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Effects of juniper removal and rainfall variation on tree transpiration in a semi-arid karst: evidence of complex water storage dynamics

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Abstract:

Brush removal is widely practiced as a tool for increasing groundwater recharge, but its efficacy depends greatly on the way in which the removed species interact with the hydrological system relative to the vegetation replacing it. We examined the effects of Ashe juniper removal in the recharge zone of the Edwards Aquifer, Texas, USA, a karst aquifer. The study was conducted in an Ashe juniper (*Juniperus ashei*)–live oak (*Quercus fusiformis*) woodland on a hill slope composed of rocky, shallow soils over fractured limestone bedrock. Ashe juniper is a native species that has been encroaching grasslands and savannas over the past century. In September 2008, a plot was cleared of 90% of its juniper trees. Tree transpiration, predawn water potentials and vegetation cover across the cleared plot and an adjacent reference site were measured from May 2009 to December 2011. Stand-level tree transpiration from May 2009 to March 2010 was diminished by a severe summer drought in 2009, from which trees were slow to recover. Subsequently, tree transpiration was 5–10× higher in the woodland compared to the clearing. For all of 2011, also a drought year, tree transpiration in the woodland exceeded precipitation inputs, indicating a high capacity for water storage at the study site. However, site differences for oak trees were generally larger than for juniper trees. While juniper removal accounted for a 431 mm year^{-1} difference in tree transpiration between sites, vegetation cover in the clearing increased from 42% to 90% over two years, suggesting that understory growth was increasingly compensating for the loss of juniper transpiration. We conclude that the removal of a relatively shallow-rooted tree, when replaced with herbaceous vegetation and low shrubs, has little effect on deep recharge. By contrast, successive years of precipitation extremes may be more effective increasing recharge by lowering the water transport capacity of trees in the aftermath of severe drought.

KEY WORDS groundwater recharge; live oak; Granier sapflow sensor; xylem water potential; stable isotopes

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INTRODUCTION

Over the last century and a half, semi-arid grasslands and savannas worldwide have been encroached by woody plants (Andela *et al.*, 2013). These structural changes have altered ecosystem processes such as rates of carbon sequestration, soil nutrient cycles (Hibbard *et al.*, 2003) and hydrological processes (Huxman *et al.*, 2005). However, a recent global meta-analyses also suggested that the ecosystem effects on woody plant encroachment are not universal and depend on the encroaching species, local climate and edaphic characteristics (Eldridge *et al.*, 2011).

In semi-arid regions with growing urban populations and declining economic importance of pastoral production, the concern about woody encroachment often focusses on hydrological effects, specifically groundwater recharge (Huddle *et al.*, 2011). Many local communities invest substantially in either controlling the rate of woody encroachment through prescribed burning of grasslands or reversing woody encroachment by mechanically removing trees and shrubs in hopes of increasing water yield. Generic hydrological models predict positive effects of shrub control on streamflow and groundwater recharge (Zhang *et al.*, 2001; Nie *et al.*, 2012) based largely on the assumption that woodlands take up more soil water than herbaceous vegetation thus reducing runoff and/or deep drainage. However, field measurements attest to great variation in the magnitude, duration and even the direction of shrub removal effects on streamflow and deep drainage (Olenick *et al.*, 2004;

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Huddle *et al*., 2011; Acosta-Martinez *et al*., 2014) (Engel *et al*., 2005; Wilcox and Huang, 2010; Dzikiti *et al*., 2016).

Theoretically, transition from woodland to grassland can increase water yield through reducing interception loss and to a greater extent through reducing transpiration rates (Zhang *et al*., 2001). But in semi-arid regions where annual potential evapotranspiration and annual precipitation are of similar magnitude, the effect of shrub control can be highly sensitive to specific properties of the ecohydrological system (Huxman *et al*., 2005; Jackson *et al*., 2009), including precipitation patterns and plant-available water capacity (PAWC) (Seyfried and Wilcox, 2006). Where PAWC is lower, the effect of brush removal on water yield is smaller, because less water is carried over from wet to dry periods to support woody plant transpiration. However, effective PAWC can be difficult to quantify, as it depends not only on rooting depth and density, but also on physical characteristics of the rhizosphere, including the hydraulic conductivity of the water-storing matrix (Romano and Santini, 2002).

Uncertainty about the magnitude of PAWC is particularly high in karst areas and challenges simple representations of PAWC as the difference between water content between field capacity and permanent wilting point in the root zone. Karst is often characterized by outcroppings of soluble rock, such as limestone, dolomite and gypsum and soils are generally thin and have a high rock content. Globally, about 10% of the terrestrial surface is characterized as karst, but collectively it contributes an estimated 30% to human freshwater supplies (Ford and Williams, 1989). Karst regions have enhanced subterranean drainage systems that develop over millennia through dissolution of carbonate bedrock by weak carbonic acid that enlarges conduits and fractures in the bedrock (Bonacci *et al*., 2009). The source of the acid is primarily CO_2 generated in the soil/root zone, which is orders of magnitude higher than atmospheric CO_2 levels, and the resulting conduit network allows fast transfer of precipitation into karst aquifers below and can limit the storage of plant-available water in semi-arid regions.

Least well-understood in the surface hydrology of karst areas is the function of the transition zone between soil and bedrock, called epikarst, which can be several metres thick (Klimchouk, 2004). The epikarst is composed of variably weathered rock, which can vary from solid rock to weathered clay residuum. Within the epikarst zone, cavities and conduits of various sizes are dispersed, some containing soil washed in from the surface, while others are open and filled with air or water depending on conditions (Estrada-Medina *et al*., 2013). The epikarst regulates infiltration and groundwater recharge via multiple, multiphasic pathways, ranging from diffusion-like, slow flow through micropores to quick conduit flow through macropores and open shafts (Klimchouk 2004, Bonacci *et al*., 2009). While the roots of shrubs and trees are known to grow into the epikarst and extract water, and may even contribute to macropore formation, it is unknown how deep they go and what fraction of the epikarst volume they occupy. The thickness of the epikarst and the sometimes great rooting depth that tree roots can attain in it, e.g. tens of metres, (Jackson *et al*., 1999), suggests that PAWC could be quite high in karst regions. Additionally, epikarst structure favours the development of perched water tables at the bottom of the epikarst. On the other hand, shallow, impenetrable bedrock layers made of less soluble materials could restrict root growth and access to water storage. In general, epikarst is a highly heterogeneous edaphic medium causing largely unpredictable variation in PAWC across the landscape and even plant-to-plant (Heilman *et al*., 2009; Sassen *et al*., 2009; Heilman *et al*., 2012; Estrada-Medina *et al*., 2013; Tokumoto *et al*., 2014).

