

The water relations of two evergreen tree species in a karst savanna

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Abstract The ecohydrology of karst has not received much attention, despite the disproportionately large contribution of karst aquifers to freshwater supplies. Karst savannas, like many savannas elsewhere, are encroached by woody plants, with possibly negative consequences on aquifer recharge. However, the role of savanna tree species in hydrological processes remains unclear, not least because the location and water absorption zones of tree roots in the spatially complex subsurface strata are unknown. This study examined the water sources and water relations of two savanna trees, *Quercus fusiformis* (Small) and *Juniperus ashei* (Buchholz) in the karst region of the eastern Edwards Plateau, Texas (USA). Stable isotope analysis of stem water revealed that both species took up evaporatively enriched water during the warm season, suggesting a relatively shallow water source in the epikarst, the transition zone between soil and bedrock. *Q. fusiformis* had consistently higher predawn water potentials than *J. ashei* during drought, and thus was probably deeper-rooted and less capable of maintaining gas exchange at low water potentials. Although the water potential of both species recovered after drought-breaking spring and summer rain events, associated shifts in stem water isotope ratios did not indicate significant uptake of rainwater from the shallow soil. A hypothesis is developed to explain this phenomenon invoking a piston-flow mechanism that pushes water stored in macropores into the active root zones of the trees. Epikarst structure varied greatly with

parent material and topography, and had strong effects on seasonal fluctuations in plant water status. The study suggests that tree species of the Edwards Plateau do not commonly reduce aquifer recharge by tapping directly into perched water tables, but more likely by reducing water storage in the epikarst. A more general conclusion is that models of savanna water relations based on Walter's two-layer model may not apply unequivocally to karst savannas.

Keywords Ecohydrology · Epikarst · *Juniperus ashei* · *Quercus fusiformis* · Stable isotopes

Introduction

The role of woody plants in the hydrological cycle and consequences of woody encroachment on water yield have been an issue of increasing interest (e.g., Scott et al. 2006; Wilcox and Thurow 2006; Williams et al. 2006). The worldwide encroachment of woody plant species into historically open grasslands and savannas is thought to reduce water yields and groundwater recharge just as human demand for water is at historic heights. However, recent reviews have made it clear that the hydrological impact of woody encroachment is by no means universal, but can vary widely with climate, physiography, and geology (Huxman et al. 2005; Jackson et al. 2000; Seyfried and Wilcox 2006).

Karst is a geologic formation for which uncertainties about the hydrological impacts of woody encroachment are particularly large. Karst regions are landscapes characterized by caves and sinkholes formed by the dissolution of highly soluble rock. Soils are often thin and rocky, while solution enlarged fissures, gaps, and channels in the

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underlying bedrock facilitate the rapid transport of surface water to groundwater. Only about 10% of the terrestrial surface area is characterized as karst, but karst aquifers contribute disproportionately more to human freshwater supplies, 25% worldwide and 40% in the US alone, according to some estimates (White 1988; Leibundgut et al. 1998). Thus, the paucity of knowledge on the ecohydrology of karst systems is particularly disconcerting.

This study describes the water use of two co-dominant tree species in the karst region of the eastern Edwards Plateau, the contributing zone of the Edwards Aquifer, one of the most productive carbonate aquifers in the United States (Maclay 1995). Studies on the water use of trees in this region are still relatively scarce and have focused chiefly on Ashe juniper (*Juniperus ashei*), this region's primary woody encroacher. Ashe juniper is predominantly shallow-rooted with an expansive fibrous root system confined to thin soils (Hall 1952). However, tap roots of juniper and most other trees have been observed in caves at 9–22 m depth (Jackson et al. 1999b; McElrone et al. 2004), and a recent stable isotope study suggested that juniper trees switch water sources from deep in summer to shallow during winter (McCole and Stern 2007).

It stands to reason that the rooting habits of trees in karst areas, thus their potential impact on karst hydrology, are strongly influenced by local geology, in particular soil thickness and the structure of the underlying epikarst. The epikarst (or the “skin of the karst”) is the transition zone between the soil and the bedrock in karst landscapes. It is a zone of enhanced permeability where weathering, dissolution, and root growth have created a substrate of highly porous rock (Bakalowicz 2003). Epikarst has recently been recognized as playing an important role in regulating aquifer recharge (Bakalowicz 2003; Perrin et al. 2003; Aquilina et al. 2006; Doctor et al. 2006). Locally, epikarst can vary greatly in thickness and structure depending on local geology among other factors, though general principles of epikarst structure have been described (Klimchouk 2004).

On the eastern Edwards Plateau, two geological formations are most commonly encountered, with characteristically different epikarst structure: at higher elevations, the Edwards limestone formation, with extremely thin and rocky soils underlain by highly fractured bedrock, and at lower elevations, the Glen Rose limestone formation, with soil depths between 10 and 100 cm and underlain by unconsolidated marl or hard dolostone (Edwards Aquifer Authority). The marl is described by some as equivalent to soil with similarly high water holding capacity and organic content (Wilding 1997) and amenable to fine and structural root growth. By contrast, dolostone layers are not readily penetrated by roots or water and may therefore form the bedding planes of streams or perched water tables.

