Species-specific water use by woody plants on the Edwards Plateau, Texas

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ABSTRACT

Woody encroachment is of great socio-economic and ecological importance in semiarid savannas because it is presumed to alter the water balance in such ecosystems. We compared two encroachers, Ashe juniper (Juniperus ashei) and honey mesquite (Prosopis glandulosa), with the less invasive live oak (Quercus fusiformis) to ascertain whether soil depth or species-specific water use strategy is most important in determining transpirational losses on shallow soils underlain by fractured limestone bedrock on the Edwards Plateau. Sap fluxes, leaf water potentials, soil moisture and meteorological information were monitored during spring 2009 at three sites with differing soil depths and were used in a non-spatial soil–vegetation–atmosphere water transfer model to predict different rooting depths. Sap flux responses and soil water stress were compared using multivariate statistical analysis. At two relatively deep-soil savanna sites, we found that dominant tree species had similar water use behaviour. However, at the shallow-soil forest containing Ashe juniper and live oak, juniper transpiration was much higher early in the season than oak transpiration, indicating that juniper benefited more from early spring rainfall than oaks. The model predicts that maximum rooting depths for the woody vegetation were mostly constrained by site soil depths. This study provides new evidence that these species perform similarly on shallow soils and that their water use is restricted by soil depth. The only species-specific strategy found important in determining transpirational losses was juniper’s ability to withstand low soil water potentials in very shallow soils. Copyright © 2012 John Wiley & Sons, Ltd.

KEY WORDS Edwards Plateau; rooting depth; Juniperus ashei; Prosopis glandulosa; Quercus fusiformis; sap flux; soil water storage

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INTRODUCTION

The increase in the abundance of woody plants in semiarid grasslands and savannas is a globally occurring trend over the past 100–200 years, which has often detrimental consequences for rangeland productivity, water resources and biodiversity (Hibbard et al., 2001; Wilcox et al., 2008). The small number of woody species that gradually outcompete native grasses has likely profited from human-induced changes in the landscape, including the introduction of livestock, suppression of wildfire, climate change and/or landscape fragmentation (Archer et al., 1988; Van Auken, 2000). However the life history strategies that make encroachers successful vary substantially. A better understanding of the characteristics that allow certain species to thrive will help in the management of them and the prediction of future vegetation changes.

The genera Juniperus (juniper) and Prosopis (mesquite) contain some of the most prolific encroaching species in North America, which may be, in part, due to their unique root architecture and physiology and phenology characteristics.

Winter deciduous mesquite trees are among the most deep-rooted species in the world (Phillips, 1963) and use deep tap roots to avoid drought. In contrast, juniper trees are evergreen drought tolerators. Ashe juniper (Juniperus ashei), for example, has a very high resistance to xylem embolism (Fonteyn et al., 1985; Willson and Jackson, 2006; Willson et al., 2008) and therefore an ability to withstand low soil water potentials.

Woody plants typically have deeper roots than grasses and therefore are presumed to have greater access to plant-available water in water-limited environments. However, considerable sections of our planet, including the karst terrain on the Edwards Plateau, are classified by shallow soil underlain by weathered bedrock. In contrast to a rooting medium consisting of homogenous soil, karst areas have highly confined pathways for root growth (Schwinning, 2010). To what extent woody plants growing on such substrates can display genetic or phenotypic differences in root distribution and thus realize hydrologic niche differentiation has not been systematically explored (Goodsheller, 2010).

On the Edwards Plateau, Ashe juniper and honey mesquite (Prosopis glandulosa) have dramatically increased in abundance in the past century in live oak (Quercus fusiformis) savannas (Archer et al., 1988; Van Auken, 2000), which
provides us with an opportunity to look for any evidence of differentiation between the root water uptake strategies of these species in response to the shallow soils that characterize this region. The roots of most species are usually confined to the shallow surface layer of soil in these systems, but some do penetrate into the fractured bedrock (Cooper, 1922; Cannon, 1924; Jackson et al., 1999; Querejeta et al., 2006; Eggemeyer and Schwinning, 2009). Juniper, mesquite and oak are known to have the ability to send roots into cracks in the limestone, possibly getting access to water sources that grasses cannot reach. Jackson et al. (1999) established that live oak was the most deep-rooted tree species on the Edwards Plateau, with roots identified in caves as deep as 21 m, whereas roots of juniper were discovered as deep as 9 m. Nevertheless, species rooting patterns can vary largely between biogeographic regions, and little is known about these root distributions or the water sources available in the cracks and channels of the bedrock at given locations.