The structural differences between epikarst and deep soil are associated with differences in the regulation of ecohydrological processes. First, the prevalence of macropore flow in epikarst means that not all infiltration results in storage. Activated by intense rainfall events, macropore flow bypasses the root zone and potential storage locations for plant-available water (Thurow and Hester, 1997; Dasgupta *et al*., 2006; Wong and Banner, 2010; Bazan *et al*., 2013). However, tree transpiration can probably decrease the amount of water storage inside large conduits, which would increase the threshold amount of precipitation needed to trigger macropore flow (Bazan *et al*., 2013; Schwartz *et al*., 2013). The larger the contribution of bypass flow to groundwater recharge, the lesser the potential for increasing recharge by vegetation manipulation (Huxman *et al*., 2005).

Relatively large quantities of water can be stored in epikarst cracks, cavities, perched water tables and the matrix of weathered rock fractions (Klimchouk, 2004). But not all of this storage is readily accessible to plant roots. Conduits through which taproots can grow are relatively scarce (Estrada-Medina *et al*., 2013), reducing the density of deep roots. Furthermore, the hydraulic conductivity of weathered rock matrix is low (Motyka *et al*., 1998), which reduced the rate with which fine roots can extract water. These impediments to water uptake from epikarst, together with a potentially high storage capacity, could create conditions in which woodland transpiration is partially uncoupled from antecedent precipitation conditions. While carry-over of stored soil moisture also happens in systems with deep soils, it is typically limited to time spans of a year or less (e.g. Flanagan and Adkinson, 2011; van der Molen *et al*., 2011). In systems where deep regolith is part of the rhizosphere, delays between recharge and extraction can be much longer, in one case generating decadal fluctuations in rhizosphere moisture storage (Ruiz *et al*., 2010).

Delayed hydrological responses with carry-over of moisture (both high and low) across years would complicate the hydrological effects of disturbances such as shrub removal, especially in regions with high rainfall variability. For example, if shrubs were removed at the end of a dry phase in the climate cycle, the immediate response of the hydrological system could be to increase water storage rather than deep drainage. Long delays between shrub removal and increased drainage could furthermore interact with successional vegetation dynamics after shrub removal.

Shrub control does not simply 'reset' an ecohydrological system from shrubland to grassland, but triggers a successional sequence with immediate, intermediate and long-term hydrological effects. The immediate effect of shrub removal may be a pulse of water recharge into the epikarst, slowly propagating downward by conduit flow, soon followed by the enhanced growth of herbaceous vegetation that should begin to limit deep recharge from then on (Dugas *et al.*, 1998; Moore and Owens, 2006). Although most reports suggest that the potential for increased streamflow or groundwater recharge is highest immediately after clear cutting, a study from New Mexico found that a regional tree die-off in pinyon-juniper woodlands actually decreased streamflow for several years, which could have been the consequence of understory growth reducing overland flow (Guardiola-Clararnonte *et al.*, 2011). At intermediate time spans, woody plants re-establish dominance through the accelerated growth of surviving saplings released from competition (Owens and Schliesing, 1995; Moore and Owens, 2006) and re-sprouting of cut trunks (Ueckert *et al.*, 2001). Dugas *et al.* (1998) attributed the short-lived effect of juniper removal from a Texas woodland to the quick recovery of woodland species. Deeper-rooted woody plants spared during the clear-cutting may be able to take advantage of the initial recharge pulse slowly travelling through the epikarst. In the long run, woodlands are expected to re-establish in the absence of continuing control measures (Rango *et al.*, 2005), and water savings could be a transient phenomenon with characteristics highly dependent on local epikarst structure.

Here we report on the ecohydrological effects of a plot-level removal of most juniper trees from an oak-juniper (*Quercus fusiformis*, *Juniperus ashei*) woodland. The manipulation was conducted on a hill slope in the Southeast of the Edwards Plateau, near San Antonio, Texas, USA. The Edwards Plateau is a limestone karst, where Ashe juniper has been encroaching for more than a century (Van Auken, 2000). In this region of the Edwards Plateau, it is still very much in question how and to what extent the karst terrain affects the relationship between vegetation and recharge (Litvak *et al.*, 2010; Moore *et al.*, 2012). With the vegetation manipulation conducted at the plot-scale, we could not quantify all components of the water balance. Instead, we quantified indicators of ecohydrological processes between a cleared and an adjacent control site over a 2.5-year observation interval just following shrub removal. Indicators included rhizosphere water status through monitoring the predawn water potentials of trees, tree transpiration through Granier sapflow sensors and annual changes in spring-time vegetation cover. We also measured the stable isotope composition of stem water in the first year of the study to examine if the use of water sources diverged between sites. Unique to our study, we focused on the consequences of brush removal on two tree species, the nuisance species Ashe juniper, which was reduced to 10% of its former tree density in the treated plot, and the iconic tree species live oak, which was not removed, in accordance with local practice.

We hypothesized that the initial effect of brush removal would manifest as an increase in the amount of water stored in epikarst, indicated by an increase in water potentials and transpiration rates of the indicator trees left standing in the clearing. We expected trees in the clearing to maintain access to deeper epikarst water sources for longer, which would be indicated through a difference in the isotopic enrichment of sap water, particularly at the end of a summer drought period. Our assumption was that, if the improved water status of trees in the clearing persisted or even increased over the study period, this could signify an accumulation of epikarst water storage that could delay and reduce the pulses of deep drainage from the bottom of the epikarst. On the other hand, if the improved water status of trees in the clearing was a transient phenomenon, this would indicate that compensatory growth of herbaceous and woody vegetation cancelled out the effect of shrub removal on deep drainage. Additionally, our experimental design allowed us to examine whether juniper removal had differential effects on juniper and live oak trees. A previous study suggested that live oak roots can grow deeper into the epikarst than juniper roots. In that study, the deepest juniper roots were observed in caves 8 m below the surface and live oak roots in caves as deep as 22 m (Jackson *et al.*, 1999). Therefore, we expected oak trees to exhibit a longer-lasting response to juniper removal, indicative of an accumulation of water in the deeper regions of the epikarst.

METHODS

Study area

The Edwards Plateau is an uplifted limestone plateau in a semiarid to sub-humid climate zone located in southwest central Texas, USA (Larkin and Bomer, 1983). The study was conducted at Camp Bullis Military Base (29°37′26.21″N, 98°34′14.86″W), 24.5 km NNW of

San Antonio, TX, in the Edwards Aquifer recharge zone. The site exemplifies the dominant landform of this area, a hill country with shallow rocky soils and a cover of mixed woodlands dominated by live oak (*Q. fusiformis*) and Ashe juniper woodlands with dispersed grassy patches. Common understory species include Texas persimmon (*Diospyros texana*) and agarita (*Berberis trifoliolata*). Mean annual precipitation is 836 mm. Average monthly temperatures range from 4.05 °C in January to 34.8 °C in August (NOAA Online Weather Data).

The study sites were located on a hillslope. One area of 2730 m^2 was cleared of most juniper trees and understory shrubs in September 2008. A reference site was located in an adjacent area of intact woodland, uphill from the clearing, with similar slope. An on-site weather station monitored rainfall and temperature continuously at 15 minute intervals since November 2004.