Consideration of such variation in epikarst structure may reconcile contradictory observations on woody plant rooting depths. For example, on sites where the Glen Rose dolostone is relatively close to the surface, the roots of juniper and other trees may indeed be confined to the shallow soil, while on Edwards limestone deep roots may develop through wide and numerous gaps in the bedrock. Such large variation in epikarst structure and consequent root distribution is likely to modify the role of trees in the hydrological budget. For example, where tree roots can tap directly into persistent recharge flows, e.g., cave streams (Jackson et al. 1999b; McElrone et al. 2004), tree encroachment is likely to reduce annual recharge. On the other hand, where tree root development is highly constrained, the evapotranspiration of a tree stand may not differ from that of herbaceous vegetation cover.

The present study is the first to investigate the water sources of the two co-dominant trees of the eastern Edwards Plateau, live oak (*Quercus fusiformis*) and Ashe juniper, across a geologically heterogeneous landscape. The study had four main objectives: first, to ascertain whether a stable isotope approach using natural abundances as tracers for water sources is suitable for this region. While this method has been very effective in regions with strong seasonal shifts in the isotope ratios of rainfall (Ehleringer et al. 1991), central Texas has little variation in precipitation isotope ratios due to its warm winters and dominant moisture input from the Gulf of Mexico. A second objective was to determine whether trees tap directly into the dominant pathways of aquifer recharge, for example solution-enhanced subsurface channels, streams, or perched water tables. A third objective was to learn whether the water sources used by the two tree species can be differentiated, i.e., whether the two species exhibit niche separation with respect to water sources. If so, they could have differential effects on hydrological budgets or respond differentially to climate drivers. Last but not least, this study explored how spatial variation in topographic position, geologic substrate, and proximity to stream channels affect the water use patterns of these tree populations. Water use patterns were quantified by tracking predawn water potentials and stem water isotope ratios over the course of a growing season. Since roots do not fractionate water during uptake, and evaporation from suberized stems is negligible, the isotope ratios of water in plant stems reflect the uptake-weighted average isotope ratio of water in the root zone (Ehleringer and Dawson 1992), and can be used to differentiate plant water sources. Predawn water potentials are measures of the root-surface-area-integrated water potentials in the root zone, on the assumption of equilibrium conditions between soil and plant at the end of the night. The comparison of plant water potentials provides additional information about root zone

separation between species, as well as about differences in plant-available water.

Materials and methods

Site characteristics

The Edwards Plateau is a 93,000 km² Cretaceous limestone plateau. Below its southeastern border lie the Edwards and Trinity Aquifers, the only sources of water to nearly 2 million people in the San Antonio–Austin corridor. Storm runoff from upland areas in the contributing zone, the Texas Hill Country, is the main contributor to aquifer recharge (Wilcox et al. 2005a). In the last 150 years, this region has been transformed from primarily open savanna dominated by live oak and Ashe juniper into closed canopy juniper-dominated woodlands (Van Auken 2000).

The study was conducted on the “Pollard Property”, an 32.3-ha (80-acre) land holding of Texas State University (29°56.5'N, 98°7.2'W) in the contributing zone of the Edwards Aquifer. The site is representative of the Texas Hill Country, the rugged eastern edge of the Edwards Plateau. It features a steep canyon with an Edwards limestone outcrop 400 m above sea level dropping to a wide valley with an ephemeral stream ~60 vertical meters below.

The Edwards limestone outcrop, estimated to be 10–15 m thick, is extremely rocky with only a few centimeters of soil cover over fractured bedrock. Underneath the Edwards limestone lies a layer (10–13 m) of Walnut Clay (Maclay 1995), a weathered limestone product with extremely high water storage capacity. Where the canyon walls cut into the clay layer, a narrow band of more water-dependent tree species such as the deciduous Texas oak (*Quercus texana*) is observed. The Walnut Clay layer lies above the Glen Rose limestone and the interface gives rise to perennial seeps, which feed into contributing channels of the ephemeral stream at the bottom of the canyon. The Glen Rose limestone formation contains alternating layers of more and less soluble rock, which has produced a stair step physiognomy (Woodruff and Wilding 2007), with steep “riser” sites associated with comparatively deep soils and marl (typically 1–3 m thick) and flat “tread” sites where hard, consolidated dolostone layers are exposed and the soil is thin.

Four sites were selected for this study: site 1 at the top of the Edwards limestone outcrop (“hill top”), a densely forested area with the overstory composed chiefly of Ashe juniper and live oak; site 2 at a Glen Rose dolostone outcrop at mid-elevation (“ledge”), where vegetation was scarce and limited to short prairie grasses and shrub-like Ashe juniper; site 3 at the canyon bottom and no more than 3 m from the ephemeral stream bed (“bottom, streamside”); and

site 4 at the canyon bottom and at least 10 m removed from the streambed (“bottom”). The canyon bottom was densely forested with Ashe juniper and live oak.

The climate of the eastern Edwards Plateau ranges from subtropical/semi-arid with an average annual precipitation of 800 mm and an average annual temperature of 19–21°C. (Larkin and Bomar 1983). Annual precipitation is variable (CV = 30%) with a bimodal tendency (peaks in May and October), but overall little seasonal predictability (average monthly rainfall CV = 83%). Multi-year droughts and severe flooding caused by intense convection storms are common. The year in which this study was conducted had average rainfall for the region (849 mm recoded from January to December at Austin’s Mueller Municipal Airport, National Weather Service Cooperative Station ID 410428, 860 mm on site). However, the months of February and July–August were much drier than average (February 37%, July–August 17% of mean monthly rainfall) which caused a moderate spring and a severe summer drought.

