water tables just above the unweathered bedrock stratum (White

2002, Klimchouk 2004). This deudritic structure of the epikarst is sometimes described

as an "upside-down root system," with many fine conduits on top that facilitate diffuse

infiltration and increasingly wider conduits at depth that consolidate flow from smaller

conduits and allow rapid turbulent flow.

The epikarst is an important temporary storage and transport system for

precipitation (White 2002, Klimchouk 2004). When rainfall saturates the soil above,

water begins to drain into the epikarst. Due to the spatial complexity of the epikarst,

water flow can be divided into several components ranging from a slow diffusion-like

flow through pores and fine fissures to rapid shaft flow through larger conduits

(Klimchouk 2004, Dasgupta et al. 2006). Eventually, water drains out of the epikarst and

into bedrock fractures and conduits that drain into the aquifer which could be hundreds of

meters below the surface (White 2002).

It is not easy to place plant roots within the complex system of water storage and

flow in the epikarst, but doing so is obviously critical to understanding both the

ecological adaptations of plants growing in karst regions and karst surface hydrology. A

limited number of recent studies have provided some insights into the location and

function of plant roots in epikarst.

First, it is not uncommon for roots of woody plants to grow into bedrock fissures.

This has been observed not just in karst, but also in other regions where soil cover is thin

and soil-stored water is not sufficient for survival (Cooper 1922, Cannon 1924, Matthes-Sears and Larson 1995, Jackson et al. 1999, Querejeta et al. 2006, Eggemeyer and Schwinning 2009). For example, woody plants in seasonally-dry environments with limited soil rely almost entirely on bedrock-stored water during the dry season (Sternberg et al. 1996, Hubbert et al. 2001, Querejeta et al. 2007, Schwinning 2008).

Rooting depths in fractured bedrock can be deeper than those in deep soils. According to one global comparison of available data, trees have a median rooting depth of 7.9 m in bedrock, compared to only 2.2 m in deep soils (Schenk 2008). Since roots follow water, the growing roots may follow the deep-reaching fractures. In addition, stem flow may funnel water towards roots, which facilitates further erosion and, in time, widens and deepens cracks and fissures allowing deeper rooting depths (Canadell et al. 1996, Klimchouk 2004).

On the Edwards Plateau, the rooting depths of trees have been examined at sites with shallow caves, where roots were observed in the cave floor and could be identified to the species level through DNA fingerprinting. This study revealed that *Quercus fusiformis* (escarpment live oak) had the deepest roots, i.e. it was found in caves as deep as 22 m below ground, while *Celtis laevigata* (net-leaf hackberry), *J. ashei* (Ashe juniper), *Ulmus crassifolia* (cedar elm) and *U. americana* (American elm) were found in caves no deeper than 9 m (Jackson et al. 1999). Another study showed, using stable isotope tracer techniques, that *J. ashei* trees accessed groundwater in perched water tables during the dry season (McCole and Stern 2007).

Even though roots are capable of growing deep into bedrock, an increasing number of studies suggest that this is rather the exception than the rule. Querejeta et al.

(2007) conducted excavations in the karst of the Yucatan peninsula (Mexico) and found that tree roots were horizontally growing in high density in a thin layer of soil and in the soil pockets of the rocks but dramatically decreased in abundance with increased depth in the weathered limestone. No roots were observed below 2 m depth, even though the water table was less than 2 m further below at some places. Studies conducted on the Edwards Plateau also found no evidence that plants used a deep, persistent water source (Schwinning 2008, Heilman et al. 2009), perhaps because perched water tables were not present at these sites, or were too deep, or separated from the root zone through impenetrable rock layers. This suggests that root development through weathered bedrock depends critically on the local bedrock structure, particularly the width, frequency and depth of fractures, fissures and bedding planes. In addition, it is possible that the relatively high porosity of highly weathered bedrock in the Edwards Plateau makes the exploration of deep fissures unnecessary. Epikarst porosity can be anywhere between 1% and 10% (Klimchouk 2004), which at the high end is on par with the porosity of sand. One study found Edwards limestone from the Edwards Limestone Trend in South Texas had an average porosity of 4 to 6% (Misak et al. 1978).

Differentiation of plant root systems in bedrock matrix

I started this chapter by discussing species differentiation of rooting depth in relation to the overall water use strategy of a species, and I will close it by discussing the evidence that this remains an important component of species differentiation for plants growing on bedrock.

One reason why species may have differential ability to grow through bedrock is related to root anatomical differences. A study from the forests of southwestern Oregon showed that not all species are equally well adapted to extract water from narrow fissures (Zwieniecki and Newton 1995). The narrowest fissures were occupied by species able to flatten the root cortex, which included two angiosperms but excluded a gymnosperm. This limitation may suggest that conifers are not deep rooted in karst regions, because fissure widths often decline with depth.

Differences in the depth of water uptake can be assessed by stable isotope methods (Ehleringer et al. 2000), but this method relies on sampling reference water from the vertical profile and comparing it to stem water isotope ratios. In bedrock, reference water is very difficult to obtain and requires destructive trenching, as was done by Querejeta et al. (2006) to obtain estimates of actual rooting depths.

When this method is unavailable, relative differences in rooting depth can still be inferred from differences in the evaporative enrichment of stem water (Jessup et al. 2003). In addition, stem water can be compared with water draining out of the epikarst in cave drips and when ground water surfaces in springs. For example, McCole and Stern (2007) inferred that *J. ashei* located at the Honey Creek State Natural Area on the Edwards Plateau used a perched water table in the dry summer by comparing its stem water isotope ratio to that of a nearby spring, but *J. ashei* used soil water (which could be directly sampled) during the wet cool months. Schwinning (2008) on the other hand found *J. ashei* and *Q. fusiformis* growing on the Edwards Plateau to take up only evaporatively enriched water, unlike water flowing from a nearby spring but less enriched than water extracted from herbaceous understory species, suggesting a rooting

depth deeper than the soil but shallower than the water table. Eggemeyer and Schwinning (2009), in a study on the Edwards Plateau, found *Prosopis glandulosa*'s rooting depth (inferred from stem water stable isotopes) increased with tree size, suggesting that it takes many years for a tree to grow roots deep into weathered bedrock of the epikarst.

In closing, there are many uncertainties concerning root development and differentiation in karst terrain. Genetic disposition for deeper roots may exist, for example, in *Q. fusiformis* or *P. glandulosa*, but may not be expressed on all karst surfaces. Some karst terrains appear to permit species differentiation in rooting depth and water source, and others do not. In this study, I investigated the water sources of three co-dominant tree species on a site on the Edwards Plateau by asking the following questions: Do the species take up water from isotopically different water sources in the soil/epikarst system? Can their water sources be matched with known water sources, including precipitation and cave drips? Does their water consumption differ in response to drought or precipitation?

CHAPTER II: VEGETATION AND SITE CHARACTERISTICS OF THE
FIELD SITE

Summary

The study site was located in central Texas (29º51´34´´N, 97 º 59´45´´W) on 5 acres of private property on the eastern Edwards Plateau within the city limits of San Marcos. The subdivision largely maintained its natural species composition associated with mixed woodland and grassland patches but has been thinned of some trees and understory for accessibility. The soil is about 30 cm thick and rocky. Below, the epikarst is derived from Edwards limestone. The site features a cave entrance leading to cave system at a depth of 5 – 10 m below ground.

The climate is semi-arid to humid sub-tropical (Dixon 2000). The mean August maximum for San Marcos is 35º C and the mean January minimum is 4º C. The average yearly precipitation for San Marcos is 86.4 cm (San Marcos Airport).

Vegetation density, vegetation cover and ground cover were measured by belt transects encompassing a 27 m x 30 m area that was located just above a shallow cave. Species and cover type were recorded along with plant height, area covered and status (alive, removed or standing dead). The most abundant species were, in the order of abundance, *Ulmus crassifolia* (cedar elm), *Quercus fusiformis* (live oak) and *Juniperus ashei* (Ashe juniper), which together accounted for 83.8 % of all stems with diameter >

2.5 cm and 88.3% of the vegetation cover. Ground cover was dominated by litter (92.9%).

Methods

Vegetation density along with ground cover and vegetation cover were measured in May 2009. Fifteen 2 m x 27 m belt transects were set up side by side to fully cover the experimental area, which is located over a shallow cave (5-10 m deep) that had been mapped at the site. Along the belt transects, all woody plants with $\geq$ 2.5 cm basal stem diameter were counted, recorded by position along the main axis of the transect, and characterized by status (live, removed or standing dead), species identity and basal diameters. Stem of woody plants $<$ 2.5 cm in diameter were counted in each 2 m wide x 50 cm long increments along the belt transect.

Cover was estimated by the line intercept method, using the long edge of the 15 belt transects (16 total). In this technique, start and end points of ground and vegetation cover type overlap with the transect line are recorded, ignoring intersect lengths of $<$ 5 cm (Bonham 1989). Woody vegetation cover was characterized by plant species (or as standing woody debris if dead) and herbaceous vegetation cover by type (sedge, grass, forb, cacti). Height of all cover classes was estimated to the nearest 10 cm.

Ground cover was characterized as bedrock, rock, woody debris or litter. Ground cover was considered "bedrock" if it had the appearance of a large unbroken rock outcrop, while "rock" consisted of cover dominated by rock fragments. I considered any dead or detached section of a woody plant over 2.5 cm diameter "woody debris."

The original composition of the forest before thinning was estimated by counting stumps and measuring their diameters.

Results/Discussion

The following woody plant species were found at the study site: *U. crassifolia* Nutt., *Q. fusiformis* Small, *J. ashei* J. Buchholz, *Diospyros texana* Scheele (Mexican persimmon), *Celtis reticulata* Torr. (netleaf hackberry) and *Berberis trifoliolata* Moric. (agarita). There were a total of 2281 woody plants in the census area, 173 of them adults (Tables 2.1 & 2.2). The total density of trees above 2.5 cm diameter was 2136 stems ha^{-1} and total canopy cover was 92% (Table 2.3). The total density of seedlings was 26025 seedlings ha^{-1}. Of the seedlings present, oak was most abundant amounting to with 57.2% of all seedlings, followed by juniper and elm.

The median diameter for each study species was as follows: 20.7 cm for oak, 17.7 cm for juniper, and 10.2 cm for elm. For the other woody species, the median diameter was 28 cm for agarita (measuring diameter of entire plant due to being multi-stem), 6.7 cm for Mexican persimmon and 9.9 cm for net-leaf hackberry. All unknown woody species were less than 2.5 cm in diameter.

Over 92% of the ground was covered by litter which mainly consisted of leaves and small twigs (Table 2.4).