Vegetation assessments

In the spring of 2009 we conducted 2-m belt transects (Bonham, 1989) covering the entire cleared area and a smaller area of 720 m^2 in the reference area to determine stem densities (the number of stems per area) and diameter distributions of all woody plants with >25-mm basal stem diameter. We counted woody plant stems that were ≤25 mm in diameter. Stumps of felled trees were recorded in the same way to estimate stem density before clearing.

In the spring of 2009, 2010 and 2011, we also determined vegetation cover types using the line intercept technique (Bonham, 1989). The canopies of all woody plants intercepting the line were recorded by species and height of cover. Other species were assessed only in terms of cover class and categorized as either grass or forb. Cover sums in excess of 100% indicate cover type overlap.

Instrumentation

Precipitation data were collected onsite (in the clearing) between 2009 and 2012 using Hobo dataloggers (Micro Station H-21-002, Onset Computer Corp., Bourne, MA, USA). Additional precipitation data for 2007 and 2008 were obtained from a nearby weather station (SAN ANTONIO 8.0 NNW, TX US). Volumetric soil water content was monitored continuously by four ECH$_2$O EC-5 soil moisture sensors (Decagon Devices, Pullman, WA, USA) per site. Soil moisture probes were installed on 5 May 2009 in the cleared site and on 24 May 2009 in the woodland site at approximately 15 (2 probes per site) and 25 cm (2 probes per site) soil depth, in patches where the soil was this deep. EC-5 sensors are not very sensitive to differences in soil texture and salinity and so we used the factory calibration to calculate soil moisture (Kizito *et al.*, 2008). On the other hand, rocks in the vicinity of the sensor can have a large impact on sensor accuracy and placing the sensors in the vicinity of rocks was unavoidable during the installation. Thus, we approached the interpretation of the soil moisture data with suitable caution. Soil moisture was monitored continuously every 60 s and logged as 15-min averages.

Sap flux of tree trunks was monitored using the heat dissipation method described by Granier (1987). At each site, six oak and six juniper trees were instrumented, each with one sensor. Thus, we optimized sampling across trees in the community, rather than obtaining more accurate estimates for individual trees. Paired reference and heated sensors were installed on the north facing side of tree trunks below the lowest branch, about 1.0–1.5 m above ground level. For insertion, we removed small areas of the bark and cortex with a leather punch. The surface of the sapwood was easily identified by its smooth appearance and greater resistance to punching. We then drilled 1-cm deep holes into the sapwood for sensor insertion, which was within the sapwood based on direct observation and our previous experience and data. The thermocouples were located half-way along the insertion depth, 5 mm into the sapwood. Thermal artefacts were minimized by wrapping the stem in reflective bubble wrap at sensor height.

According to Granier (1987), the temperature difference between these two probes varies with sap velocity, u (m s^{-1}):

$$u = 119\, x\, 10^{-6} K^{1.231} \tag{1}$$

where

$$K = (\varDelta T_{Max} - \varDelta T)/\varDelta T. \tag{2}$$

Thermocouple voltage was measured every 60 s and 15-min averages were logged. Sap velocities were integrated daily and reported as sap flux density (J_s) in kg m^{-2} sapwood area d^{-1}.

On 19 February 2010, the two-sensor design described above was replaced with a four-sensor design (Goulden and Field, 1994). This involved adding two reference sensor probes approximately 10 cm parallel to the heated and reference sensors of the original setup. This modification was expected to reduce artifacts because of temperature gradients along the stem not associated with the heat source. We observed no discontinuities in the sensor data before and after the installation of the new probe design.

Stand-level transpiration of oak and juniper trees (T, mm d^{-1}) was calculated from average sap velocities for the two species ($\bar{u}_{jun}$ and $\bar{u}_{oak}$) and stand characteristics as follows:

$$T = \frac{1}{1000}\left(\frac{\overline{u}_{jun}\ \sum_{i=1}^{n} S_{jun,i}}{A_{plot}} + \frac{\overline{u}_{oak} \sum_{j=1}^{m} S_{oak,j}}{A_{plot}}\right) \tag{3}$$

in which $S_{jun,i}$ and $S_{oak,j}$ are the estimated sapwood areas of the i'th juniper tree and the j'th oak tree, respectively, in the censused plot area of A_{plot}; n and m are the total number of juniper and oak trees, respectively, in the plot area with basal stem diameters > 2.5 cm. Detailed census information is shown in Table I. Sapwood areas were calculated by applying allometric equations for live oak and Ashe juniper that scale S, the sapwood area of a tree to D, the diameter. The equation for juniper was taken from (Owens *et al*., 2006). For oak we derived an equation based on data collected by G. Moore (personal communication) at another site:

$$S_{jun,i} = 0.672 D_i^{1.7409} \quad \left(R^2 = 0.94\right) \tag{4}$$

$$S_{oak,j} = 0.245 D_j^{1.9524} \quad \left(R^2 = 0.90\right). \tag{5}$$

To estimate continuous transpiration rates within the reporting interval, we had to fill some gaps in the sapflow data. Over the reporting period, gaps existed only at one of the two sites, never on both sites simultaneously. Including 10 days of data before and 10 days after the gap, we developed regression equations to predict missing sapflow data at one site from the existing data at the other site. We also used this technique at the beginning of the reporting period, using 20 days of subsequent data in the regression. Overall, we gap-filled 256 out of a total of 939 days.

Water potential measurements and stable isotope collections

Predawn water potentials of instrumented oak and juniper stem segments were taken periodically (usually monthly) using a Scholander pressure bomb (PMS Instrument Co., Model 1000, Albany, OR, USA). At predawn, the water potential of plants are assumed to be in equilibrium with the water potential of the rhizosphere. Thus, predawn water potentials can serve as a soil-root conductance-weighted average root-zone water potential. The equilibrium assumption is not always met, for example, some plants transpire at night (Dawson *et al*., 2007) and during drought conditions, plants may not reach equilibrium by dawn (Donovan *et al*., 1999). Nonetheless, the predawn water potential is often the only available and most meaningful proxy for plant-available water in the root zone.

Stem samples for the determination of water stable isotope ratios (Ehleringer and Dawson, 1992) were collected on the same days at predawn water potentials, usually at mid-morning. Cumulative precipitation was also collected at the site, in irregular intervals as dictated by precipitation. Evaporation of the collections were prevented by adding mineral oil to the collection vessel. Stem samples were taken from small branches below attaching leaves. They were placed in glass vials, capped and sealed with parafilm and stored in a freezer until extraction by cryogenic vacuum distillation (Ehleringer and Dawson, 1992). Stem and rain water samples were analysed on a liquid water isotope analyser (Los Gatos Research, Inc., Mountain View, CA, USA). Stable isotope ratios of hydrogen and oxygen are presented in delta notation:

$$\delta = \left(R_{sample}/R_{standard} - 1\right) * 1000‰ \tag{5}$$

where R_{sample} and $R_{standard}$ represent the molar ratio of D/H for δD or O^{18}/O^{16} for $\delta^{18}O$ of the sample and a water standard, Vienna Standard Mean Ocean Water (V-SMOW), respectively (Ehleringer and Dawson, 1992). Samples for

Table I. Basal area density (the sum of the basal stem area per ground area; $10^{-6}\,m\,m^{-1}$) and stem densities (the number of stems per ha) in three size categories for woody plants at the sites. Densities before clearing were inferred by counting tree stumps. The values in parenthesis are estimated sapflow area densities for *J. ashei* and *Q. fusiformis* only.