Study species

Ashe juniper (*Juniperus ashei* Buchholz) is a drought-tolerant evergreen deciduous shrub or small tree, native to northeastern Mexico and the south-central United States. It forms dense to open communities, on the eastern Edwards Plateau primarily with live oak. In the absence of fire, Ashe juniper stands (“cedar brakes”) grow outward and invade adjacent grassland patches (Van Auken et al. 2004). Grazing does not control its spread, as cattle and deer avoid eating the bitter and spiny seedlings. Texas live oak (*Quercus fusiformis* Small), by some authors considered a subspecies of southern live oak [*Quercus virginiana* Miller var. *fusiformis* (Small) Sargent; Harms 1990] is a subevergreen tree, which can become up to 25 m tall, but on the Edwards Plateau, forms small trees with rhizomatous copses (shinneries) and rarely reproduces from seed due to high grazing pressure (Russell and Fowler 2004).

Rainwater sampling

A Hobo tipping bucket rain gauge (Onset Computer, Pocasset, MA, USA) was installed in an open meadow at the top of the Pollard Property. Rainwater was collected in a mineral oil capped 20-l bucket about 5 km from the study site. As much as practical, water samples for individual storm events were collected separately. Precipitation intervals were considered separate if they were at least 12 h apart. Water samples were stored in screw cap vials that were parafilm around the cap for additional leak protection and frozen until sent out for stable isotope analysis. A total of 28 water samples were used to construct the local meteoric water line, accounting for ~74% of total annual

precipitation. After high rainfall periods, seep and stream samples were also taken at the Pollard Property, as well as occasional samples from a deep well 5 km from the field site to represent aquifer water.

Plant sampling

Stem samples of Ashe juniper and live oak for the measurement of predawn water potentials and stem water stable isotope analysis were taken every 2–4 weeks from February to September 2006. Samples were taken repeatedly from marked trees. From January to August, 3 trees per species were sampled from sites 1–3. In August, the sample size was doubled and site 4 was included. In addition, three samples of understory grasses and sedges were taken from sites 1 to 3, as a bioassay for the isotope ratio of plant-available shallow soil water. Because of their physical proximity, it was assumed that understory samples of sites 3 and 4 would not be different.

Stem samples for water potential analysis were taken before dawn and contained in ziplock bags until measured with a Scholander pressure bomb (PMS Instrument, Albany, OR, USA). Stem samples for water isotope analysis were collected within 2 days of the water potential measurements and often on the same day. Samples were taken at mid-morning on dry days from stems upstream of the most proximal evaporation sites (i.e., leaves or green stems) to reduce the risk of back-diffusion of evaporatively enriched water. Only a subset of four sampling dates was sent out for analysis. These include samples taken on March 9, March 23, August 23 and September 9. Analysis concentrated on these dates to focus on two questions: are there species differences in rooting depth, and to what extent do species utilize water stored in shallow soil layers? To answer question one, I selected samples taken near the peak of two drought periods (March 9, August 23), hoping that the establishment of a vertical evaporation gradient through soil and epikarst would allow me to distinguish deeper from more shallow rooted species on the basis of their stem water isotope ratios. To answer the second question, I selected two dates right after the two respective drought-breaking rain events (March 23, September 9) to determine to what extent stem water isotope ratios shifted in the direction of rainwater isotope ratios, as a means to quantify the uptake of shallow versus deeper water sources.

Stem water was extracted by the cryogenic vacuum method described by Ehleringer et al. (2000). Samples were analyzed at the SIRFER facility at the University of Utah on a Thermo Finnigan Delta Plus XL Isotope Ratio Mass Spectrometer along with internal standards that were calibrated against Vienna standard mean ocean water (VSMOW) for quality assurance. Isotope ratios are reported in delta notation in units of per mil (‰):

$$\delta D = \left(\frac{(D/H)_{\text{sample}}}{(D/H)_{\text{VSMOW}}} - 1 \right) \times 1000$$

$$\delta^{18}O = \left(\frac{(^{18}O/^{16}O)_{\text{sample}}}{(^{18}O/^{16}O)_{\text{VSMOW}}} - 1 \right) \times 1000$$

where D, H, ^{18}O , and ^{16}O are the abundances of the respective isotopes.

In this study, it was not possible to compare stem water isotope ratios with the isotope ratios of below-ground water sources directly, as this would have required digging multiple pits, some in locations inaccessible to the necessary equipment. More importantly, such activities would have caused permanent damage to the research site. Therefore, alternative methods were sought to interpret the stem water isotope ratios of the target species, such as the collection of rainfall and seep samples, and of grass and sedge samples as a root-zone integrated reference point for shallow soil water.

To collect grass and sedge samples, parts of the root or rhizome systems were pulled out of the soil, attached soil was briefly shaken off, and all green biomass was carefully clipped off. Thus, samples consisted of a mixture of non-green above ground biomass, below-ground biomass, and some soil contaminant. Water extracted from these materials would have been dominated by water taken up from the entire grass root zone, not just the immediate surface soil.