In forest surveys completed in 1980 in Bandera County, 80 mi west of my study site, juniper had a density of 668 plants per hectare in an evergreen forest while oak and persimmon had a density of 39 and 207 plants per hectare, respectively (Van Auken et al. 1981). The site had a total of 970 plants ha^{-1}. Another study (Van Auken et al. 1979),

surveying a dry upland community in the eastern adjacent county of the previous study, found juniper to have a density of 1459 plants per hectare, oak at 632 ha^{-1}, persimmon at 702 ha^{-1}, agarita at 132 ha^{-1} and elm at a density of 104 plants per hectare. The total density was 3605 plants ha^{-1}. Both of these studies included only plants with a diameter over 1 cm. Total tree density at my study site fell about midway between these two sites, however, juniper was not the most abundant species. Instead, cedar elm had the highest density of the woody species present. Although juniper had been selectively removed at my study site, reducing juniper density by about 30%, based on counting the stumps of removed trees, even adding these juniper trees back into the total stem density made juniper only the second-most abundant tree species at the site, with 528 ha^{-1}.

Table 2.1. Density of stems > 2.5 cm diameter.

Name	Adult density (ha⁻¹)	Adult density (%)
Cedar elm	1000	47
Live oak	420	20
Ashe juniper	370	17
Mex. persimmon	284	13
Netleaf hackberry	49	2
Agarita	12	0.6
TOTAL	**2136**	**100**

Table 2.2. Density of stems < 2.5 cm diameter.

Species	Seedling density (ha⁻¹)	Seedling density (%)
Live oak	14877	57
Ashe juniper	4889	19
Cedar elm	4309	17
Mex. persimmon	901	3
Agarita	531	2
Unk woody sp	333	1
Netleaf hackberry	185	0.7
TOTAL	**26025**	**100**

Table 2.3. Woody and herbaceous species cover (%).

Species	Cover (%)
Woody species:	
Cedar elm	37
Live oak	30
Ashe juniper	22
Mex. persimmon	5
Netleaf hackberry	2
Standing woody debris	1.5
Agarita	0.09
Unknown woody species	0.01
Herbaceous species:	
Forb	0.8
Cacti	0.05
Sedge	0.6
Grass	0.6

Table 2.4. Percentage of each ground cover class at the field site.

Cover Class	Ground cover (%)
Litter	92.90
Rock	3.02
Woody debris	2.10
Bedrock	1.39
Soil	0.59

CHAPTER III: WATER SOURCES OF THREE COEXISTING TREE SPECIES ROOTED IN FRACTURED BEDROCK DURING AN EXTREME DROUGHT

Abstract

Woody plant species that exhibit differences in root distribution are able to partition available water sources. This happens quite commonly in regions with deep soils, but are species still able to develop differences in root distribution when rooted in fractured bedrock? I examined this question by comparing three tree species, cedar elm (*Ulmus crassifolia*), a winter-deciduous broadleaf, live oak (*Quercus fusiformis*), an evergreen oak, and Ashe juniper (*Juniperus ashei*), an evergreen conifer, growing in a mixed stand on a site with shallow soil over fractured bedrock on the eastern Edwards Plateau, Texas, USA. For one growing season, which included a severe summer drought, I recorded monthly variation in predawn water potentials and the stable isotope ratios of stem water. I also continuously measured sap flow velocities. Minimum predawn water potentials differed between the species, reaching -8 MPa for both juniper and elm, and -5 MPa in oak. As the summer drought developed, sap flow velocities of the three species declined synchronously and stem water isotope ratios increased, reflecting the evaporative enrichment of a shared, diminishing water source. Thus, maximal rooting depths and access to stored water appeared to be similarly constrained across the three species. However, species exhibited differences in drought tolerance and response: oak appeared to hydraulically disconnect from water sources at water potentials of -4 to -5 MPa, at

which point stem hydraulic conductivity was reduced by 75%. Both elm and juniper continued to extract water, but this was more detrimental to elm, which approached 90% loss of stem hydraulic conductivity and shed leaves by the end of August, instead of October in wet years. Juniper had the smallest loss of stem hydraulic conductivity (15-30%). These differences in drought response in species similarly constrained by storage capacity for water may suggest differences in species vulnerability to drought intensity and duration that may cause the eventual shift of species composition on the Edwards Plateau in a climate regime with a more frequent occurrence of extended or intense drought.

Introduction

Plant species typically differentiate in the use of limiting shared resources. This is usually interpreted as having the effect of reducing competitive interactions and facilitating stable coexistence (Packham et al. 1992, Chesson 2000). In climate zones where water is limiting at least during part of the year, one typically sees a wide range of water use strategies with species diversifying in when, where, and how much water is taken up (Walter 1971, Burgess 1995, Casper and Jackson 1997, Meinzer et al. 1999, Williams and Ehleringer 2000).

The potential for niche differentiation through differences in root distribution seems nearly universal, and has indeed been demonstrated from the moist tropics (Lopez et al. 2005) to hyper-arid deserts (Schultze et al. 1996, 1998). The classic niche contrast in rooting depth is between shallow-rooted herbaceous species and woody species whose root systems, while not always truly "deep," typically exceed the rooting depth of

herbaceous species (Walter 1971). However, differences in maximum and median

rooting depth are also common among woody plant species and have been linked to other

aspects of their water use strategy, e.g. drought tolerance and deciduousness, which

together work as an integrated suite of adaptive traits (Smith et al. 1997, Schwinning and

Ehleringer 2001, McDowell et al. 2008), although these linkages are not universal

(Schenk and Jackson 2002a).

In the development of the physiological ecology of plants, little or no

consideration has been given to constraints that could limit the expression of hydrologic

niche differentiation, other than rainfall amount itself. Thus, the almost unanimous

assumption has been that rainfall limits infiltration depth, which in turn limits maximal

rooting depth (Schenk and Jackson 2002b). By contrast, there are many types of

environments where vertical root development is limited by hard layers that are

impassible for roots, or nearly so. These include bedrock (Jones and Graham 1993) and

caliche (Shreve and Mallery 1933, Duniway et al. 2007). While these hard layers, when

they are close to the surface, often contain fractures wide enough for root proliferation,

they nevertheless represent a physically highly constraining rooting medium (Schwinning

2010). It is unclear whether species can still express differences in root distribution in

such media. Does the distribution and accessibility of cracks and fissures force

limitations on the shape and depth of root systems, and if so, what consequences might

this have on water use and drought response?

In this study, I observed for one growing season the water use of three co-

dominant tree species growing in mixture on a site with a shallow soil depth of 30 cm

underlain by fractured and karstified limestone bedrock. The site was located on the

eastern edge of the Edwards Plateau in central Texas, USA. The co-dominance of these species would suggest gross differences in resource use to reduce competitive interactions, including competition for water which is episodically limiting in this ecosystem (Casper and Jackson 1997, Chesson et al. 2004). Phenological differences between these species suggest differences in peak demand for resources. Cedar elm is winter deciduous, suggesting a peak demand for water in spring and early summer after leaves first emerge. Further, Ashe juniper flowers and sets seeds in late winter, while live oak completes seed production in late summer, suggesting a peak resource demand for juniper in winter, and for oak in summer. Species may also differ in drought responses: cedar elm is considered moderately drought tolerant (Wrede 2005) and is frequently associated with riparian zones throughout Texas (Van Auken et al. 1979, Lonard and Judd 2002, Bush et al. 2006) and cedar brakes. Ashe juniper is highly drought-tolerant with one of the highest known resistances to xylem embolism (Fonteyn et al. 1985, Willson and Jackson 2006, Willson et al. 2008), while live oak is much less so and responds to severe drought by shedding leaves.

Differences in drought tolerance and seasons of peak resource demand are normally complemented by differences in rooting depth (Davis and Mooney 1986, Schenk and Jackson 2002a). For example, one would expect oak to be deep-rooted in order to access a more stable water source to limit water stress during its reproductive period, while juniper could remain comparatively shallow-rooted since its reproductive cycle is complete by summer and its exceptional drought tolerance protects from drought damage. An earlier study indeed identified live oak as being the most deep-rooted tree species found on the Edwards Plateau (Jackson et al. 1999). Maximal rooting depths of

several tree species were examined at sites with shallow caves, where roots in caves were identified to species through DNA fingerprinting. Only the roots of live oak were found in caves as deep as 22 m, while no roots of juniper and elm were found in caves deeper than 9 m.

My study site was also located on the eastern edge of the Edwards Plateau in central Texas, and also featured a cave, but no roots were found protruding from the cave walls even though the cave was comparatively shallow at 5-10 m. This suggests a more constraining geology than that at Jackson et al.'s (1999) site.

In both Jackson et al.'s (1999) and the present study, tree roots were located in a transition zone between the soil and the unweathered bedrock at depth that is called "epikarst" (Klimchouk 2004). Epikarst has some predictable structural characteristics due to the common process of its formation by solutional weathering. At the top, the epikarst is more soil-like, water transport is diffuse and the epikarst has high porosity and permeability (Bonacci et al. 2007). However, flow paths become increasingly consolidated with depth, such that diffuse infiltration at the top of the epikarst is gradually replaced by shaft flow towards the bottom (Aquilina et al. 2006). This structure suggests that plant roots, while being able to easily penetrate into the highly weathered top of the epikarst, are soon obstructed from going deeper due to an increasing frequency of large, solid blocks of bedrock and a decreasing frequency of cracks in the rock.

Questions of rooting depth and water source are a sensitive matter in karst regions because of the potential for trees to consume significant amounts of water that would otherwise recharge the karst aquifer. This is especially true in the Edwards

Plateau region of central Texas where karst aquifers provide freshwater to two million

people in the Austin-San Antonio corridor. Some believe that landscape transformation

from open grassland to woodland drastically reduced recharge rates by replacing the

predominantly shallow root systems of grasses with the deeper root systems of trees

(Tennesen 2008). Others suspect that the consequences, particularly of Ashe juniper

encroachment, are minor because of the shallow-rootedness of this species (Heilman et

al. 2009). Thus, by characterizing the water use and water sources of three dominant tree

species of the Edwards Plateau, my study addresses not only a question of academic

interest, but one with potential management implications.

The goal of the present study was 1) to determine whether three species, whose

differences in ecophysiological strategy and phenology would normally suggest

differences in rooting depth, are able to establish such differences in epikarst, and if not,

2) to examine how this lack of differentiation affects their responses to seasonal water

deficits. The water status of the three study species were tracked by taking monthly

measurements of predawn water potentials. The relative impact of water deficit on

whole-plant water use was determined by continuous measurement of sap velocity, and

plant water sources were characterized by analysis of stable isotope composition of stem

water. The effect of the drought on stem hydraulic conductivity was measured at the end

of the growing season. The study took place during a year of record drought in central

Texas, which enabled us to follow the uninterrupted depletion of ecosystem water stores

between June and August, 2009.

Methods

Study Site and Species

The study site was located in central Texas (29º51´34´´N, 97 º 59´45´´W) on 5 acres of

private property on the eastern Edwards Plateau within the city limits of San Marcos.

The subdivision largely maintained its natural species composition associated with mixed

woodland and grassland patches but had been thinned of some trees and understory for

accessibility. The soil was about 30 cm thick and rocky. Below, the epikarst was derived

from Edwards limestone. The site featured a cave entrance leading to cave system at a

depth of 5 – 10 m below ground.