An increasing number of studies suggest that roots growing deep into bedrock are quite unusual (Querejeta et al., 2007). Schwinning (2008) and Heilman et al. (2009) conducted studies on the Edwards Plateau that found no indication that woody plants exploited a deep, persistent water source. Schwinning (2008) suggested that Ashe juniper and live oak have roots that delve deeper than the soil but do not reach the perched water table. Eggemeyer and Schwinning (2009) found that the rooting depth of honey mesquite increased with tree size and therefore hypothesized that the absence of large mesquite trees at shallow-soil sites is explained by their inability to send down deep tap roots and access a deep stable soil water source. Juniper has also been found to survive in caves as deep as 21 m, whereas roots of juniper were discovered as deep as 9 m. Nevertheless, species rooting patterns can vary largely between biogeographic regions, and little is known about these root distributions or the water sources available in the cracks and channels of the bedrock at given locations.

Whether some species’ roots penetrate rocks more than others has consequences for belowground competition for water and the impact of woody plant encroachment of invasive species on water resources. Studies that directly compare the water use of both encroaching and non-encroaching trees in the Edwards Plateau region are still relatively scarce. The present study is the first to investigate whether three such co-dominant woody species have an equally stable supply of available soil water in shallow soils, where roots can possibly penetrate cracks in the fractured bedrock, in comparison with deeper soils in the same area, using both species-specific sap flux and pre-dawn leaf water potential measurements.

We hypothesize that deeper soils have the capacity to store more water, which would otherwise be drained quickly away through the fractured bedrock in a shallower soil profile. Therefore, as soils dry out between rain events, trees found at deeper soil sites will transpire more than those found on shallow-soil sites. However, because water is episodically limiting in this ecosystem, we also expect co-dominant trees to optimize their rooting profiles and hydraulic architecture (e.g. Dekker et al., 2011) to sustain growth during drought by varying their water uptake patterns temporally and by penetrating roots as deep as possible into the fractured bedrock.

The main objective of this investigation is to understand which factors are driving differences in woody plant transpiration and water uptake patterns in a heterogeneous landscape on the Edwards Plateau during two distinct drydown cycles of spring 2009. More specifically, our first goal is to ascertain whether soil depth or species-specific water use strategy is most important in determining transpirational losses in semiarid savannas. We compared differences in sap flux responses and soil water stress using a multivariate statistical analysis among these three species at three sites with differing soil depths. We use the daily integral of sap flow per sapwood area, as a measure of tree transpiration per sapwood area.

The second goal is to predict different water use strategies in terms of rooting depth. Because it is difficult to measure directly how the water moves through the soil in this complex rocky terrain, we used a one-dimensional soil-plant-atmosphere model. We focus on the actual transpiration and plant water stress that are experienced by juniper, mesquite and oak. The sap flux responses, soil water measurements, soil water stress and meteorological information were used in a non-spatial vegetation model (1-dimensional Water and Tracer Balance (1DWTB); Rebel et al., 2005) to understand species-specific water use and rooting strategies.

METHODS

Study area and site characteristics

The sites chosen for this investigation are located on the Freeman Ranch, a 1700-ha research station in the eastern Edwards Plateau in central Texas (29°9′N, 097°9′W). The area has a mean annual precipitation of 913 mm; however, periodic droughts occur often. We have selected three different sites, one forested site (FOR) and two savanna sites with different soil depths (SAVshallow and SAVdeep).

Our sites are underlain by two soil types: Rumple–Comfort Association, which is dominated by Rumple gravelly clay loam, and Comfort–Rock Outcrop, which is composed of approximately 15% rock, with stones that reach up to 80 cm across. Both soil types are relatively shallow, rocky soils that develop over hardened limestone, typical of a karst terrain (Barnes et al., 2000).