Statistical analysis

All statistical tests were conducted with SPSS (SPSS, Chicago, IL, USA) using parametric methods. Since the same individuals were repeatedly sampled throughout the study, repeated measures analyses were conducted on water potential data. The data significantly deviated from the assumption of sphericity, thus *p* values are reported based on the lower bound estimate, a conservative method that does not assume sphericity.

Shifts in stem water isotope ratios between two close sampling dates (before and after rain) were quantified for individual trees as the Euclidian distance between the δD and $\delta^{18}O$ coordinates. Significant shifts, as well as the effects of species and site on the magnitude of the shift were evaluated by analysis of variance.

Results

Precipitation and local meteoric water line

Two distinct growing season dry periods were observed, one in March, with <1 mm rainfall recorded within a 21-day period, and a more severe dry period from early July to early September, with <10 mm rainfall recorded

within a 63-day period (Fig. 1). There was only a slight seasonal trend from more enriched rain in February to more depleted rain water in October. The local meteoric water line determined from local rainfall samples was indistinguishable from the global meteoric water line (Craig 1961; Fig. 2). Occasional samples taken from the site's perennial seep, a deep well, and creek water, when water was flowing (June 19), did not depart from the meteoric water line. Water samples taken from a deep well showed little variation in isotope ratios and were consistent with values reported for the confined portion of the Edwards aquifer in

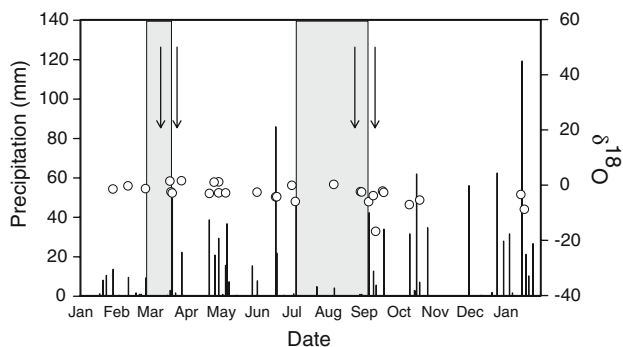


Fig. 1 Rainfall measured on site and $\delta^{18}\text{O}$ values of rainfall samples in 2006. The extremely low value sampled in September was associated with a hail storm. The four arrows indicate dates for which stem isotope samples were analyzed. The two shaded regions mark spring and summer drought periods

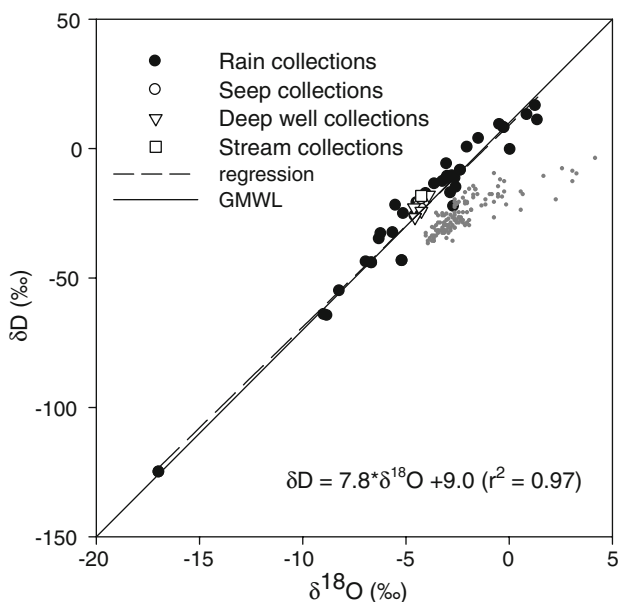


Fig. 2 Local Meteoric Water Line constructed from 28 rainfall samples taken between January 16, 2006 and January 24, 2007. The regression equation is shown in the figure. Also shown are the isotope ratios of water samples taken from other water sources, the isotope ratios of all plant stem samples taken in the course of this study (gray symbols) and the Global Meteoric Water Line $\delta\text{D} = 8\delta^{18}\text{O} + 10$

other studies (Fahlquist and Ardis 2004; Groschen and Buszka 1997).

Plant water potentials

The predawn water potentials (PWP) of live oak and Ashe juniper trees at the beginning of the observation interval were relatively low and then increased after several moderate rainfall events in January and February (Fig. 3). Subsequent early spring and mid-summer dry spells caused PWP to drop in both species. Repeated measures analysis suggested highly significant effects of date ($P = 0.006$), species ($P = 0.001$), site ($P = 0.006$), date \times species ($P = 0.004$), date \times site ($P = 0.01$), but overall no significant effects involving site \times species interactions.

However, during peak drought periods, site ($P < 0.001$, both seasons), species ($P < 0.001$, both seasons) and site \times species interactions (spring: $P = 0.039$; summer: $P = 0.028$) were significant (Fig. 4). With a few exceptions, oak trees had higher PWP than juniper trees. In spring, the two species had similar PWP on the Edwards outcrop site at the top of the canyon but, in summer, juniper had the lowest recorded PWP at this site. The ledge site, which had no oak trees, was consistently the wettest site for juniper, and in summer was the only site where juniper could achieve PWP similar to those of oak. In general, juniper trees on the ledge site were highly buffered against precipitation variability (Fig. 3).