The climate is semi-arid to humid sub-tropical (Dixon 2000). The mean August

maximum for San Marcos is 35º C and the mean January minimum is 4º C. The average

yearly precipitation for San Marcos is 86.4 cm (San Marcos Airport).

Dominant tree and shrub species at the site, in the order of their frequency, were:

Ulmus crassifolia Nutt. (cedar elm), *Quercus fusiformis* Small (escarpment live oak),

Juniperus ashei Buchholz (Ashe juniper), *Diospyros texana* Scheele (Mexican

persimmon), *Celtis laevigata* var. *reticulata* (Torr.) L. Benson (netleaf hackberry)*,* and

Berberis trifoliolata (agarita), all representative of the oak/juniper woodlands that are

widely distributed throughout the Edwards Plateau (Van Auken 1979, Wills 2005).

For this study, I chose the three most common tree species at the site; elm, oak

and juniper, which together accounted for 84% of adult woody plant stem density. The

density of juniper was comparatively low at this site since it had been selectively thinned.

Ashe juniper is normally the most common component of woodlands in this region, as it

has encroached grasslands and savannas over the past 150 years, probably as a consequence of fire suppression and grazing (Van Auken 2000).

Experimental Design

The study was conducted from February to December, 2009. Six trees of each study species were randomly selected from an area of approximately 800 m^2 directly over the cave system. All trees were mature and healthy, over 3 m tall and with diameters between 16.6 and 35.8 cm for oak, 14.3 and 33.8 cm for elm, and 16.7 and 44.9 cm for juniper.

Granier sap flow sensors (Granier 1987, Phillips 2002) were installed and tested on all 18 trees by May 3, 2009. Sensors were installed at breast height on the north facing side of the tree trunks. Sensor leads were connected to an AM 16/32B relay multiplexer controlled by a CR1000 data-logger (both Campbell Scientific, Logan, UT, USA). Data were collected at 60 second intervals, averaged over 15 minutes and logged. Datalogger, multiplexer and the Granier sensors were powered by three 125 W solar panels. After September 10, at the beginning of a rain-intensive period, the system experienced intermittent power outages, which made the calculation of sap flow values impossible.

Soil moisture at 25 cm depth was measured with four EC-5 sensors (Decagon Devices Inc, Pullman, WA). Measurements were taken every 60 s, averaged over 15 min intervals and logged along with the Granier sensor readings. Due to malfunction, I lost data from July 6th to August 5th, when all sensors were replaced and also after September 10th due to power outages. Starting November 23rd, I report only the data segments that

could be salvaged, which representing soil moisture snapshots rather than daily average values.

Predawn xylem water potentials (Ψ_{pre}) were taken monthly on all 18 experimental trees using a Scholander pressure bomb (Model 1000 Pressure Chamber Instrument, PMS Instruments, Albany, OR, USA). Since elm is winter-deciduous, samples were only taken when trees were in foliage (April-November). Only four elm trees had leaves in November. In August, three elm trees had Ψ_{pre} values that exceeded residual tank pressure (>8 MPa) and were not used in statistical analysis. In September, two oak trees had only brown leaves and were not measured. One of the trees did not recover after the onset of rain and was left out of the next two months measurement for Ψ_{pre}.

Stem samples for stable isotope analysis of stem water were collected between 9 and 11 am on the same days that Ψ_{pre} was measured, again omitting trees without green leaves. Samples were not collected in October due to time constraints. I followed the stem collection protocol described in Schwinning (2008). Three outliers, identified as having inconsistent $\delta^{18}O$ and δD isotope ratios, were removed from analysis.

Weather Data and in-cave measurements

A weather station installed on site on January 5, 2009, recorded rainfall, wind speed and direction, solar radiation, temperature and relative humidity (Onset Computer Corp., Bourne, MA, USA). Measurements were logged at 10 minute intervals.

Precipitation samples and cave drips were collected continuously, stored under exclusion of evaporation, and sampled periodically (typically monthly). In addition, drip rates from speleothems were determined by collecting drips on a tarp and routing the

water to a tipping bucket rain gauge connected to an Onset Computer Micro-station data logger (Onset Computer Corp., Bourne, MA, USA).

Sap flow sensor design

Briefly, sap flow sensors consisted of two copper-constantan thermocouples each mounted inside an 11 mm long, 19 gauge stainless steel needle shaft. About midway along the needle, the thermocouple connection was exposed through a cut slit. One of the probes, called the "heated probe" was wrapped in a tight coil of 0.0125 cm diameter constantan wire to provide a heat source when an electric current was applied. This probe was inserted into the sapwood of trees (after removing bark and phloem layers) inside an aluminum sleeve to promote heat dissipation. The other "reference probe" was inserted in the same position 10 cm below the heated probe but without the aluminum sleeve. To minimize temperature fluctuations, tree trunks and sensors were double-wrapped in aluminum insulated heat shielding.

The heat coil of the heated sensor was supplied with a constant current between 110 and 130 mAmp, adjusted to the heat coil resistance to produce the same heat output across sensors. The thermocouples' leads were wired in series, so that the resulting mV signal was proportional to the temperature difference between the reference and heated thermocouples. This also eliminated the need for a reference temperature reading.

Sap flow Analysis

Sap flow velocity (u, m s^{-1}) was estimated from the temperature difference between the heated and the reference sensor. Granier (1985) developed an empirical relationship for this:

$$u = 119 * 10^{-6} K^{-1.231} \qquad \text{eq. 1}$$

where

$$K = \frac{\Delta T_M - \Delta T}{\Delta T} \qquad \text{eq. 2}$$

with ΔT_M as the temperature difference between the heated and reference probe when sap

flow is zero, and ΔT as the temperature difference for u > 0, i.e. at any other time. For

the trees in our study, ΔT values remained relatively flat between 1 and 5 am, and I

determined for each probe and day the maximal value measured within this time interval

to use as ΔT_M in eq. 2.

Stable Isotope Analysis

Stem samples were frozen until cryogenic vacuum extraction (Ehleringer et al. 2000).

Extracts were analyzed at Texas State University-San Marcos on a LGR DLT-100 (Los

Gatos Research, Inc., Mountain View, CA, USA) along with internal standards created

using the LGR certified standards and expressed in delta notation in parts per thousand

(‰) relative to the V-SMOW standard (Gonfiantini 1978):

$$\delta D \text{ or } \delta^{18}O = (\frac{R_{sample}}{R_{standard}} - 1) \bullet 1000 \qquad \text{eq. 3}$$

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

Native embolism and hydraulic conductivity

Native embolism was estimated after the peak of the summer drought, from late

September to early October by taking stem samples either from marked trees or nearby

trees of equivalent size, totaling 6-8 samples per species. I selected 15 cm long segments

of straight unbranched wood of uniform thickness (~0.5 cm in diameter). Branches were

initially cut 15 cm below the target segment to prevent embolism by cutting. Cut branches were enclosed in a dark moist container for transport to the lab. Before measurement, target segments were excised under water and recut with a sharp razor blade to remove crushed xylem elements.

Hydraulic conductivity was determined following the method described by Sperry et al. (1988). Briefly, stem segments were inserted into a hydraulic pathway of known pressure head running with ultra-clean water. Water was collected onto a micro-balance connected to a computer to calculate the rate of water flow. Pressure-driven flow rates were corrected by flow rates measured at zero pressure to correct for leakage. Hydraulic conductivities (k_h, MPa kg s^{-1} m^{-1}) were calculated from Darcy's Law (Tyree and Sperry 1988):

$$k_h = \frac{v}{\left(\dfrac{dP}{dl}\right)} \qquad \text{eq. 4}$$

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

The degree of native embolism was determined by comparing the hydraulic conductivity of a stem segment just after collection from the field with their hydraulic conductivity after "flushing." Stems were flushed with clean water for 20 – 30 min at high pressure (5-10 PSI) to drive air out of embolized vessels and tracheids thus restoring maximal hydraulic conductivity. The percent loss of conductivity was then expressed as:

$$Loss(\%) = (1 - \frac{G_{native}}{G_{max}}) * 100 \qquad \text{eq. 5}$$

The method worked well for oak and elm, but I had difficulties producing acceptable values for juniper, as hydraulic conductivities often decreased, rather than increases after flushing, a problem specific to conifers mentioned by Sperry and Tyree (1990). I did not solve this problem in 2009, and instead report on laboratory values I obtained in 2010 with stems pressurized to 8 – 9 MPa (reflecting minimum field values for 2009) using a pressure sleeve (PMS instruments, Albany, OR, USA). To obtain consistent measurements, I recut stems of juniper after flushing at both ends by about 0.5 cm, making sure to modify the calculation of maximal hydraulic conductivity based on the new stem length. I also included elm and oak in this analysis, using pressures of 4 – 5 MPa for oak and of 8 – 9 MPa for elm, to test if artificially induced embolism was comparable to the native embolism measured in 2009.

Data Analysis

To test for species and time effects in water potential and stable isotope data, I used repeated measures ANOVA for the months April through August, when I had maximal sample sizes for all three species. I also applied repeated measures ANOVA on sap flow data, averaged by tree over 7 day intervals between May 2nd and September 10th.

The sphericity assumption was usually rejected by Mauchly's test, and data transformation did not improve conformity to assumptions. I therefore report lower-bound p-values which do not depend on the sphericity assumption. In addition, I used univariate ANOVA for each month to individually test for species effects for both predawn water potentials and stable isotopes data. Fisher's LSD was used for all post hoc tests. For all statistical tests, I used SPSS (SPSS, Chicago, Il, USA).

Results

In 2009, central Texas experienced exceptional drought conditions according to the

Palmer Drought Index published at NOAA's National Climate Data Center

(http://www.ncdc.noaa.gov). The Edwards Plateau was in a moderate to extreme drought

from May 16th to September 12th. From June 1st to September 1st, cumulative

precipitation was 41.9 mm at the field site, which was 75% below the long-term average

for these months (Fig. 3.1a). Accordingly, soil moisture at the field site showed an

uninterrupted downward trend from May to August (Fig. 3.1b). Frequency and amount

of precipitation increased greatly in early September and conditions remained wet until

well into the following year.

Predawn water potentials (Ψ_{pre}) reflected this decline in water availability (Fig.

3.2), and repeated analysis of variance indicated highly significant effects of date, species

and date*species (Table 3.1). The year started out relatively wet with $\Psi_{pre} > -2$ MPa for

all species, but then dropped for three consecutive months from early June to late August,

and finally recovered due to heavy rain falls in September (Fig. 3.2). In February, oak

had a slightly but significantly lower Ψ_{pre} than juniper (p= 0.012). In April, there was a

significant species difference in Ψ_{pre} (p=0.044), specifically between juniper and elm

according to Fisher's LSD post hoc test. Starting in June, species differences in Ψ_{pre}

increased with oak maintaining consistently more negative Ψ_{pre} than juniper and elm.