	Basal area density			Stem density (>65 mm)			Stem density (25 – 65 mm)			Stem density (<25 mm)		
Species	Wood-land	Clearing	Before clearing	Wood-land	Clearing	Before clearing	Wood-land	Clearing	Before clearing	Wood-land	Clearing	Before clearing
Juniperus ashei	2112 (799)	548 (159)	3782 (1341)	1125	186	1979	500	172	1334	1944	2545	3119
Quercus fusiformis	2637 (697)	624 (166)	688 (184)	556	323	373	14	624	638	95 820	74 701	74 744
Diospyros texana	506	121	169	431	165	172	1069	989	997	1625	3341	3370
Celtis reticulata	488	85	85	97	36	36	0	0	0	889	445	445
Quercus buckleyi	128	23	23	28	14	14	0	0	0	8028	825	825
Acacia roemeriana	4	14	14	0	36	36	14	29	29	28	1054	1061
Berberis trifoliolata	0	5	5	0	0	0	0	22	29	2250	4123	4130
Cercis canadensis	2	1	1	0	0	0	14	14	14	347	93	93
Rhus virens	0	4	7	0	0	0	0	65	72	528	1506	1506
Other	2	0	0	0	0	0	0	7	7	111	452	452
Total	5879	1425	4774	2236	760	2609	1611	1921	3119	111 570	89 084	89 743

stable isotope analysis were collected only in the first year of the study (2009).

Statistical analyses

We separated the data set into 6-month periods from October to March and April to September to test for site differences within those periods using ANOVA. For predawn water potentials measured within each interval, if there was more than one measurement, we used repeated measures analyses, reporting between-subjects effects with lower bound p-values. For sap flux, we calculated interval averages for individual trees and used ANOVA on the tree averages. We only compared time intervals for which data were collected on both sites (i.e., excluding gap filled periods). All statistical analyses were done using PASW Statistics 18, (SPSS Inc., Chicago, IL).

RESULTS

Based on the survey of remaining trees and tree stumps in the clearing, the intact woodland site and the adjacent site before the clearing had similar species composition, with Ashe juniper being the most common tree in the >25-mm diameter categories, followed by live oak and persimmon (Table I). However, before clearing, 79% of total basal stem area had been contributed by juniper trees, compared to 36% in the adjacent woodland. For oak, the basal stem area percentages were 14% before clearing and 45% in the woodland. Not counting trees <25 mm in diameter, most oak trees in the woodland (98%) were larger than 65 mm in diameter, some much larger, compared to only 37% in the clearing. Thus, the downslope site before it was cleared had a higher density of juniper trees and fewer, smaller oak trees.

The thinning treatment took out 90% of all juniper trees, and live oak became the most abundant species in the clearing. Basal stem and sapwood areas became more evenly divided between oak and juniper (Table I).

Precipitation during the water years from October to September was 378 mm (2007/2008; the year of the treatment), 415 mm (2008/2009), 1365 mm (2009/2010) and 248 (2010/2011). At a mean annual precipitation in San Antonio of 836 mm, two severe drought years fell into the observation period, with <50% of annual mean precipitation separated by one exceptionally wet year, 60% above average annual precipitation. The NOAA Drought Monitor classified conditions for central Texas as extreme to exceptional in mid-August 2009 and the Texas Drought of 2011 was record-setting both in terms of low rainfall and high temperatures lingering into September (Hoerling *et al*., 2013). Year type differences in terms of precipitation are highlighted in Figure 1A by showing the annual as well as the biennial cumulative precipitation from 2009 to 2011. The biennial accumulation of precipitation highlights potential differences in the water storage status of the site.

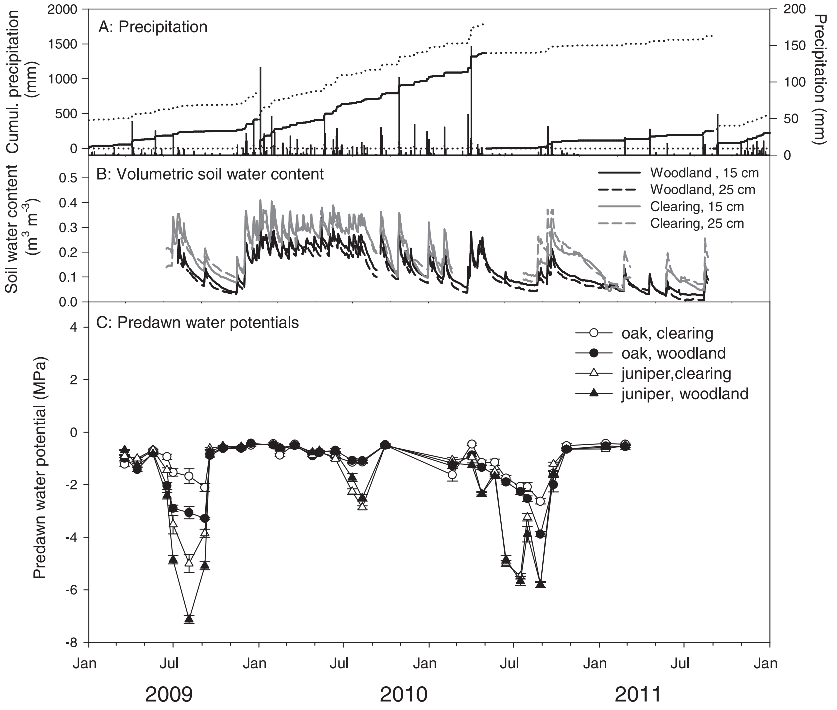

Figure 1. Precipitation and cumulative precipitation (October to September) over one year (solid lines) and two years (dotted lines) during the study period (A), volumetric soil water content at two depths (B) and predawn water potentials of oak and juniper (C)

Volumetric soil water content at 15 and 25 cm indicated higher soil moisture for most periods in the cleared site (Figure 1B). Based on our observations during sensor installation, these differences may have been in part caused by a difference in the rockiness of the soil, which was greater in the woodland site. However, by the end of the 2011 drought, soil moisture had declined to the same uniformly low values at both sites, indicating the nearly complete depletion of soil moisture to 25-cm depth at least.