The FOR site is a closed-canopy forest, approximately composed equally of Ashe juniper (J. ashei) and plateau live oak (Quercus virginiana var. fusciformis). The FOR site consists of a Comfort–Rock Outcrop soil. The SAVshallow Site is a mesquite-juniper savanna, which is undergoing woody plant encroachment. This site is in the transition phase between grassland and Ashe juniper-dominated woodland. Besides juniper, the other dominant woody species are the deciduous honey mesquite (P. glandulosa) and two dominant perennial grass species: king ranch bluestem (Bothriochloa ischaemum (L.) Keng.), an introduced C4 species that has become invasive on the plateau, and Texas wintergrass [Nassella leucotricha (Trin. & Rupr.) Pohl], a C3 species. The SAVshallow site consists of a Rumple–Comfort soil. The SAVdeep site is a savanna of similar vegetation composition and woody plant cover as that of SAVshallow. However,
SAVdeep also has live oak trees present and an abundance of surface rocks. The SAVdeep soil consists of a combination of Rumple–Comfort and Comfort–Rock Outcrop soil. Table I outlines the three sites investigated, and a more detailed description of the area can be found at the Freeman Ranch website.1 Figure 1 shows an overview of the data collected from the three sites.

**Soil depth survey.** Depth to rock was estimated from electrical conductivity measurements (EM38DD, Geonics Limited, Mississauga, Ontario, Canada). The three sites were surveyed on the same day and re-calibrated for each site to reduce variation from soil moisture (θ) and temperature drift (Sudduth et al., 2001). Spatial variation in soil temperature (open vs under the canopy), soil moisture, salinity and soil texture had likely only a small effect on the electromagnetic (EM) readings, and it is reasonable to assume that variation in the EM readings is mainly due to variation in soil depth (Bork et al., 1998). An area of approximately 90 m² was surveyed at each site, encompassing the sap flow trees (section on Sap Flux). Vertical dipole measurements were recorded on a Polycorder 720 data logger every second; results are shown in Figure 2. EM measures indicate that FOR soils are distinctly shallower compared with the savanna sites. SAVdeep appears to have the deepest soils according to the EM survey, as well as the largest depth variation compared with the other sites.

To estimate the actual soil depths, we also conducted a physical survey of the soil depth by pounding a pole into the ground until it ‘hit’ rock within a randomly selected 20 m × 20 m grid at 5-m intervals. The recorded depth to an impenetrable layer at each of the 25 locations within each site showed that FOR soils were indeed very shallow (average 17 ± 14 cm). The average recorded depth to rock at the two savanna sites was very similar (SAVdeep 27 ± 12 cm and SAVshallow 30 ± 14 cm), despite SAVdeep appearing to have the

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1Freeman Ranch website: http://www.txstate.edu/freemanranch

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<table>
<thead>
<tr>
<th>Description</th>
<th>FOR</th>
<th>SAVshallow</th>
<th>SAVdeep</th>
</tr>
</thead>
<tbody>
<tr>
<td>Surface rocks</td>
<td>Shallow</td>
<td>Not present</td>
<td>Abundant</td>
</tr>
<tr>
<td>Soil type</td>
<td>CrD</td>
<td>RuD</td>
<td>RuD</td>
</tr>
<tr>
<td>Slope</td>
<td>Level</td>
<td>Level</td>
<td>Slight decline</td>
</tr>
<tr>
<td>Woody plant cover (%)</td>
<td>100</td>
<td>~50</td>
<td>~50</td>
</tr>
</tbody>
</table>

Table I. An overview of the three sites located on the Freeman Ranch.
Vegetation survey. A survey of the woody vegetation was conducted at each site. We surveyed the basal diameters and species of all woody vegetation within four randomly placed 20 m x 20 m quadrats at SAVshallow and FOR and from six quadrats at SAVdeep. Only vegetation with a basal diameter greater than 2 cm was included.

We measured the leaf area index (LAI) periodically over a 10-week period during the ‘greening up’, from late February until April 2009. Weekly digital hemispherical photographs were taken at each savanna site with a Sigma 4.5-5 mm F2.8 EX DC Circular Fish eye HSM lens, directly under each of the sap flow trees (section on Sap Flux), in accordance with methods outlined by Chen et al. (2006) and Campbell and Norman (1998). The photos were then cropped to include only the canopy of the targeted tree when needed. At FOR, the vegetation was entirely evergreen, so hemispherical photos were only taken once every 3 weeks to monitor the oak trees, which are known to replace their leaves during spring time. Under the canopy at FOR, five locations along a randomly placed 20-m transect were repeatedly sampled. All hemispherical photos were then processed using Hemisview 2.1 SR2 software to determine the raw ‘plant area index’ (PAI). The LAI was then estimated by subtracting the ‘wood area index’ (WAI) and incorporating an appropriate leaf clumping factor for the relevant species,

\[ LAI = (PAI - WAI) \times \text{clumping factor} \] (1)