Also in July, elm exhibited lower Ψ_{pre} than juniper (p=0.022). The most negative Ψ_{pre}

were measured on August 17th, when juniper had an average Ψ_{pre} of -8.0 MPa and oak of

-5.2 MPa. Three elm tree were also measured at -8 MPa, but the three other trees had

Ψ_{pre} values < -8 MPa, which could not measure on that day. Thus, the true average Ψ_{pre}

for elm was likely < -8 MPa.

Stem water stable isotope ratios

The stable isotope ratios of hydrogen and oxygen in stem water varied significantly over

the course of the measurement period, becoming more enriched between June and August

(Fig. 3.3). In a repeated analysis of variance, applied from April to August when samples

of all three species were available in sufficient numbers, species effects on δD were not

significant, but species effects on $δ^{18}$O were, including significant time*species

interactions and between subjects species effects (Table 3.1). Analyzing the data by

month indicated significant differences between juniper and oak in four months for δD

and in five months for $δ^{18}$O, between juniper and elm in two months for δD and in four

months for $δ^{18}$O and between oak and elm in one month for δD and in four months for

$δ^{18}$O (Table 3.2). In general, whenever significant species differences were found,

juniper had the least enriched stem water isotope ratios.

The sap extracted from trees all plotted under the local meteoric water line

(LMWL), suggesting evaporatively enriched water sources for plants. Further, the degree

of evaporative enrichment generally increased as Ψ_{pre} values declined (Fig. 3.4). Water

dripping out of the epikarst consistently plotted on or above the meteoric water line. The

location of points above the LMWL indicated that drip collections at the driest time of

the year probably originated in condensation of moist air on the collection tarp, rather

than by drip from speloethems. With the rain in September, sap water stable isotope

values were drawn back to the LMWL, indicating that the species took up the fresh input

of rain water. Drawing a regression line through the stem water stable isotope ratios from

the months of June to August to estimate the isotope ratios of the precipitation that originally recharged the soil/epikarst layers that plants were using at that time (Barnes and Turner 1998), indicated a relatively depleted and identical precipitation source for all three species.

Sap flow

Sap flow velocities of the three species declined steeply in the month of June and remained at very low levels until September, when the rain set in (Fig. 3.5). The long summer drought was interrupted only by two isolated rain events in July, each of nearly 10 mm, to which all three species clearly responded, increasing sap flow velocities for at least one day. Repeated measures analysis of variance on weekly averaged sap flow velocities indicated a significant effect of time, but no significant species effects, suggesting no difference in species transpiration response to drought or rain.

However, species experienced different rates of decline in relation to Ψ_{pre} (Fig. 3.6). For example the comparably low sap flow velocity of about 0.2 m d^{-1} were reached at -3.6 MPa for oak, at -6.2 MPa for elm and -8 MPa for juniper. Oak and elm reached this level of water stress in July, while juniper reached it in August.

Hydraulic conductivity

By the end of the 2009 summer drought, the hydraulic conductivity of stems was reduced the most in elm (89%), followed by oak (76%), and these values were similar to those obtained in the laboratory in 2010 (Table 3.3). The laboratory estimate for juniper indicated a 15-30% loss of hydraulic conductivity.

Discussion

The purpose of this study was to identify species differences in rooting depth and seasonal variation water use. In general, I found evidence for neither. Differences in maximal rooting depth would have been expressed in diverging stem water isotope ratios during the summer drought with deeper-rooted species switching to less enriched water sources stored at greater depth. Instead, I observed that the sap of all three species became more enriched from June to August (Fig. 3.3, Fig. 3.4). Concurrently, sap flow in all three species declined sharply in June and then stayed low until it began to rain again in early September (Fig. 3.5). Both observations together suggest that all three species shared the same water source, which became gradually depleted and enriched by evaporation. Thus, the shared water source was not only limited in abundance but close enough to the surface to lose water by evaporation.

All three species apparently maintained the capacity to respond to small rainfall events in mid-summer, which due to their small size could have wetted only the shallow soil layer and not entered the epikarst. Thus, all three species maintained functional uptake roots in the soil during the hottest and driest time of the year.

However, there were some species differences in stem water isotope ratios in spring and late summer potentially indicating a separation of water sources among species. In spring, juniper had more negative stem water isotope ratios than oak and elm, which could indicate comparatively deeper water sources. But this could also indicate that juniper is more actively obtaining precipitation in the upper layers indicating active shallow roots more so than elm and oak. Juniper would be more active during winter and

early spring due to being in its reproductive cycle. On February 9th, there was 9.63 mm of rainfall and isotope samples were collected on February 18th. This rainfall event could have been enough to invert the vertical profile so that a sample with more enriched isotope ratio would actually indicate a deeper water source. The $\delta^{18}O$ value for precipitation collected on February 12th has a value of -1.55, similar to that of juniper's average $\delta^{18}O$ of -1.84, but not of oak's average $\delta^{18}O$ of -0.425.

In July and August $\delta^{18}O$ values for oak were higher than for juniper (Fig. 3.3, Table 3.2). I do not think that this pattern was generated by a more shallow water source for oak, since oak had higher, not lower predawn water potentials at that time. Consistent with the concurrent very low sap velocities, I think that oak had ceased most water uptake at that time, isolating itself hydraulically from the soil and epikarst by shedding fine roots to maintain higher plant water potentials. However, since transpiration was not zero at the time, oak stem tissues would have become gradually enriched by residual evaporation from leaf surfaces and back-diffusion of enriched leaf into the xylem at night.

The same may have been true for elm, although the very negative Ψ_{pre} values observed in elm suggested that elm continued to take up water in the root zone, albeit at very low rates that may have been too slow to completely replace stem water, which may have become enriched at night, with soil water during the course of one day.

In September, just after rain, juniper had the most negative stem water isotope ratios, coming very close to the meteoric water line, while the isotope ratios of elm and oak remained higher. This might suggest that junipers were able to replace stem-stored water very quickly with the new input of rain water, while rain water mixed with stored stem water in oak and elm, suggesting that these species took up much less water. This

would be consistent with the observed severely reduced transport capacity for water in these two species (Table 3.3). By the end of the summer drought, oak and elm had lost an estimated 76% and 89%, respectively, of their stem hydraulic conductivity and presumably an even greater percentage of the root hydraulic conductivity, as roots tend to be more vulnerable to cavitation than stems (Sperry and Saliendra 1994, Sperry and Ikeda 1997).

Reduced transport capacity would have also been observable in sap flow rates, but unfortunately, the equipment for measuring sap flow velocities failed just when it began to rain again.

It is very uncommon to see *Quercus* species exceed -5.0 MPa in predawn water potentials (Fonteyn et al. 1985, Filella and Peñuelas 2003, David et al. 2007, Bendevis et al. 2010). In other locations, *Quercus* species often have a "dimorphic" root system, involving both a deep tap root and an extensive system of shallow lateral roots (Kurz-Besson et al. 2006, Duan et al. 2008). Thus, they are capable of "switching" water sources, for example, from shallow soil layers during the wet season to deep soil layers during the dry season. For most *Quercus* species, there is a wide range of ecological plasticity for depth of water uptake (Asbjornsen et al. 2008).

The oaks at my sites clearly could not express this plasticity and as a consequence, became severely water stressed over the course of summer. Past some point during the summer drought, they may have supported leaf transpiration through stem-stored water, more so than by water uptake from the root zone, but there are obviously limits to how long an oak tree can sustain gas exchange from stored water. Past this point, total leaf abscission is a last resort for this species. In August 2009, I observed three of

the six marked trees abscise leaves. However, with the return of rain in rain in September, all of the oak trees immediately put out new leaves.

This drought response is consistent with live oak acting as an "isohydric" species, i.e. a species that attempts to control tissue water potentials by regulating gas exchange rates (McDowell et al. 2008). Although oak allowed its water potential to become quite low, it remained surprisingly high compared to the other species, not because it had more water to take up, but because it must have isolated itself hydraulically from the increasingly water-depleted epikarst. According to theory, such species are less likely to die from catastrophic xylem failure than from carbon starvation, which might explain why oaks maintained leaves apparently beyond their capacity to take up water, and why they greened up immediately after rain.

By contrast, elm and juniper apparently continued to extract water from the increasingly depleted water source, forcing tissue water potentials to drop with the matrix potentials in the soil/epikarst system. This caused, in the case of elm, very high levels of stem xylem embolism by the end of the season, but much less embolism in juniper. Elm did not appear to safeguard against almost total hydraulic failure to the same extent that oaks did. Thus elm acted more like an "anisohydric" species, perhaps out of a need to maximize carbon gain while in foliage (Pockman and Sperry 2000). This could make elm more susceptible to death by hydraulic failure.

Juniper appeared least drought stressed, and, according to the stem water isotope ratio data and the low loss of hydraulic conductivity, was able to maintain water uptake throughout summer, and presumably could have persisted through an even longer, more intense drought. A study by Willson et al. (2008) indicated that the water potential

producing 50% loss in hydraulic conductivity for Ashe juniper is -9.4 MPa for roots and -13.1 MPa for stems. Although I observed some juniper mortality in other areas during the summer of 2009, no juniper at the study site died. Perhaps drought mortality in juniper for the exceptional drought conditions of 2009 requires an even more constraining root environment.

Climate models predict the occurrence of more severe drought, as well as longer lasting drought events by the middle of this century (IPCC 2007). Drought severity and drought length could have differential effects on tree species of the Edwards Plateau, based on the manner of their regulation of water status. According to McDowell et al. (2008), isohydric species such as live oak are more negatively impacted by long, moderate drought conditions, which drains them of carbon reserves, while anisohydric species such as juniper and elm, are endangered by short, severe droughts that could cause runaway cavitation.

On the Edwards Plateau, precipitation patterns interact strongly with local geology, in most places, decreasing the storage capacity for water. Where water storage is limited, water availability can decline very rapidly, as seen in the sharp decline of sap flow in June 2009. Steep, unbounded decline in soil/epikarst water potential would be more problematic for anisohydric species, especially if they lacked a mechanism for shedding transpiring surfaces, as may be the case for scaly-leafed juniper. However, as my data show, it would take summer droughts longer than 3 months to induce a 50% or more loss of hydraulic conductivity in Ashe juniper. However, isohydric species such as oak may come through long summer drought events relatively less harmed.

Increases in the occurrence of chronic drought conditions, as may be caused by several consecutive years with below-average rainfall, while observed to increase mortality in isohydric species in some regions (Breshears et al. 2009), may have relatively less effect in storage-limited ecosystems, where resident species are already adapted to chronic water limitation. Thus, it might take relatively greater reductions in average annual rainfall to exert significantly more stress and induce stand-level mortality in escarpment oak. Chronic, low level stress would be even less problematic for juniper.

The interaction of drought character (chronic or acute) with local geology and constraints on root system development is an interesting new perspective for climate science, but one that has to await better models of water depletion and recharge, before consequences for community composition can be made with sufficient confidence.