Predawn water potentials of juniper and oak trees reflected variation in precipitation inputs (Figure 1C, Table II). In fall/winter, the predawn water potentials of both species were generally closer to zero and not significantly different between sites. In summer, juniper trees consistently obtained lower water potentials than oak trees, but site effects differed between years. In the dry summer of 2009, both species had significantly lower water potentials at the woodland site but in the wet summer of 2010, juniper trees had slightly but significantly lower water potentials at the woodland site, while there was no site difference for oak trees. In the summer of 2011, only oak trees exhibited significant site differences in water potentials (Table II). The site difference for juniper was marginally different and attributable to a single measurement that followed a precipitation event August. For juniper, the most negative average water potential was measured in 2009 at -7 MPa, and the minimal water potential for oak occurred in 2011 and was -3.9 MPa.

Site effects on the δ^{18}O composition of stem water were apparent but variable in size and direction in the first half of 2009 (Figure 2, Table III). The dissociation of stem water stable isotope values by site and species towards the end of the summer drought was more informative: Juniper trees in the woodland reach a maximal enrichment value first, indicating water uptake from a relatively shallow water source that had become enriched by evaporation or enrichment of stem water in the absence of transpiration. Even though a precipitation event occurring around that time had an even higher δ^{18}O value, this was not the source of the water extracting from the plant xylem (based on the comparison also of δD values). In addition, the amount of precipitation was too little to do more than wet the soil surface, consisting of a 2.5-mm event two weeks before and a 1.8-mm event 4 days before precipitation was collected.

Juniper trees in the clearing and oak trees in the woodland reached this seasonally highest level of enrichment only a month later, while oak trees in the clearing never reached at the level before plant water sources were renewed by a series of storm events from late August to September. Towards the end of the year, species effects prevailed, with slightly higher δ^{18}O values observed in oak trees.

Table II. ANOVA results for predawn water potentials by semi-annual periods. Repeated measures ANOVA was used for when there were more than one observation per period. *N* is the total sample number within the time interval, *k* is the replication number through time, *n* is the number of subjects and *F* is the value of the *F*-statistic. Within subjects, a degree of freedom of 1 was assumed using the lower-bound estimate method, which does not require the sphericity assumption to be met. *P*-values below the a=0.05 criterion were considered significant and are printed in bold letters.

Predawn water potentials in live oak

				Time		Time×site		Site (between subjects)	
	N	*k*	*n*	*F*	*p*	*F*	*p*	*F*	*p*
4/09–9/09	84	7	12	80.50	<0.001	12.13	**0.006**	54.89	**<0.001**
10/09–3/10	72	6	12	13.79	0.004	4.31	0.065	3.68	0.084
4/10–9/10	72	6	12	46.45	<0.001	2.43	0.150	2.053	0.182
10/10–3/11	12	1	12	—	—	—	—	1.736	0.217
4/11–9/11	96	8	12	93.29	<0.001	4.73	0.055	35.50	**<0.001**
10/11–3/12	36	3	12	2.00	0.188	0.098	0.761	2.38	0.154

Predawn water potentials in Ashe juniper

				Time		Time×site		Site (between subjects)	
	N	*k*	*n*	*F*	*p*	*F*	*p*	*F*	*p*
4/09–9/09	84	7	12	477.37	<0.001	14.69	**0.003**	38.65	**<0.001**
10/09–3/10	72	6	12	13.66	0.004	0.62	0.45	0.001	0.976
4/10–9/10	72	6	12	320.96	<0.001	4.56	0.059	**14.57**	**0.003**
10/10–3/11	12	1	12	—	—	—	—	1.201	0.299
4/11–9/11	96	8	12	562.19	<0.001	1.675	0.228	4.577	0.061
10/11–3/12	36	3	12	9.44	0.012	2.12	0.176	0.01	0.921

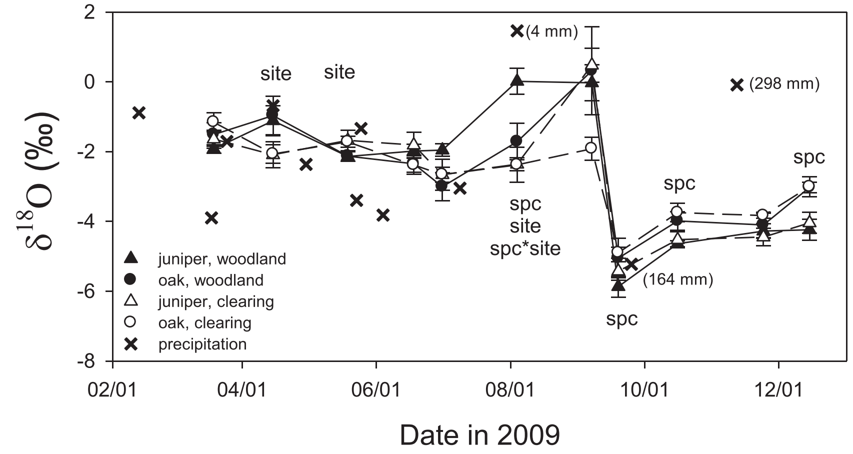

Figure 2. Stable isotope ratios of oxygen in sap water and precipitation collections ($\delta^{18}O$) for the year 2009. The labels 'site' indicate significant site effects, 'spc' significant species effects and 'site × spc' a significant interaction between the two at the $a = 0.05$ level. The isotope ratios of rainwater collections are shown for the day of collection. For the last three collections, we also indicated the cumulative precipitation over the collection interval

Sap flux densities were lower in 2009 than in 2011, and much higher in the intervening wet year (Figure 3). Semi-annual averages showed significant site differences for oak, but not for juniper (Table III): During the two dry summers, oak trees had significantly higher J_s in the clearing, with no difference during the wet summer of 2010. Averaged over the entire length of the observation period, J_s of oak was 80% higher in the clearing ($p = 0.011$).

In the woodland, stand-level transpiration by the juniper population far exceeded that of the oak population and was more even between the two species at the cleared site because of more similar sapwood area density (Figure 4). Over the 939-day interval, a tree transpiration difference between the woodland and the cleared site of 1507 mm was accumulated, 76% of actual precipitation. Of this difference, 1109 mm could be attributed to a difference in juniper transpiration between sites and the remaining 399 mm to a difference in oak transpiration, because oak trees had lower density in the clearing compared to the woodland (Table I). The site difference was primarily accumulated in 2010 and 2011, in spite of the drought conditions that dominated the second of the two years.

Table III. ANOVA results for sap flux density averaged across by tree across semi-annual periods. Included in the analysis are only time intervals for which data from both species in both sites were available. n is the sample size and F is the value of the F-statistic. P-values below the $a = 0.05$ criterion were considered significant and are printed in bold letters.