Stem water isotope ratios

All stem water samples collected in the course of this study fell below the local meteoric water line (Fig. 2), a sign that all plants took up water predominantly from sources that had been evaporatively enriched. During the height of the spring and summer drought events, stem water samples taken from oak and juniper were not significantly different in their δD - or $\delta^{18}\text{O}$ -values. There were also no significant site effects on stem water isotope ratios.

Stem water isotope ratios shifted significantly after the intervening rain events. In spring, the shift was statistically significant only for the two species combined ($P = 0.002$), while site effects were non-significant. On all sites, stem water isotope ratios appeared to shift by a similar amount, except for oak trees on the hill top site, which had similar isotope ratios before and after rain. Data are shown pooled across sites in Fig. 5.

Stem water isotope ratios also shifted after the summer-drought-ending rain event, and species effects were again non-significant (Fig. 6). Site effects were marginally significant ($P = 0.074$). When juniper, which was distributed across four sites instead of just three for oak, was analyzed separately, site effects on the magnitude of the isotopic

Fig. 3 Predawn water potentials collected in 2006. The two shaded regions mark spring and summer drought periods, as in Fig. 1

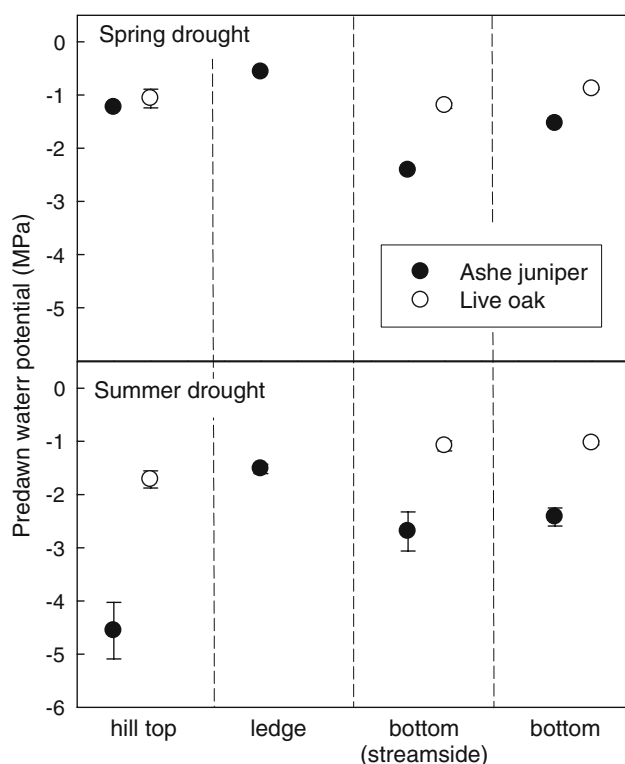
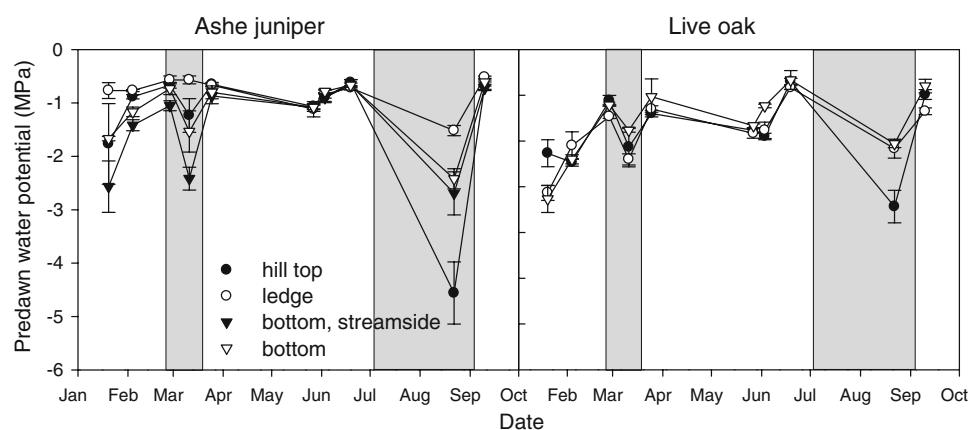


Fig. 4 Site and species comparison of predawn water potentials during the spring (March 9) and summer (August 23) drought

shift were significant ($P = 0.02$). Isotope ratios clearly shifted in response to rainfall inputs at only two sites, the Edwards outcrop hill top, and the near-stream site at the canyon bottom. Isotope shift patterns for oak tended to follow those for juniper, though site effects on the magnitude of shift were non-significant for oak.

If trees took up rainwater, one would expect their stem water to shift in the direction of the isotope ratios of the rainwater input, or a slightly evaporatively enriched derivative of it, as “new” water taken up by shallow roots would have mixed with “older” stem water. This pattern was indeed observed for grasses and sedges in summer, but