Table 3.1. Repeated measures ANOVA results for predawn water potentials (Ψ_{pre}), stem water stable isotope δD, stem water stable isotope δ^{18}O and sap flow velocity for within-subject effects of time and time by species interaction and between subject effects of species. F, degrees of freedom (df) and p values are shown. For Ψ_{pre}, n=6 for both juniper and oak and n=3 for elm. For δD and δ^{18}O, n=5 for oak, n=5 for juniper, and n=2 for elm. For sap flow velocity, n=6 for all three species.

	Ψ_{pre}			δD			δ^{18}O			Sap flow velocity		
	F	df	p	F	df	p	F	df	p	F	df	p
Within Subjects												
Time	692.695	1	<0.001	21.543	1	<0.001	53.937	1	<0.001	27.645	1	<0.001
Time*Species	12.782	2	<0.001	2.491	2	0.121	5.001	2	0.025	1.179	2	0.334
Between Subjects												
Species	67.259	2	<0.001	2.819	2	0.096	6.021	2	0.014	0.968	2	0.402

Table 3.2. Univariate ANOVA results for individual months for both δD and δ¹⁸O stem water stable isotope ratios. Fisher's LSD post hoc tests were performed for pair-wise comparisons if the p-value was equal or less than 0.05 and if data were available for all three species (i.e. April to September) Significant and marginally significant differences are bolded.

	δD					δ¹⁸O				
	F	p	Oak/juniper	Oak/elm	Elm/juniper	F	p	Oak/juniper	Oak/elm	Elm/juniper
February	54.106	**<0.001**				47.094	**<0.001**			
March	67.54	**<0.001**				2.744	0.129			
April	4.7	**0.026**	0.327	0.064	**0.009**	5.007	**0.022**	0.648	**0.026**	**0.01**
May	0.92	0.420				3.66	**0.051**	0.506	**0.02**	0.073
June	1.196	0.332				1.608	0.235			
July	2.794	0.093				6.473	**0.009**	**0.003**	0.162	**0.052**
August	4.1	**0.04**	**0.021**	**0.03**	0.855	7.123	**0.007**	**0.002**	**0.029**	0.193
September	25.705	**<0.001**	**<0.001**	0.429	**<0.001**	18.592	**<0.001**	**0.039**	**0.008**	**<0.001**
November	3.258	0.077				7.473	**0.009**	**0.003**	0.27	**0.032**
December	2.533	0.143				1.297	0.281			

Table 3.3. Mean (SE) embolism (%) for each species at native (fall 2009) and induced (fall 2010). Values reported at both the predawn maximum (-5MPa for oak, -8MPa for juniper and elm) and the predawn maximum plus 1 MPa.

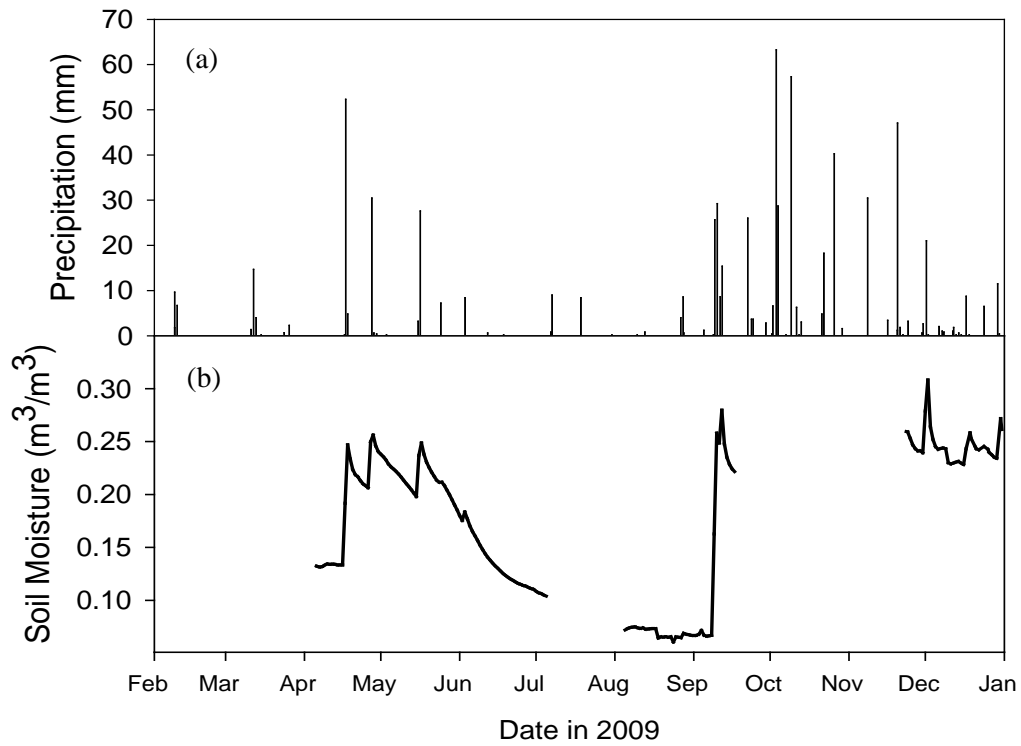| Species	Native embolism (%)	n	Induced embolism	n	Induced embolism +1MPa	n
Live oak	76 (9)	6	71 (19)	5	88 (9)	5
Ashe juniper			16 (12)	7	27 (12)	7
Cedar elm	89 (11)	6	36 (15)	6	55 (13)	6