where juniper has a clumping factor of 1.6 due to its distinctive scale-like leaf structure (Gower et al., 1999), whereas mesquite and oak had a clumping factor of 1.0. Mesquite WAI was taken to be the PAI prior to bud break (WAI range: SAVshallow, 0.3-0.7 m² m⁻² and SAVdeep, 0.5-0.8 m² m⁻²; day 71, March 7). Oak and juniper were estimated from the hemispherical photographs to have a WAI of 0.5 m² m⁻², which falls within the range of 5–35% of PAI reported by Gower et al. (1999). FOR canopy LAI increased only slightly over the season from 1.33 to 1.60 m² m⁻², most likely as a result of oak trees replacing their leaves during this time. The average LAI of the individual juniper trees at the savanna sites was reasonably constant over the duration of spring at 1.82 ± 0.21 m² m⁻² for SAVshallow and 1.41 ± 0.13 m² m⁻² for SAVdeep. Oak at SAVshallow had an LAI of 0.72 ± 0.14 m² m⁻². Much larger changes in mesquite LAI were observed at the two savanna sites over the season (Figure 3). Leaf out began around day 77 at both sites and reached a maximum value by day 105. Trees from SAVshallow accumulated more leaf area (a maximum of 0.65 m² m⁻²) than those from SAVdeep (a maximum of 0.38 m² m⁻²) over the season. This difference is unexpected and could be explained by the size of the mesquite trees at SAVshallow which were on average larger (0.049 m² basal area/tree) than that at SAVdeep (0.018 m² basal area/tree). Table II summarizes the measured ranges in LAI.

Climate. Ambient temperature, relative humidity, net radiation, precipitation and wind speed were recorded at SAVshallow and FOR sites and from a third climate station approximately 500 m from SAVdeep. Gaps in precipitation data recorded at FOR between days 70 and 80 were filled from the next geographically closest climate station, SAVshallow, approximately 1 km away. The year before this study, 2008, was a relatively dry year with precipitation totals 44% below normal. Further, there were approximately 100 days without a rain event over 10 mm, leading up to the study period in 2009.

Table II. The range in LAI, k and Vegfac for each species at each site.

<table>
<thead>
<tr>
<th>Species</th>
<th>SAVshallow</th>
<th>SAVdeep</th>
</tr>
</thead>
<tbody>
<tr>
<td>FOR</td>
<td>Juniper, live oak</td>
<td>1.33–1.60</td>
</tr>
<tr>
<td></td>
<td>Juniper</td>
<td>1.82</td>
</tr>
<tr>
<td></td>
<td>Mesquite</td>
<td>0.00–0.65</td>
</tr>
<tr>
<td></td>
<td>Juniper</td>
<td>1.41</td>
</tr>
<tr>
<td></td>
<td>Mesquite</td>
<td>0.00–0.38</td>
</tr>
<tr>
<td></td>
<td>Live oak</td>
<td>0.72</td>
</tr>
</tbody>
</table>

* Extinction coefficient values, k, were taken from Kiniry (1998) (honey mesquite 0.34, Eastern red cedar 0.37) and Etienne et al. (2008) (evergreen oak 0.7). At the savanna sites, LAI is measured per square metre of the projected canopy area, and at the FOR site, LAI is measured per square metre of the ground area.
In the studied period, between days 50 and 150, eight precipitation events were recorded at similar times for all three sites. Recorded precipitation events at $SAV_{\text{shallow}}$ were smaller relative to the other sites on day 71 ($SAV_{\text{shallow}}$ 50 mm and $SAV_{\text{deep}}$ 55 mm), day 107 ($SAV_{\text{shallow}}$ 30 mm, $SAV_{\text{deep}}$ 37 mm and FOR 49 mm) and day 117 ($SAV_{\text{shallow}}$ 41 mm, $SAV_{\text{deep}}$ 52 mm and FOR 52 mm). More precipitation was recorded at FOR relative to the other sites on day 136 ($FOR_{66}$ mm, $SAV_{\text{shallow}}$ 49 mm and $SAV_{\text{deep}}$ 50 mm).

**Monitoring plant water use**

The plant water use strategies of the three dominant woody species, live oak, Ashe juniper and honey mesquite, were examined directly by measuring sap flux and pre-dawn water potential and indirectly by recording trends in soil moisture for use in the modelling of rooting depths.