	Sap flux density in live oak			Sap flux density in Ashe juniper		
	n	*F*	*p*	*N*	*F*	*p*
4/09–9/09	12	11.07	**0.008**	11	1.72	0.222
10/09–3/10	12	3.45	0.093	12	1.99	0.189
4/10–9/10	12	0.009	0.925	12	1.31	0.279
10/10–3/11	11	11.76	**0.008**	10	0.473	0.511
4/11–9/11	11	8.39	**0.018**	8	1.45	0.273

Over the observation interval, transpiration was frequently uncoupled from precipitation (Figure 5). For example, at the end of the 2009, precipitation inputs were high starting in September, but stand transpiration remained low even in the woodland until March of the following year. From June 2010 to November 2011, woodland transpiration exceeded precipitation inputs, suggesting that trees transpired water stored in the epikarst, perhaps for more than a year.

Between the spring of 2009 and 2011, the vegetation cover of over- and understory in the cleared site more than doubled to 90% in the spring of 2011 (Table IV). About one third of this increase was contributed by woody plants, the rest by herbaceous species. Total cover in the woodland changed comparatively little over the same interval and had a negligible herbaceous component. Vegetation cover in the woodland was lowest in 2010, the year that followed the second of two drought years and juniper cover showed the greatest decline (~6%), while live oak cover increased slightly (~4%). These trends are not statistically testable, but they are consistent with our observation that juniper trees experienced branch dieback in 2009 while live oak flushed out new epicormic sprouts (water sprouts) soon after the return of rain in fall and winter 2009/10.

DISCUSSION

Did epikarst water content increase after clearing?

We confirmed our hypothesis that juniper removal increased water storage in the epikarst, but the patterns were complex and changed during the years of observation. Our overall interpretation of the data is illustrated in Figure 6.

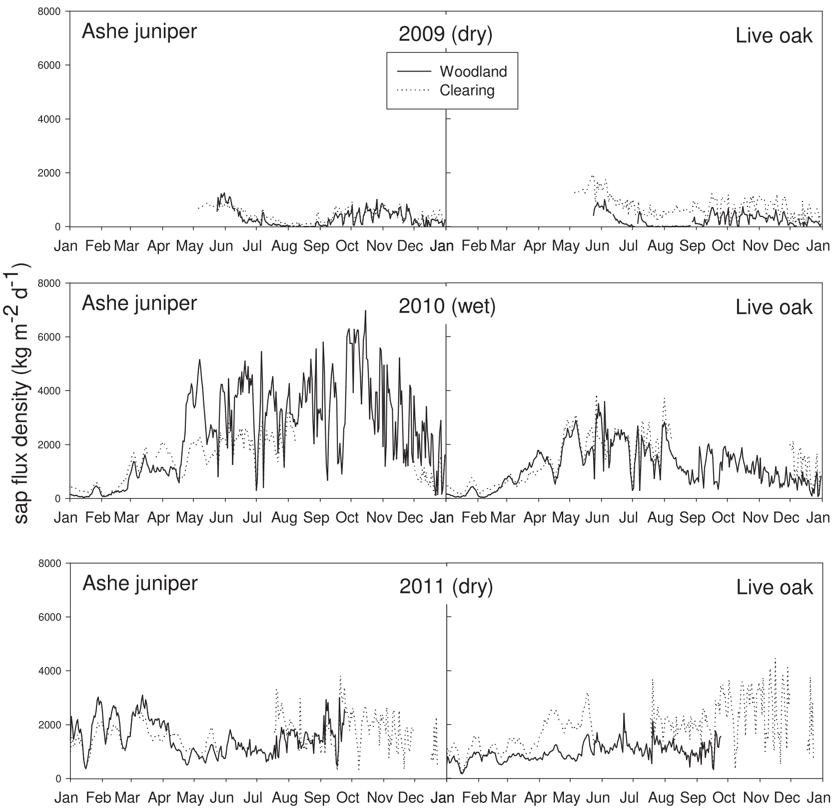

Figure 3. Average sap flux density (J_s) as 7-day running averages. The results of significance tests are presented in Table III

First, the shrub removal took place in the first of two successive dry years, which limited additional recharge into the epikarst immediately after shrub removal. In the summer of 2009, the low predawn water potentials indicated significant water stress in trees across sites. Still, predawn water potentials in both species and J_s in oak trees were significantly lower in the woodland compared to the clearing. This indicated slightly greater water availability because of brush removal, but only enough to moderate drought stress for the remaining woody plants and unlikely to produce deep drainage. In addition, sap water became increasingly enriched, indicating dwindling water reserves in soil and plant. The enrichment occurred sooner for juniper than oak trees in the woodland, and sooner for juniper trees in the woodland than in the clearing, while oak trees in the clearing did not show signs of evaporative enrichment at all, even at the end of the 2009 summer drought. This indicated that the recharge pulse that occurred right after brush removal in the winter and spring of 2008/09 persisted through summer only in deeper regions of the epikarst accessible to oak roots but below the root zone of juniper trees (Figure 6).

What followed was an exceptionally wet period from April 2010 to March 2011. During this period predawn water potentials and sap flux densities recovered, but there were no significant site differences, except a small difference in juniper predawn water potentials during a late summer dry spell (Figure 1C, Table II). However, juniper trees in the clearing had slightly *lower* water potentials, suggesting a decrease in water availability in the root zone of juniper trees, likely because of water uptake by herbaceous vegetation, which had greatly increased in the spring of 2010. Ashe juniper root density peaks at about 40-cm depth (Tokumoto *et al*., 2014), thus is widely overlapping with the root zone of forbs and grasses.

Excess precipitation in 2010 resulted in substantial increases in epikarst storage made evident by the much higher J_s of trees in 2010 through 2011, even though 2011 was an even hotter and drier year than 2009. Storage occurred at both sites and the site differences in predawn water potentials and J_s observed for oak trees indicated greater storage and slower decline of stored water in the clearing compared to the control site. However, juniper trees showed little difference in predawn water potentials between the two sites, except just after a mid-summer rainfall event, which could be attributed to greater throughfall in the clearing producing a slightly greater soil moisture pulse. Together, these observations indicated that juniper removal had increased water storage primarily in deeper regions of the epikarst, within the root