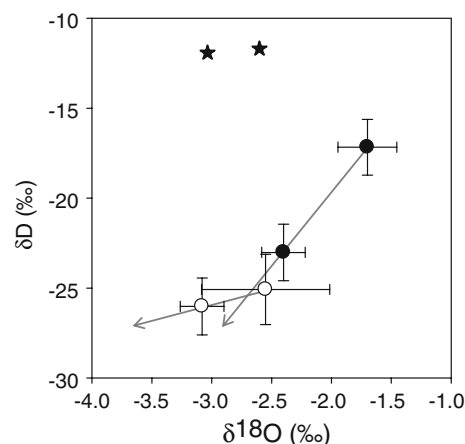


Fig. 5 Shifts in stem water isotope ratios observed between March 9 (before rain) and 23 (after rain), pooled across sites. The arrows indicate the direction of change. Solid symbol Ashe juniper, open symbol live oak. The star symbols mark the isotope ratio of two intervening rainfall events: a 16.2-mm event on March 19 with $\delta D = -11.7\text{‰}$, $\delta^{18}O = -2.6\text{‰}$ and a 33.6-mm event on March 20 with $\delta D = -11.9\text{‰}$, $\delta^{18}O = -3.0\text{‰}$

it was not observed for the two tree species (Figs. 5, 6). Nevertheless, the stem water isotope ratios of the tree species shifted in some locations, and water potentials recovered in all locations (except for juniper on the ledge site in spring; Fig. 3), clearly indicating a significant input of water into the active root zones of trees. Based on the direction of the stem water shifts, the source and location of this water input appeared to be different for the trees than for the understory grasses and sedges, and was most likely not shallow soil water.

Discussion

Comparison of oak and juniper zones of water uptake

During the dry periods of 2006, on almost every site where Ashe juniper and live oak co-occurred (with the exception

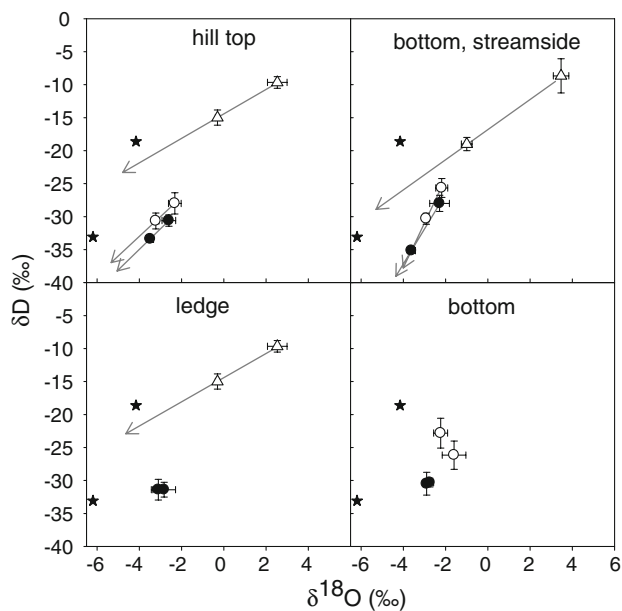


Fig. 6 Shifts in stem water isotope ratios observed between August 23 (before) and September 9 (after rain). Symbols as in Fig. 5. Open triangles Grass or sedge understory samples. The two intervening rainfall events were a 42.4-mm event on September 5 with $\delta D = -33.1\text{‰}$, $\delta^{18}O = -6.19\text{‰}$ and a 12.7-mm event in the early hours of September 9 with $\delta D = -19.0\text{‰}$, $\delta^{18}O = -4.2\text{‰}$. Arrows were drawn only where shifts in isotope ratios were statistically significant

of the hill top in spring), juniper had 0.5–1.5 MPa lower PWP than oak trees, indicating that the roots of oak trees were not confined to the root zone of juniper trees and possibly reached deeper, as seen at other sites on the Edwards Plateau (Jackson et al. 1999b). Stem water stable isotope ratios for the two species were statistically indistinguishable where they grew side-by-side, both during and after drought. Thus, species must have tapped into the same relatively well-mixed water source within a stratum that allowed the establishment of a water potential gradient during drought. This water source was evaporatively enriched relative to local meteoric water, indicating that it resided in the evaporation zone or exchanged water with it by diffusion.

Although rainfall increased PWPs to pre-drought levels, necessitating a water input into the root zone, the associated shifts in stem water isotope ratios were inconsistent with uptake of rainwater from the intervening rainfall events. While it could have been the case that the rainwater collection was not representative of the rainfall input at the site, or that isotope exchanges between rock and water somehow altered the isotope ratios of the rainwater, this explanation was ruled out in summer by checking the stem water isotope ratios in the herbaceous understory, which did shift in the expected direction. Assuming then that the isotope ratio of the rain event was recorded correctly, the direction of change in the stem water isotope ratios begs

further explanation. The data would suggest that another water source was pushed into the active root zone of the trees, enough to cause plant water potentials to recover. Near-surface roots would have taken up no or just small amounts of water, but water input at the top may have pushed stored water into the active root zone of trees, perhaps through a piston flow mechanism. Piston flow phenomena occur in hydrological systems with substantial subsurface flow (Hewlett and Hibbert 1963), including karst regions (Lastennet and Mudry 1997; Aquilina et al. 2006). Alternatively, the observed shift in stem water isotope ratios could have been the result of 2 or more water sources entering the tree root zone simultaneously, one of which could have been rainwater, thus explaining the improved water status. The problem with this explanation is that, to explain the observed shift in stem water isotope ratios, the hypothetical second water source would have to have been “off the chart” in terms of isotope composition, i.e., far off any other water source observed during 2006 (Fig. 2). Thus, I consider the first explanation, involving some form of piston flow, the more likely scenario.