Figure 3.1. (a) Precipitation (mm) and (b) average soil moisture (m^3/m^3) at 25 cm depth. Weather station recorded each rainfall event at field site, San Marcos, TX, USA. Data loss for soil moisture occurred from July 6th to August 6th and September 18th to November 23rd.
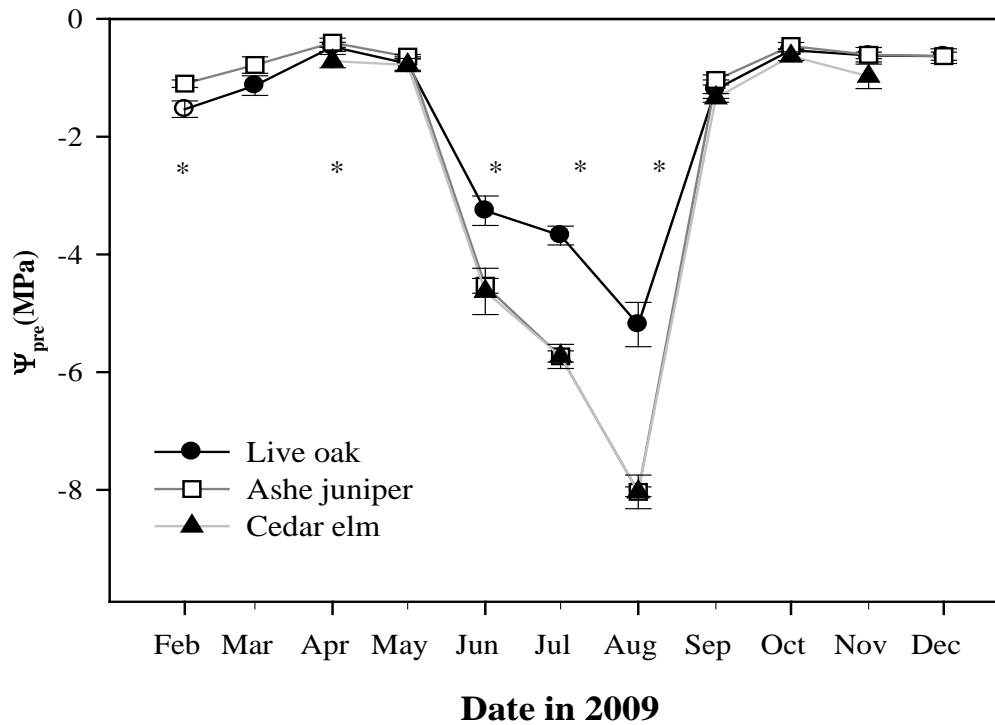
Figure 3.2. Average predawn water potential (Ψ_{pre}, MPa) from February to December 2009. Standard error bars are shown for each. Asterisks (*) show the dates that had a significant difference (p<0.05) between the species: February: between oak and juniper*;* April: between juniper and elm; June: between oak and elm and between oak and juniper; July and August: between oak and the other two species. For the August measurement only three elm trees entered into the calculation of the mean, while the three other trees had Ψ_{pre} < -8 MPa and could not be measured on that day.
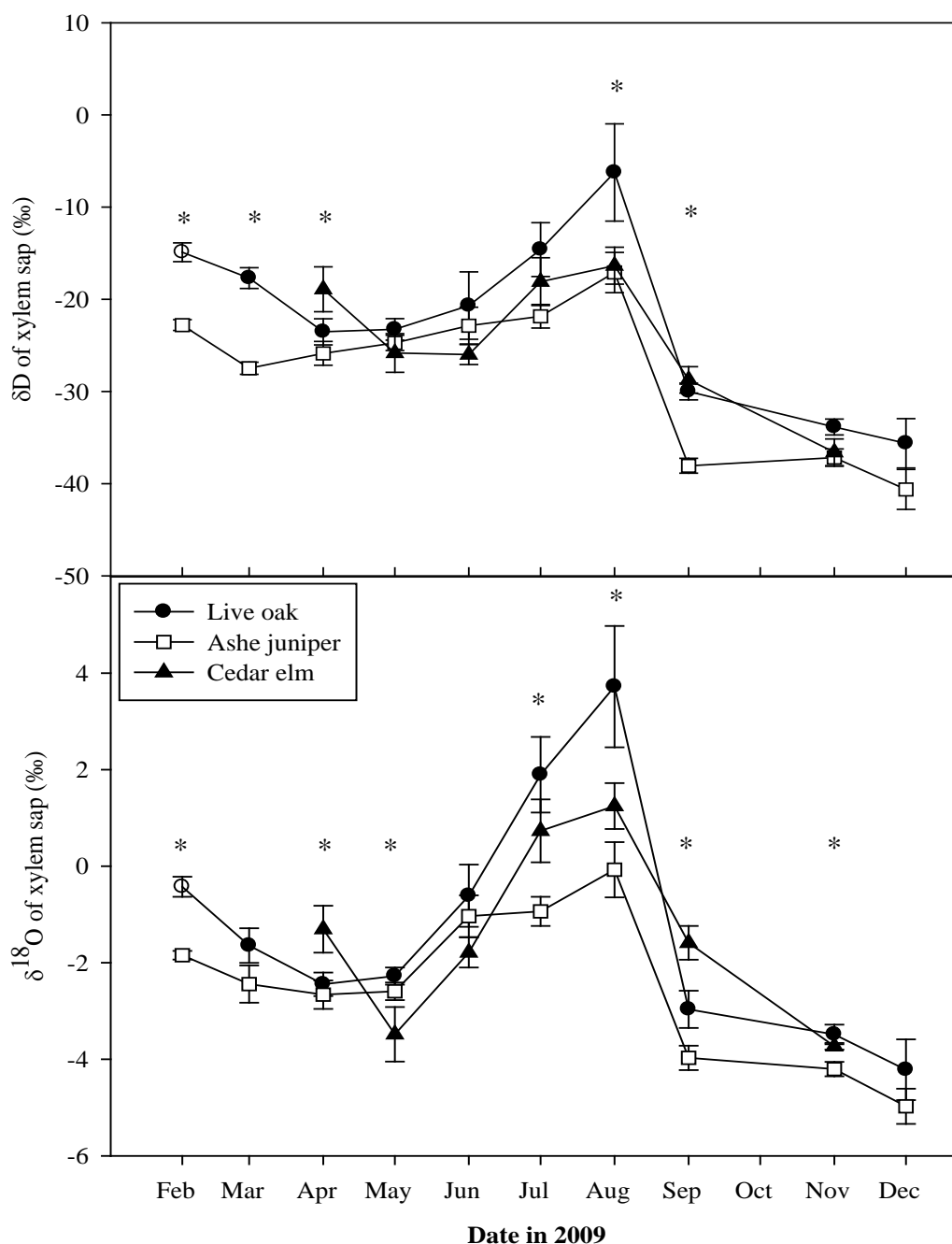
Figure 3.3. Average (a) δD and (b) δ^{18}O isotope ratios (‰) of xylem sap from February to December 2009. Standard error bars are shown for each. Asterisks (*) show the dates that had a significant difference (p<0.05) between the species: February δD and δ^{18}O: between oak and juniper; March δD: between oak and juniper; April δD and δ^{18}O: between juniper and elm and δ^{18}O: oak and elm; May δ^{18}O: oak and elm; July δ^{18}O: between juniper and oak and juniper and elm; August δD and δ^{18}O: between oak and the other two species; September δD and δ^{18}O: between juniper and the two other species and δ^{18}O: between oak and elm; November δ^{18}O: between juniper and the other two species.
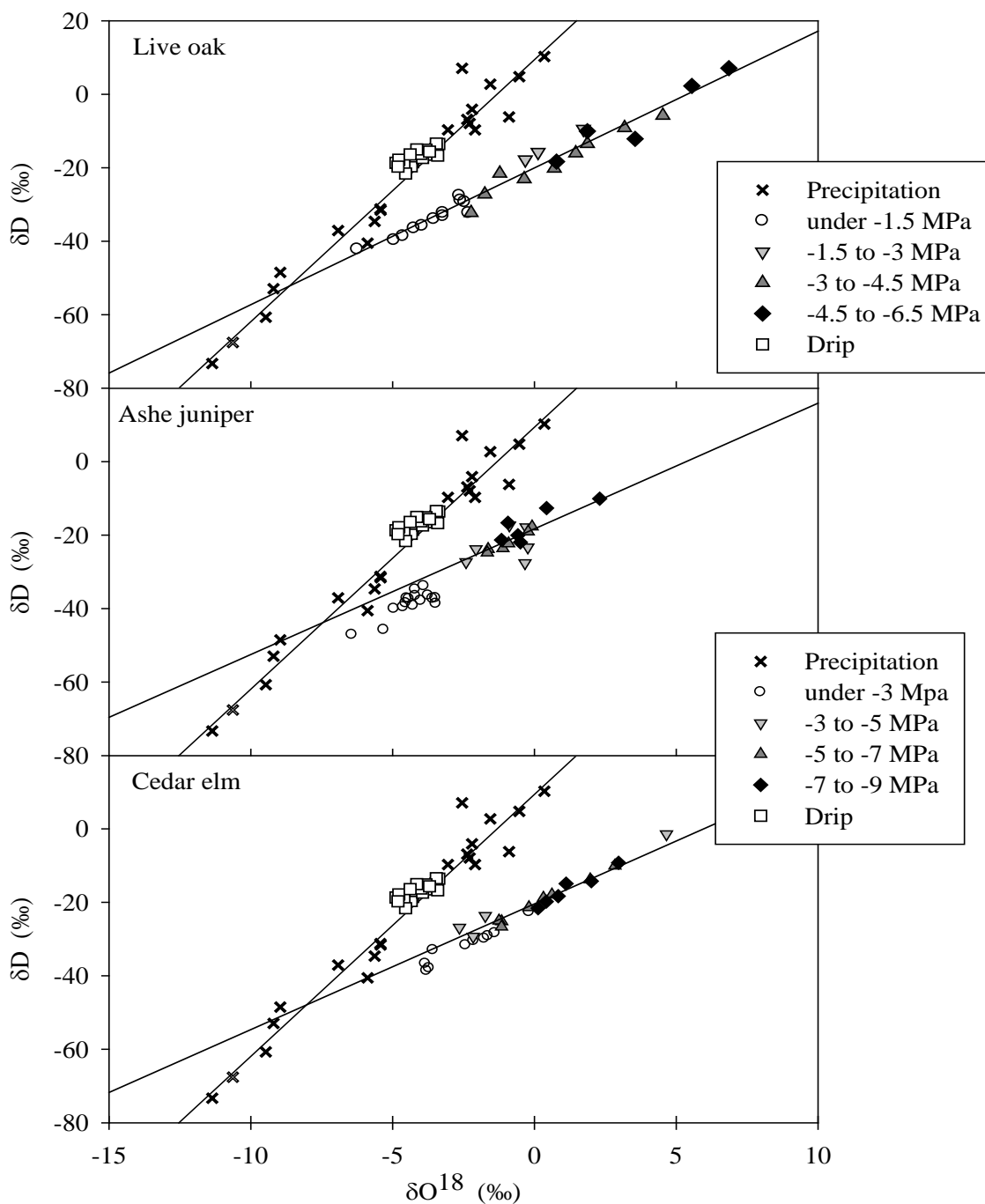
Figure 3.4. Individual isotope ratio of cave drip and each tree for live oak, Ashe juniper, cedar elm against local meteoric water line (LMWL) created from precipitation samples taken from the field site. Data are from June to September 2009 for the tree data and February to December for the precipitation and drip data. Symbol shading is characterized by the predawn water potential. Regression line intersecting the LMWL represents water source for the samples taken between June and August.
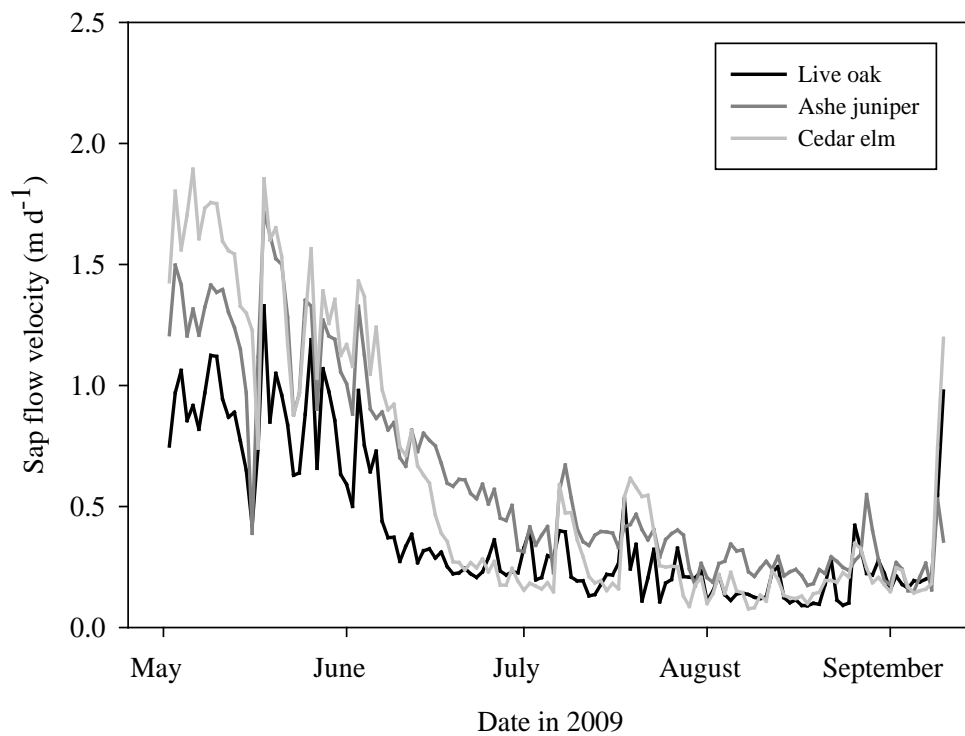
Figure 3.5. Average daily sap flow velocity (m d^{-1}) for each species from May to September 2009.
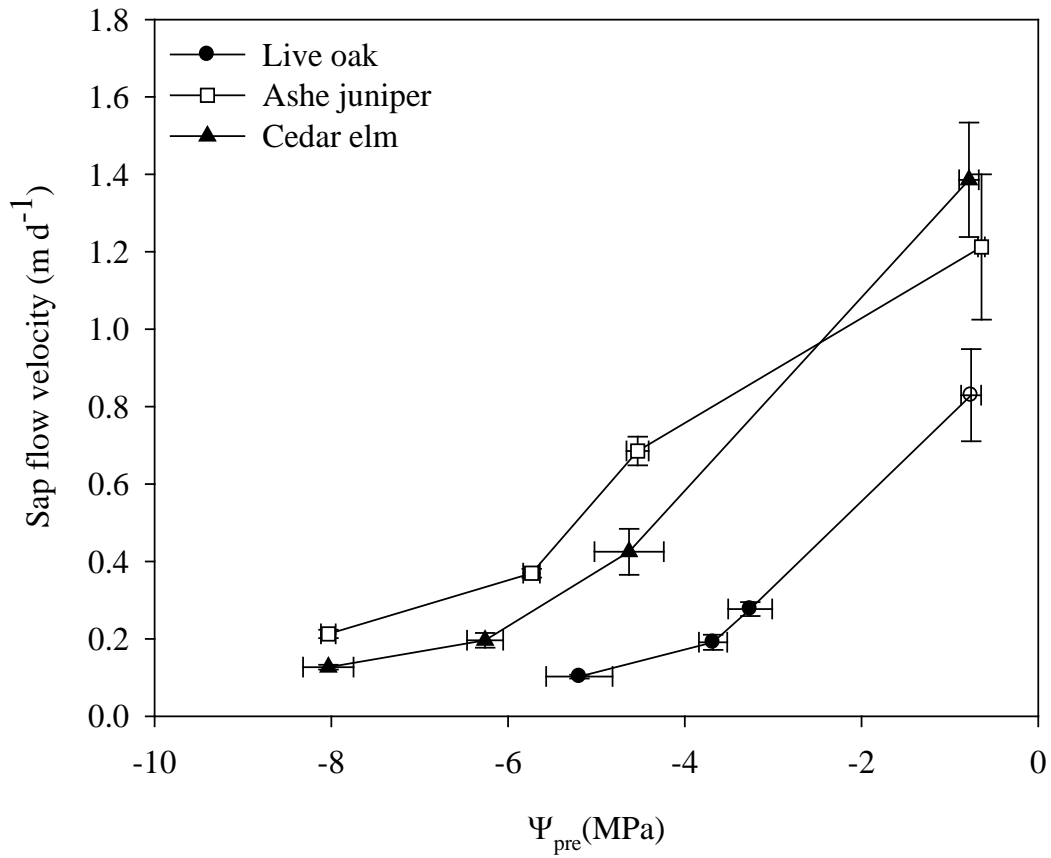
Figure 3.6. Sap flow velocity (m d^{-1}) as a function of predawn water potential (Ψ_{pre}, MPa) values for May, June, July and August 2009. Sap flow data were averaged from three days before and after the days that the Ψ_{pre} values were collected. The bidirectional error bars are based on standard errors of the mean.