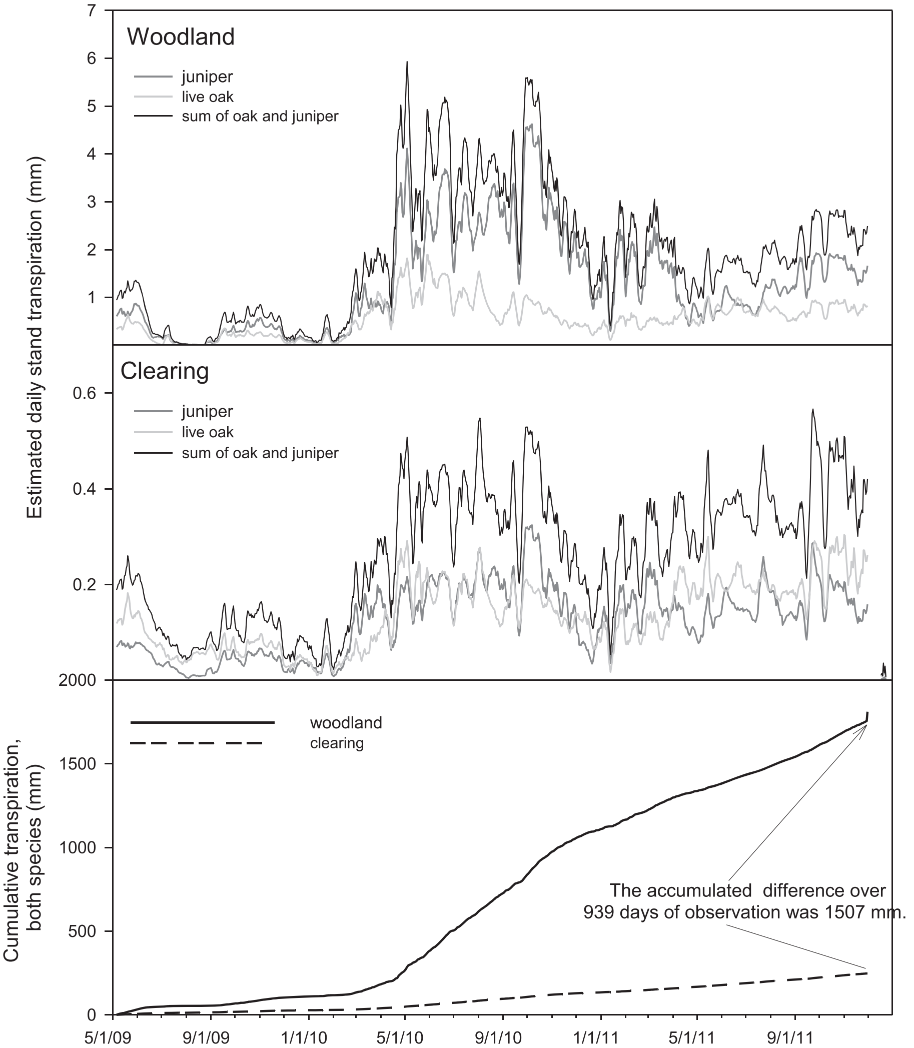

Figure 4. Estimated values for stand-level tree transpiration as 7-day running averages after gap-filling. The bottom graph shows cumulative transpiration over the 939-day observation interval

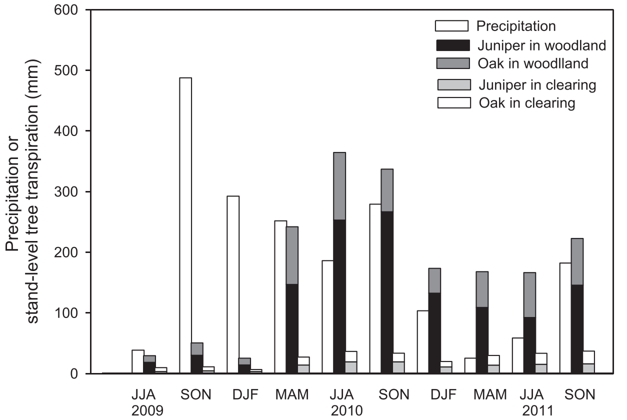

Figure 5. Comparison of total precipitation and stand-level tree transpiration in three month intervals (JJA = June–August, SON = September–November, DJF = December–February, MAM = March–May). Stacked bars are divided into contributions from juniper and oak trees

system of oak trees but below the root zone juniper trees (Figure 6).

Changes in stand transpiration

We calculated that tree transpiration was reduced by an average of 431 mm year^{-1} relative to the reference site because of the reduction in juniper density over the observation period (with another 155 mm year^{-1} attributable to the lower oak density). Evapotranspiration rates for grassland on the Edwards Plateau are frequently higher than this, ranging from 587 mm year^{-1} to 816 mm year^{-1} (Litvak *et al*., 2010). Thus, it is at least theoretically possible that the herbaceous vegetation that eventually spread in the cleared area was capable of transpiring just as much as an intact juniper stand, and furthermore taking up water from similarly shallow depths. Moore and Owens (2006) found that juniper

Table IV. Percent vegetation cover over three years for the most common woody plant species, combined herbaceous plant species and total vegetation cover. Herbaceous species includes grasses, cedar sedge, forbs and a small percentage of *Yucca rupicola*.

Cover class	Site	Spring 2009	Spring 2010	Spring 2011
Juniperus ashei	Clearing	4.6	4.2	5.5
	Woodland	60.1	53.9	58.6
Quercus fusiformis	Clearing	14.2	15.0	23.1
	Woodland	47.7	52.1	54.6
Diospyros texana	Clearing	5.5	5.2	11.0
	Woodland	22.2	18.8	25.9
Celtis reticulata	Clearing	3.7	3.9	4.3
	Woodland	4.7	3.4	3.7
Berberis trifoliolata	Clearing	0.9	1.2	1.5
	Woodland	2.5	2.3	3.0
Rhus virens	Clearing	0.6	0.6	0.7
	Woodland	0.1	0.0	2.2
Total woody	Clearing	34.6	35.4	48.9
	Woodland	145.6	138.0	149.7
Total herbaceous	Clearing	8.1	24.1	41.2
	Woodland	1.2	2.5	0.8
All cover classes	Clearing	42.6	59.5	90.2
	Woodland	146.8	140.5	150.5

seedlings released from overstory competition had higher rates of photosynthesis and transpiration, so that they too could have compensated for losses in transpiration by mature juniper trees. Thus, compensatory transpiration from herbaceous species, low shrubs and juniper saplings, drawing water from largely the same soil/epikarst zone as juniper trees, could explain the lack of site difference in the water status of juniper trees between sites. The rapid spread of understory vegetation after brush removal suggested that there was a limited 'window of opportunity' for epikarst recharge in our study, starting right after shrub removal and ending with the establishment of continuous herbaceous cover. While the high rainfall in 2010 may have allowed more water to infiltrate into the epikarst beneath the cleared site, it also contributed to closing the window by facilitating understory growth.

Epikarst water status and deep drainage

Our study showed that shrub removal increased the water storage in the epikarst, which could have had consequences for deep drainage and groundwater recharge. The linkage between storage and deep drainage was previously examined in a series of experiments near our study site. In 2008, Bazan *et al*. (2013) conducted several rainfall simulation experiments just after juniper removal and measured the amount of water entering a shallow cave through its ceiling, 3–5 m beneath the cleared area, as a proxy for deep drainage. Data were compared with an earlier study by Gregory *et al*. (2009) who measured cave recharge at the same site in 2005, before juniper removal. Both studies found that a higher proportion of water entered the cave when the ground had been wet from previous rainfall, but juniper removal, despite decreasing interception loss, had no apparent effect on cave recharge. Thus, initial precipitation increased water storage in the soil and epikarst, while subsequent precipitation flowed through the epikarst by way of macropores, bypassing the juniper root zone. Neither process was significantly affected by the presence of juniper. Furthermore, an astonishing proportion of the applied irrigation water (>80% or ~40 mm per event) remained unaccounted for and must have bypassed the cave and/or remained stored in the epikarst above the cave.