A basic challenge for applying a piston flow mechanism in the present situation involves explaining why the active root zone of trees can run out of water (and induce low plant water potentials), while significant amounts of water are still stored somewhere else in the epikarst and can be “pushed through” into active root zones after rain. This explanation would require that (1) the epikarst is not uniformly occupied by roots, so that some water-filled macropores can remain untapped, and (2) flow pathways between rooted and non-rooted portions of the epikarst break when water potentials are declining due to root water uptake, but become reconnected when rainfall causes slightly increased hydrostatic pressures in the water-filled macropores.

Hydrological observations made by Dasgupta et al. (2006) in the context of a rainfall simulation study in the contributing zone of the Edwards Plateau provide some degree of support for this model. First, the group observed that larger rainfall events activated rapid preferential flow pathways. Secondly, soil moisture probes installed in the pseudomatrix (soil-filled gaps between rock layers) responded heterogeneously to rainfall, i.e., some probes did not respond to smaller rainfall events, and response times generally decreased with event size. This suggested to Dasgupta et al. (2006) that substantial water potential gradients can be maintained between the pseudomatrix and macropores, and that slight pressure differentials caused by rainfall inputs facilitated lateral flow of water from the macropores into the pseudomatrix. Thus, if the fine root system of trees were predominantly associated with the “pseudomatrix” of Dasgupta et al.’s (2006) conceptual model, then the phenomena recorded in this study would

have a consistent mechanistic explanation. Whether it is the correct explanation can only be shown by future studies, perhaps using a combination of rainfall simulation and water isotope tracers to provide further insights into the potentially complex transport mechanisms and pathways of this fascinating landform.

Independent of the considerations above, one other important finding is that the rainfall responses of savanna trees on karst may be quite different from those on deep soils, due to the predominance of preferential, or macropore, flow. In this study, live oak and Ashe juniper, the two co-dominant tree species of the eastern Edwards Plateau, responded hydraulically to spring and summer rainfall, possibly with the involvement of deeper rather than near-surface roots. This is in stark contrast with the patterns found in systems with deep soils where the magnitude of a species' physiological response to rainfall input is correlated with the capacity to take up shallow soil water (e.g., Lin et al. 1996; Schwinning et al. 2003; Fravolini et al. 2005). Simply speaking, a deep-rooted plant that lacks shallow uptake-roots would simply not "notice" changes in shallow soil water availability. In this karst system, however, changes in the water status of the soil/epikarst system appear to be rapidly communicated throughout, such that all members of the plant community are affected by rain, almost independent of the vertical extent of their root zones.

The results of this study may suggest an essential difference between the ecohydrology of savanna systems on deep soils versus in karst regions with shallow soil. In deep soils, trees are relatively buffered against high frequency variation in rainfall inputs, in accordance with Walter's (1971) two-layer model but, in karst systems, rainfall input may affect herbaceous layer and canopy layer species simultaneously. Thus, the functional tradeoff between deep roots (with steady but limited water supply) and shallow roots (infrequent saturating water supply; see Schwinning and Ehleringer 2001) may not necessarily apply to plants on karst. Aside from situations where woody plants on karst have access to a relatively large, or well-buffered, perched water table, all roots on karst may require adaptations that would allow them to tolerate large amplitude variation in root zone water potential, in a way making all roots functionally more like "shallow roots" in deep soil systems.

Site effects on water use

The study demonstrated the unexpected, complex and sometimes counter-intuitive water relations of karst sites. For example, the Edwards limestone outcrop at the hill top was an example of a large but leaky (by way of seeps at its bottom) epikarst water reservoir. The site did not impose

very negative PWP's on either juniper or oak during the spring drought, when presumably it was charged from winter precipitation, but it was the driest site for juniper during the summer drought (Fig. 4), indicating that winter recharge did not carry over well compared to, for example, the canyon bottom sites.

In stark contrast, the Glen Rose limestone ledge was greatly buffered from rainfall variation and afforded the resident juniper population a favorable water status year-round (Fig. 3). This site was located just below the Edwards and Walnut Clay limestone layers and was different from all other sites in several aspects: it almost completely lacked soil cover, juniper density was much lower than above or below this site, juniper had a shrublike rather than treelike growth habit, and there were no oak trees. The much reduced potential for intraspecific competition for water may in part explain the continuously high PWP's in juniper, but this does not explain why tree density was low or juniper plants were stunted. With limited soil cover, this site may have provided limited establishment opportunities, and the stunted growth habit may have been caused by nutrient rather than by water limitations. The tree density at this site may have also been limited by the availability of gaps through the hard dolostone layer. If a tree root made it through, it could have encountered a permanently wet layer underneath.

Conspicuous as well is the absence of oak trees on this site. Due to high grazing pressure, oak trees almost never establish from seed but instead sprout saplings from shallow roots (Russell and Fowler 1999). This suggests that oak roots do not grow into the exposed ledge site, or that saplings cannot develop without a minimal soil cover.

Lastly, this study provided no evidence that trees growing near the creek took up stream water. This would have been indicated by a stem water isotope ratio shift towards rainwater, as creek water isotope ratios were very close to rainwater ratios when observed. However, following the drought-breaking rain events in spring and summer, the creek may have run only for a brief period of time, if at all, and was not running at the time that the stem water samples were collected. Thus, the study was inconclusive with respect to stream water use and future observations will have to ascertain if trees growing near the stream have access to stream water.