LITERATURE CITED

Aquilina, L., B. Ladouche and N. Dorfliger. 2006. Water storage and transfer in the epikarst of karstic systems during high flow periods. *Journal of Hydrology*, 327: 472-485.

Asbjornsen, H., G. Shepherd, M. Helmers and G. Mora. 2008. Seasonal patterns in depth of water uptake under contrasting annual and perennial systems in the Corn Belt Region of the Midwestern U.S. *Plant Soil*, 308: 69-92.

Barnes C.J. and J.V. Turner. 1998. Isotopic exchange in soil water. In *Isotope Tracers in Catchment Hydrology*, Kendall C. and J.J. McDonnell (eds). Elsevier: Amsterdam; 165–202.

Bendevis, M.A., M. K. Owens, J.L. Heilman and K.J. McInnes. 2010. Carbon exchange and water loss from two evergreen trees in a semiarid woodland. *Ecohydrology*, 3: 107-115.

Bonacci, O., T. Pipan and D.C. Culver. 2009. A framework for karst ecohydrology. *Environmental Geology,* 56: 891-900.

Bonham, C.D. 1989. *Measurements for Terrestrial Vegetation.* John Wiley & Sons, Inc, NY, pp.108-119.

Breshears, D.D., O.B. Myers, C.W. Meyer, F. J. Barnes, C.B. Zou, C.D. Allen, N.G. McDowell and W.T. Pockman. 2009. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Frontiers for Ecology and the Environment,* 7: 185-189.

Brodribb, T.J., N.M. Holbrook and M.V. Gutierrez. 2002. Hydraulic and photosynthetic co-ordination in seasonally dry tropical forest trees. *Plant, Cell and Environment,* 25: 1435-1444.

Burgess, T.L. 1995. Desert Grassland, Mixed Shrub Savanna, Shrub steppe, or semidesert scrub? The dilemma of coexisting growth forms. In: *The Desert Grassland* (McClaran, M.P., Van Devender, T.R., eds). The University of Arizona Press, AZ, pp.31-67.

Bush, J.K., F.A. Richter and O.W. Van Auken. 2006. Two decades of vegetation change on terraces of a South Texas River. *Journal of the Torrey Botanical Society*, 133: 280-288.

Canadell, J., R.B. Jackson, J.R. Ehleringer, H.A. Mooney, O.E. Sala and E.D. Schulze. 1996. Rooting depth of vegetation types at the global scale. *Oecologia,* 108: 583-595.

Cannon, W.A. 1924. General and physiological features of the vegetation of the more arid portions of southern Africa, with motes on the climatic environment. *Carnegie Institute of Washington Publication,* 354: 159.

Casper, B.B. and R.B. Jackson. 1997. Plant competition underground. *Annual Review of Ecology and Systematics*, 28: 545-570.

Casper, B.B., H.J. Schenk and R.B. Jackson. 2003. Defining a plant's belowground zone of influence. *Ecology,* 84: 2313-2321.

Chen, J.-W., Q. Zhang, X.-S. Li and K.-F. Cao. 2009. Independence of stem and leaf hydraulic traits in six Euphorbiaceae tree species with contrasting leaf phenology. *Planta,* 230: 459-468.

Chesson, P. 2000. General theory of competitive coexistence in spatially – varying environments. *Theoretical Population Biology,* 58: 211-237.

Chesson, P., R.L.E. Gebauer, S. Schwinning, N. Huntly, K. Wiegand, M.S.K. Ernest, A. Sher, A. Novoplansky and J. F. Welzin. 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia*, 141: 236-253.

Collins, D.B.G. and R.L. Bras. 2007. Plant rooting strategies in water-limited ecosystems. *Water Resources Research,* 43: Art. No. W06407.

Cooper, W.S. 1922. The broad-sclerophyll vegetation of California. An ecological study of the chaparral and its related communities. *Carnegie Institute of Washington Publication,* 319: 124.

Dasgupta, S., B.P. Mohanty, J.M. Kohne. 2006. Impacts of juniper vegetation and karst geology on subsurface flow processes in the Edwards Plateau, Texas. *Vadose Zone Journal,* 5: 1076-1085.

David, T.S., M.O. Henriques, C. Kurz-Besson, J. Nunes, F. Valente, M. Vaz, J.S. Pereira, R. Siegwolf, M.M. Chaves, L.C. Gazarini and J.S. David. 2007. Water-use strategies in two co-occurring Mediterranean evergreen oaks: surviving the summer drought. *Tree Physiology*, 27: 793-803.

Davis, S.D. and H.A. Mooney. 1986. Water-use patterns of 4 co-occurring chaparral shrubs. *Oecologia,* 70: 172-177.

Dawson, T.E. and J.R. Ehleringer. 1991. Streamside trees that do not use stream water. *Nature,* 350: 335-337.

Dixon R. 2000. Climatology of the Freeman Ranch, Hays County, Texas, Freeman Ranch Publication Series No. 3-2000. Southwest Texas State University Press: San Marcos, Texas; 2–3.

Duan, D.-Y., H. Ouyang, M.-H. Song and Q.-W. Hu. 2008. Water sources of dominant species in three alpine ecosystems on the Tibetan Plateau, China. *Journal of Integrative Plant Biology,* 50: 257-264.

Duniway, M.C., J.E. Herrick and H.C. Monger. 2007. The high water-holding capacity of petrocalcic horizons. *Soil Science of America Journal*, 71: 812-819.

Eggemeyer, K.D., T. Awada, F.E. Harvey, D.A. Wedin, X. Zhou and C.W. Zanner. 2009. Seasonal changes in depth of water uptake for encroaching trees *Juniperus virginiana* and *Pinus ponderosa* and two dominant C-4 grasses in a semiarid grassland. *Tree Physiology,* 29: 157-169.

Eggemeyer, K.D. and S. Schwinning. 2009. Biography of woody encroachment: why is mesquite excluded from shallow soils? *Ecohydrology,* 2: 81-87.

Ehleringer, J.R., S.L. Phillips, W.S.F. Schuster and D.R. Sandquist. 1991. Differential utilization of summer rains by desert plants. *Oecologia,* 88: 430-434.

Ehleringer J.R., J. Roden, T.E. Dawson. 2000. Assessing ecosystem-level water relations through stable isotope ratio analyses. In Methods in Ecosystem Science, Sala O, Jackson R, Mooney HA, Howarth R (eds).Springer Verlag: New York; 181–198.

Filella, I. and J. Peñuelas. 2003. Partitioning of water and nitrogen in co-occurring Mediterranean woody shrub species of different evolutionary history. *Oecologia,* 137: 51-61.

Flanagan, L.B., J.R. Ehleringer and J.D. Marshall. 1992. Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland. *Plant Cell and Environment,* 15 (7): 831-836.

Fonteyn, P.J., T.M. McClean and R.E. Akridge. 1985. Xylem pressure potentials of three dominant trees of the Edwards Plateau of Texas. *The Southwestern Naturalist,* 30: 141-146.

Gardner, W.R. 1960. Soil water relations in arid and semi-arid conditions. In: *Plant-Water Relationships in Arid and Semi-Arid Conditions Reviews of Research* UNESCO, Switzerland. pp. 37-54

Gonfiantini R. 1978. Standards for stable isotope measurements in natural compounds. *Nature,* 271: 534–536.

Granier, A. 1985. A new method of sap flow measurements in tree stems. *Annales des Sciences Forestieres,* 42: 193-200.

Granier, A. 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiology,* 3: 309-320.

Hacke, U.G. and J.S. Sperry. 2001. Functional and ecological xylem anatomy. *Perspectives in Plant Ecology, Evolution and Systematics,* 4/2: 97-115.

Hacke, U.G., J.S. Sperry, W.T. Pockman, S.D. Davis and K.A. McColloh. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia,* 126: 457-461.

Heilman, J.L., K.J. McInnes, J.F. Kjelgaard, M.K. Owens and S. Schwinning. 2009. Energy balance and water use in a subtropical karst woodland. *Journal of Hydrology,* 373: 426-435.

Horton, J.L., T.E. Kolb and S.C. Hart. 2001. Physiological response to groundwater depth varies among species and with river flow regulation. *Ecological Applications,* 11: 1046-1059.

Hubbert, K.R., J.L. Beyers and R.C. Graham. 2001. Roles of weathered bedrock and soil in seasonal water relations of *Pinus jeffreyi* and *Arctostaphylos patula. Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestiere,* 31: 1947-1957.

IPCC (Intergovernmental Panel on Climate Change). 2007. Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the fourth assessment report of the Intergovernmental Panel on Climate Change. New York, NY: Cambridge University Press.

Jackson, P.C., F.C. Meinzer, M. Bustamante, G. Goldstein, A. Franco, P.W. Rundel, L. Caldas, E. Igler and F. Causin. 1999. Partitioning of soil water among tree species in a Brazilian Cerrado ecosystem. *Tree Physiology,* 19: 717-724.

Jackson, R.B., L.A. Moore, W.A. Hoffmann, W.T. Pockman and C.R. Linder. 1999. Ecosystem rooting depth determined with caves and DNA. *Proceedings of National Academy of Science of USA,* 96: 11387-11392.

Jacobsen, A.L., R.B. Pratt, S.D. Davis and F.W. Ewers. 2007. Cavitation resistance and seasonal hydraulics differ among three arid Californian plant communities. *Plant, Cell and Environment,* 30: 1599-1609.

Jessup, K.E., P.W. Barnes and T.W. Boutton. 2003. Vegetation dynamics in a Quercus-Juniperus savanna: An isotopic assessment. *Journal of Vegetation Science*, 14: 841-852.

Jones, D.P. and R.C. Graham. 1993. Water-holding characteristics of weathered granitic rock in chaparral and forest ecosystems. *Soil Science Society of America Journal,* 57: 256-261.

Klimchouk, A. 2004. Towards defining, delimiting and classifying epikarst: its origin, processes and variants of geomorphic evolution. *Speleogenesis and Evolution of Karst Aquifers,* 2: 1-12.

Kurz-Besson, C., D. Otieno, R. Lobo do Vale, R. Siegwolf, M. Schmidt, A. Herd, C. Nogueira, T. Soares David, J. Soares , J. Tenhunen, J. Santos Pereira and M. Chaves. 2006. Hydraulic lift in cork oak trees in a savannah-type Mediterranean ecosystem and its contribution to the local water balance. *Plant and Soil*, 282: 361-378.