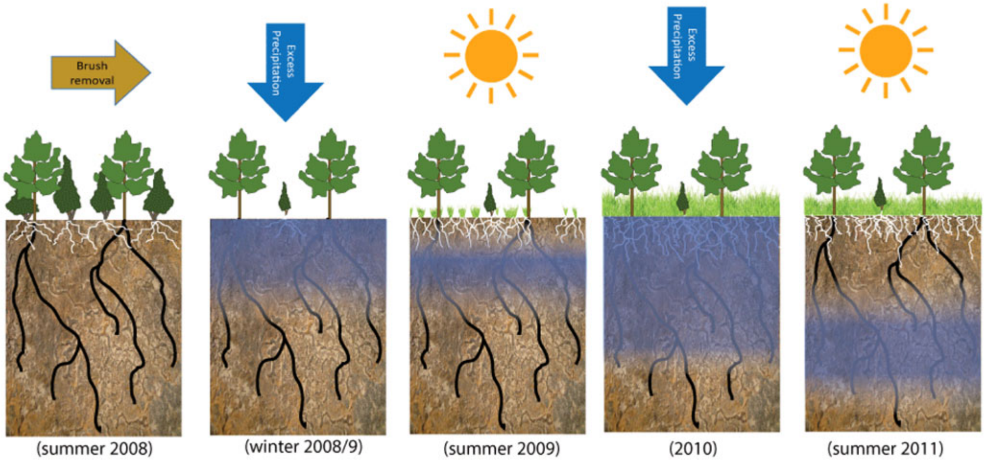

Figure 6. Illustration of the hypothesized effect of brush removal at the study site. Desirable trees (deep-rooted live oak trees with 'black roots') are spared while undesirable trees (shallow-rooted juniper trees with 'white roots') are culled. Before brush removal, soil and shallow layers of the epikarst dry up rapidly and tend to maintain high precipitation thresholds for triggering bypass flow and deep drainage. Right after brush removal, there is a window of opportunity in which shallow water uptake is diminished, water is retained longer and precipitation thresholds for bypass flow are lower. This window closes when forbs and grasses take over bare soil. The removal of deep-rooted trees could have a longer-lasting effect, but is not practiced because of aesthetic considerations

The study showed that water storage in the epikarst can be a significant barrier to deep drainage. While juniper removal may slow the rate of water depletion in upper regions of the epikarst and decrease bypass flow thresholds at least initially, the transfer of stored water to the bottom of the epikarst, where it would contribute to deep drainage, could be quite slow. Long residence times, together with the practice of sparing deep-rooted trees such as live oak, which utilize epikarst storage during drought, could further undermine the effect of brush clearing on recharge.

The role of precipitation patterns

Earth system models predict more extreme rainfall patterns in the near future, with longer, hotter droughts and larger, more intense precipitation events (IPCC, 2013). Our study period happened to be characterized by a succession of extreme year types with both exceptionally high and low precipitation, thus allowing us to speculate on the consequences of this aspect to climate change on groundwater recharge. The 2011 Texas Drought was widely regarded as the worst regional drought in over a century (Hoerling *et al.*, 2013). Unlike many other sites on the Edwards Plateau, where tree mortality peaked in 2011 (Kukowski *et al.*, 2013; Moore *et al.*, 2015), there was no tree mortality spike at the site of this study. In fact, physiological measurements on the study species attested that the 2009 drought generated more intense water stress than the 2011 drought. The carry-over of stored water from 2010 into 2011 clearly prevented worse drought effects at the study site.

In 2009, drought effects on transpiration outlasted meteorological drought conditions by several months. At our study site, the 2009 drought was broken in early September by a series of large rainfall events, yet transpiration in both juniper and oak trees remained low compared to the same time period in 2010, and this condition lasted until March. This suggested that both species recovered from drought impacts only during the subsequent growing season, presumably by growing new leaf area and xylem conduits.

The low predawn water potentials we recorded in 2009, especially in the intact woodland, were of a magnitude that could have impaired water transport capacity. According to data reported by McElrone *et al.* (2004), a xylem water potential of $-3.3\,\mathrm{MPa}$ in live oak would have reduced the hydraulic conductance of shallow roots to nothing and that of deep roots and stems to about 10%. The juniper water potential of $-7.1\,\mathrm{MPa}$ would not have reduced the hydraulic conductivity of stems but would have reduced the conductivity of shallow roots by 20%. Coniferous species, while having a more cavitation-resistant sapwood, respond to acute drought stress by sacrificing distal organs, such as fine roots, leaves and branches (Johnson *et al.*, 2012). Canopy die-back in juniper was indeed noticeable and was also reflected in the decline of juniper cover between the spring of 2009 and 2010, particularly in the woodland. Over the same interval, the slight increase in oak cover could be attributed to a burst of epicormic shoot growth, a typical response to xylem embolism (Meier *et al.*, 2012). Irrespective of the many morphological and physiological differences between juniper and oak that determined drought response and recovery (Zwieniecki and Secchi, 2015), it appeared that both species were too severely damaged by drought in 2009 to recover instantaneously with the onset of precipitation in September. This is consistent with the general observation that more severe droughts require longer recovery times for gas exchange to resume to pre-drought levels (Wang *et al.*, 2015; Ruehr *et al.*, 2015).

Intense summer drought conditions, by reducing the water transport capacity of trees, set the stage for a subsequent wet fall and winter to saturate the rhizosphere and increase the chance of deep drainage by bypass flow, further reducing the hydrological differences between intact and cleared woodlands. In this light, the global trend towards more extreme precipitation patterns, combined with warming, may ultimately have a pronounced impact on groundwater recharge in karst and other regions where focused recharge is important (Ries *et al.*, 2015; Meixner *et al.*, 2016; Thomas *et al.*, 2016). Additional effects imposed by spatially and temporally confined reductions of woody plant cover may be small in comparison.

CONCLUSION

Our results add to the mounting evidence that the removal of shallow-rooted shrubs such as juniper as a method of water management might be of limited utility in karst areas. In karst, deep drainage is primarily produced by bypass flow during intense rainfall events and is enhanced when the soil and epikarst have a high water content from previous precipitation. The benefits of shrub removal may then be contingent on the occurrence of rainfall patterns sufficient to cause an increase in epikarst water storage during a window of opportunity between shrub removal and the establishment of a continuous herbaceous cover. Deeper-rooted trees, such as live oak, have a greater potential to interfere with deep drainage, but because of their relatively sparse and unchanging distribution, as well as iconic status to local people, are not considered targets for shrub control. Given the importance of bypass flow in karst regions, it is conceivable that a shift to more extreme precipitation patterns will increase deep drainage in karst regions irrespective of vegetation management and further reduce the relative benefits of brush removal.

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