Niche separation between juniper and oak

This study is consistent with previous work suggesting that live oak and Ashe juniper exhibit different water use strategies. The predawn water potentials of juniper trees dropped to very low values during drought, indicating that juniper canopies continued to transpire as water availability in their root zone declined. By contrast, predawn water

potentials in oak trees rarely dropped below -3 MPa. While this could indicate a much larger water reservoir available to oak but not juniper, alternatively it could indicate that oak trees cut back gas exchange rates as root zone water availability declines below -2 to -3 MPa. Owens and Schreiber (1992) observed that Ashe juniper gas exchange rates stayed fairly constant over the course of a growing season, while live oak gas exchange rates varied sixfold. On a canopy basis, the variation in gas exchange rates may even be greater as live oak trees readily drop leaf area during drought (personal observation). Differences in the hydraulic architecture of juniper and oak roots and stems also suggest far greater drought tolerance in juniper. Oak trees suffer a 90% loss of hydraulic conductivity at -2 MPa, while the most vulnerable part of juniper's hydraulic pathway, deep roots, suffer only a 50% loss in hydraulic conductivity (McElrone et al. 2004). While these estimates are not directly transferable to trees at the present study site, the data provide strong evidence for large systematic differences in the two species' tolerance to low water availability. Thus, Ashe juniper and live oak are an example of an evergreen species pair with distinct rooting habits and regulation of gas exchange. This should create a fairly large amount of niche separation, despite their shared evergreen phenology, and begins to explain their intimate association in the Texas Hill Country.

There are interesting parallels between the Edwards Plateau and the dry-forest karst system of the Yucatan peninsula, recently studied by Querejeta et al. (2006, 2007), where none of six tree species investigated relied heavily on groundwater during the dry season and all stem water isotope samples fell upon a regression line below the local meteoric water line. Furthermore, two deciduous species derived a majority of water from the 15-cm-thick soil layer that lay above the epikarst, while another one made extensive use of epikarst water. Among the evergreen species, two used the same deep water source and one used almost exclusively soil water. Thus, in general, rooting depth and drought tolerance do not appear to be strongly associated with the evergreen–deciduous dichotomy (see also Jackson et al. 1999a).

McCole and Stern (2007) observed that Ashe juniper on a Glen Rose site on the Edwards Plateau switched between shallow soil water from November to April (a period not considered in this study) to deeper epikarst water from May to October. Similarly, Utah juniper (*J. osteosperma*) shifts between shallow soil water in winter and deeper soil water in summer (Leffler and Caldwell 2005), though it continues to take up substantial amounts of shallow soil moisture when it becomes available intermittently in summer (Flanagan et al. 1992; Evans and Ehleringer 1994; Williams and Ehleringer 2000). One must assume that the maintenance of active uptake-roots in the shallow soil in summer is a relatively

costly undertaking, due to the higher temperatures (which increases maintenance respiration) and low water potentials (which necessitate thicker xylem walls). Perhaps Ashe juniper foregoes this cost because the environment of the eastern Edwards Plateau is more mesic. In addition, if precipitation inputs can be expected to “push through” to deeper soil layers, the “lost opportunity costs”, incurred by not having functional shallow roots, would be small. It would be interesting to examine more generally in future studies whether and in what respect root system form and function differs systematically between plant species adapted to deep soils and those adapted to epikarst environments.

Is juniper a “water thief”?

The State of Texas spends multiple millions of dollars per year in shrub removal programs on the eastern Edwards Plateau, primarily targeted at Ashe juniper (Olenick et al. 2004). However, the evidence that juniper encroachment on the Edwards Plateau reduces streamflow or aquifer recharge is weak (Wilcox et al. 2005b). A common misconception is that deep juniper roots commonly tap into perennial water sources such as perched water tables and cave streams, as reported by Jackson et al. (1999b), a study that was for some time the only window into the root zones of the Edwards Plateau. However, the present study suggests that juniper's water sources are restricted to rather limited and ephemeral epikarst water stores that recharge and deplete in rapid succession. The extreme drought tolerance of juniper and the low water potentials measured in 2006 provide further support that juniper's water sources are readily depleted. That said, there is little doubt that juniper accesses water beyond the root zone of the herbaceous understory and reduces water storage in the epikarst. As shown in other karst areas, epikarst storage contributes to aquifer recharge during high flow periods (Perrin et al. 2003; Aquilina et al. 2006; Doctor et al. 2006). Thus, to the extent that juniper reduces epikarst water storage, woody encroachment on the eastern Edwards Plateau can be expected to reduce aquifer recharge somewhat, but a quantification must await a better understanding of the role of epikarst in aquifer recharge in this region.

Conclusion

Much remains to be learnt about the ecohydrology of karst regions. As karst geohydrologists are beginning to understand the function of epikarst in watershed hydrology, the time is right for ecologists to pay closer attention to plant–epikarst interactions. Until recently, ecologists have nearly ignored the study of plant communities on non-soil substrates, though the phenomenon and ecological significance of roots growing through bedrock has been known for some

time (Cooper 1922; Cannon 1924). With respect to savanna systems, there remains an open question whether knowledge gleaned from savannas in deep soil systems, particularly their hydrological approximation as two-layer systems (Walter 1971), can be unequivocally transferred to karst savannas.

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