Leffler, A.J. and M.M. Caldwell. 2005. Shifts in depth of water extraction and photosynthetic capacity inferred from stable isotope proxies across an ecotone of *Juniperus osteosperma* (Utah juniper) and *Artemisia tridentata* (big sagebrush). *Journal of Ecology*, 93: 783-793.

Lonard, R.I. and F.W. Judd. 2002. Riparian vegetation of the lower Rio Grande. *The Southwestern Naturalist*, 47: 420-432.

Lopez, O.R., T. A. Kursar, H. Cochard and M.T. Tyree. 2005. Interspecific variation in xylem vulnerability to cavitation among tropical tree and shrub species. *Tree Physiology*, 25: 1553-1562.

Maherali, H., W.T. Pockman and R.B. Jackson. 2004. Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology,* 85: 2184-2199.

Matthes-Sears, U. and D.W. Larson. 1995. Rooting characteristics of trees in rock - a study of *Thuja occidentalis* on cliff faces. *International Journal of Plant Sciences*, 156: 679-686.

McCole, A.A. and L.A. Stern. 2007. Seasonal water use patterns of *Juniperus ashei* on the Edwards Plateau, Texas, based on stable isotopes in water. *Journal of Hydrolog*y, 342: 238-248.

McDowell, N., W.T. Pockman, C.D. Allen, D.D. Breshears, N. Cobb, T. Kolb, J. Plaut, J. Sperry, A. West, D.G. Williams and E.A. Yepez. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist*, 178: 719-739.

McElrone, A.J., W.T. Pockman, J. Martinez-Vilalta and R.B. Jackson. 2004. Variation in xylem structure and function in stems and roots of trees to 20 m depth. *New Phytologist*, 163: 507-517.

Meinzer, F.C., J.L. Andrade, G. Goldstein, N.M. Holbrook, J. Cavelier and S.J. Wright. 1999. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia,* 121: 293-301.

Misak, M.D., R.D. Atteberry, J.J. Venditto and S.E. Fredrickson. Edwards Limestone completions improved by new stimulation technique [abstract]. In: SPE Southwest Texas Regional Meeting; 1978 April 14; Corpus Christi, Texas. American Institute of Mining, Metallurgical, and Petroleum Engineers; 1978; 7115-MS.

NOAA. 2009 Drought Severity Index by Division (Long-term Palmer) Archive. U.S. Department of Commerce, National Climatic Data Center, Camp Springs, Maryland.

Otieno, D.O., C. Kurz-Besson, J. Liu, M.W.T. Schmidt, R. Vale-Lobo do, T.S. David, R. Siegwolf, J.S. Pereira and J.D. Tenhunen. 2006. Seasonal variations in soil and plant water status in a *Quercus suber* L. Stand: roots as determinants of tree productivity and survival in the Mediterranean-type ecosystem. *Plant and Soil,* 283: 119-135.

Packham, J.R., D.J.L. Harding, G.M. Hilton and R.A. Studdard. 1992. *Functional Ecology of Woodlands and Forest,* Chapman &Hall, London, pp.107-115.

Phillips, N., B. Bond, N. McDowell and M.G. Ryan. 2002. Canopy and hydraulic conductance in young, mature, and old Douglas-fir trees. *Tree Physiology*, 22: 205–211.

Pockman, W.T. and J.S. Sperry. 2000. Vulnerability to xylem cavitation and the distribution of Sonoran Desert vegetation. *American Journal of Botany,* 87: 1287-1299.

Querejeta, J.I., H. Estrada-Medina, M.F. Allen, J.J. Jimenez-Osornio and R. Ruenes. 2006. Utilitzation of bedrock water by *Brosimum alicastrum* trees growing on shallow soil atop limestone in a dry tropical climate. *Plant Soil,* 287: 187-197.

Querejeta, J.I., H. Estrada-Medina, M.F. Allen and J.J. Jimenez-Osornio. 2007. Water source partitioning among trees growing on shallow karst soils in a seasonally dry tropical climate. *Oecologia,* 152: 26-36.

Retzlaff, W.A., G.K. Blaisdell and M.A. Topa. 2001. Seasonal charges in water source of four families of loblolly pine (*Pinus taeda* L.). *Trees-Structure and Function*, 15: 154-162.

Schenk, H.J. 2008. The shallowest possible water extraction profile: A null model for global root distributions. *Vadose Zone Journal*, 7: 1119-1124.

Schenk, H.J. and R.B. Jackson. 2002a. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology*, 90: 480-494.

Schenk, H.J. and R.B. Jackson. 2002b. The global biogeography of roots. *Ecological Monographs*, 72: 311-328.

Schulze, E.-D., H.A. Mooney, O.E. Sala, E. Jobbagy, N. Buchmann, G. Bauer, J. Canadell, R.B. Jackson, J. Loreti, M. Oesterheld and J.R. Ehleringer. 1996. Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. *Oecologia*, 108: 503-511.

Schulze, E.-D., R.J. Williams, G.D. Farquhar, W. Schulze, J. Langridge, J.M. Miller and B.H. Walker. 1998. Carbon and nitrogen isotope discrimination and nitrogen nutrition of trees along a rainfall gradient in northern Australia. *Australian Journal of Plant Physiology*, 25: 413-425.

Schwinning, S. 2008. The water relations of two evergreen tree species in a karst savanna. *Oecologia*, 158: 373-383.

Schwinning, S. 2010. Ecohydrology bearings- Invited commentary- The ecohydrology of roots in rock. *Ecohydrology*, 3: Special Issue. SI: 238-245.

Schwinning, S., K. Davis, L. Richardson and J.R. Ehleringer. 2002. Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau. *Oecologia,* 130: 345-355.

Schwinning, S. and J. R. Ehleringer. 2001. Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *Journal of Ecology,* 89: 464-480.

Seyfried, M.S. and B.P. Wilcox. 2006. Soil water storage and rooting depth: key factors controlling recharge on rangelands. *Hydrological Processes,* 20: 3261-3275.

Shreve, F. and T.D. Mallery. 1933. The relation of caliche to desert plants. *Soil Science,* 35: 99-113.

Smith, S.D., R.K. Monson and J.E. Anderson. 1997. *Physiological Ecology of North American Desert Plants.* Springer-Verlag, Berlin, pp. 109-120.

Sobrado, M.A. 1993. Trade-off between water transport efficiency and leaf life-span in a tropical dry forest. *Oecologia,* 96: 19-23.

Sperry, J.S., F.R. Adler, G.S. Campbell and J.P. Comstock. 1998. Limitation of plant water use by rhizosphere and xylem conductance: results from a model. *Plant, Cell and Environment,* 21: 347-359.

Sperry J.S., J.R. Donnelly and M.T. Tyree. 1988. Seasonal occurrence of xylem embolism in sugar maple (*Acer saccharum*). *American Journal of Botany,* 75: 1212–1218.

Sperry, J.S. and T. Ikeda. 1997. Xylem cavitation in roots and stems of Douglas-fir and white fir. *Tree Physiology*, 17: 275-280.

Sperry, J.S. and N. Z. Saliendra. 1994. Intra- and inter-plant variation in xylem cavitation in *Betula occidentalis*. *Plant, Cell and Environment,* 17: 1233-1241.

Sperry, J.S. and M.T. Tyree. 1990. Water-stress-induced xylem embolism in three species of conifers. *Plant, Cell and Environment*, 13: 427-436.

Sternberg, P.D.. M.A. Anderson, R.C. Graham, J.L. Beyers and K.R. Tice. 1996. Root distribution and seasonal water status in weathered granitic bedrock under chaparral. *Geoderma*, 72: 89-98.

Tennesen, M. 2008. When juniper and woody plants invade, water may retreat. *Science*, 322: 1630-1631.

Tyree, M.T. and F.W. Ewers. 1991. Tansley Review no. 34. The hydraulic architecture of trees and other woody plants. *New Phytologist,* 119: 345-360.

Tyree M.T. and J.S. Sperry. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. *Plant Physiology,* 88: 574–580.

Tyree, M.T. and M.H. Zimmermann. 2002. *Xylem Structure and the Ascent of Sap*, 2nd ed. Springer, Berlin, Germany, pp. 89-141.

Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. *Annual Review of Ecological Systems,* 31: 197-215.

Van Auken, O.W., A.L. Ford and J.L. Allen. 1981. An ecological comparison of upland deciduous and evergreen forests of central Texas. *American Journal of Botany*, 68: 1249-1256.

Van Auken, O.W., A. L. Ford and A. Stein. 1979. A comparison of some woody upland and riparian plant communities of the Southern Edwards Plateau. *The Southwestern Naturalist*, 24: 165-180.

Walter, H. 1971. *Ecology of Tropical and Subtropical Vegetation*. Oliver & Boyd, Edinburgh, pp. 266-296.

Wan, C., R.E. Sosebee and B.L. McMichael. 1994. Hydraulic properties of shallow vs. deep lateral roots in a semiarid shrub, *Gutierrezia sarothrae*. *American Midland Naturalist,* 131: 120-127.

Weaver, J.E. and J. Kramer. 1932. Root system of *Quercus macrocarpa* in relation to the invasion of prairie. *Botanical Gazette*, 94: 51-85.

White, W.B. 1988. *Geomorphology and Hydrology of Karst Terrains.* Oxford University Press, NY, pp. 1-7.

White, W.B. 2002. Karst hydrology: recent developments and open questions. *Engineering Geology*, 65: 85-105.

White, W.B., D.C. Culver, J.S. Herman, T. C. Kanes and J. E. Mylroie. 1995. Karst lands. *American Scientist*, 83: 450-461.

Wilcox, B.P., M.K. Owens, W.A. Dugas, D.N. Ueckert and C.R. Hart. 2006. Shrubs, streamflow, and the paradox of scale. *Hydrological Processes*, 20: 3245-3259.

Williams, D.G. and J.R. Ehleringer. 2000. Intra- and interspecific variation for summer precipitation use in pinyon-juniper woodlands. *Ecological Monographs*, 70: 517-537.

Wills, F.H. 2005. Structure of historic vegetation on Kerr Wildlife Management Area, Kerr Country, Texas. *Texas Journal of Science*, 57: 137-152.

Willson, C.J. and R.B. Jackson. 2006. Xylem cavitation caused by drought and freezing stress in four co-occurring *Juniperus* species. *Physiologia Plantarum,* 127: 374-382.

Willson, C.J., P.S. Manos and R.B. Jackson. 2008. Hydraulic traits are influenced by phylogenetic history in the drought-resistant, invasive genus *Juniperus* (Cupressaceae). *American Journal of Botany,* 95: 299-314.

Wrede, J. 2005. *Trees, Shrubs, and Vines of the Texas Hill Country,* 1st ed. Texas A&M University Press, TX, pp. 168.

Zwieniecki, M.A. and M. Newton. 1995. Roots growing in rock fissures: their morphological adaption. *Plant and Soil,* 172: 181-187.

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