**Soil moisture.** Soil access tubes were installed at $SAV_{\text{deep}}$ to allow periodic measurements of soil water content ($\theta$) using a PR2 capacitance probe (Delta-T Devices, Ltd., Cambridge, UK). Measurements using the PR2 probe were made at least once a week to a depth of 20 to 40 cm, depending on depth to rock. One location was chosen under each of the targeted woody species. The PR2 capacitance probe was calibrated using a similar clayey soil, Slidell silty clay, collected approximately 150 km from the study area.

$\theta$ measurements from $SAV_{\text{shallow}}$ and FOR were obtained from ECH20 EC-5, 5TE capacitance soil moisture sensors (Decagon Devices, Pullman, WA), recorded on a Campbell Scientific CR10X data logger every 30 min and calibrated using the default manufacturer’s equation. At $SAV_{\text{shallow}}$, two sensors were located under an isolated juniper tree at depths of 5 and 10 cm, and two sensors were located under an isolated mesquite tree at depths of 5 and 15 cm. At FOR, two sensors were located under the mixed canopy at depths of 10 and 20 cm. Daily averages were then calculated for use in model parameterization. Because different soil moisture techniques were used between the three sites, we did not make absolute comparisons between sites; rather we focused on the relative differences in soil moisture dynamics.

**Sap flux.** Sap flux rates were measured by the heat dissipation method using both the original Granier (1987) technique and the Goulden and Field (1994) method. All sap flow sensors were 10 mm in length. Instantaneous measurements taken from sap flow gauges at 30-s intervals were averaged every 30 min using a model CR10X data logger (Campbell Scientific, Logan, UT). Background temperature fluxes (BTF) affecting the original-type Granier sensors were compensated for by subtracting a separately measured average diurnal BTF for each species and site. Goulden and Field-type sensors were found to be significantly less susceptible to BTF and were therefore not compensated. Sap flux per sapwood area per second (kg m$^{-2}$ s$^{-1}$) for each sensor was found according to the Granier method (Lu et al., 2004) and then summed to find the daily total sap flux per sensor. An average daily sap flux rate was then based on four sensors for mesquite and five sensors for juniper and oak that were functioning consistently throughout the entire study period at each site. Minimal gap filling was performed using species-specific equations derived from working sensors. In the case of oaks, both sites had about the same amount of gap filling (<25%). Even less gap filling was needed for juniper at the $SAV_{\text{shallow}}$ site, but slightly more was needed at FOR. Juniper sensors at $SAV_{\text{deep}}$ and mesquite sensors at both sites required minimal gap filling (<5%).

The sapwood area for each tree was estimated from basal diameters (section on Sap Flux) using species-specific correlations found as a result of a comprehensive sapwood area survey (G. Moore, personal communication). In this survey, the sapwood area of nearby mesquite trees was delineated from digital photos of 18 cut stumps and correlated with their basal area ($R^2 = 0.78$). The sapwood area of 13 oak trees was estimated from 5-mm-diameter core samples (two per tree) and correlated with basal diameters ($R^2 = 0.66$; G. Moore, personal communication). Juniper sapwood area was estimated from basal area using a pre-established relationship ($R^2 = 0.94$) developed from a very large ($N \sim 100$) set of cut trees with similar growing conditions at a site located approximately 40 km south-west (Owens et al., 2006). Finally, an average sapwood area per ground area was found for each of the dominant species from the vegetation surveys. In addition, the projected canopy area of all sap flux trees was estimated from two perpendicular crown radius measurements per sapwood tree to estimate canopy sap flux at the savanna sites. Figure 4 shows the sapwood area of the woody vegetation for the three sites. Sapwood area per ground area is highest at FOR, whereas on average, almost no difference was found between $SAV_{\text{shallow}}$ and $SAV_{\text{deep}}$. $SAV_{\text{deep}}$ had considerably more spatial variation in vegetation type and abundance, compared with the other sites, as a result of larger clumped vegetation patches and larger open areas than $SAV_{\text{shallow}}$. Both savanna sites had a similar spatial extent of juniper, whereas FOR had approximately twice as much juniper sapwood per ground.

Figure 4. Results of the woody vegetation survey at the three sites. Error bars represent one standard deviation from the mean for all species combined. FOR, forested site; $SAV_{\text{deep}}$, savanna site with deep soil; $SAV_{\text{shallow}}$, savanna site with shallow soil.
area compared with oak, and a total of nearly three times more woody vegetation sapwood than the savanna sites.

Leaf water potential. Because soil water instruments could not be installed below a depth of 20 cm owing to the rocky terrain, water stress was assessed by taking pre-dawn leaf water potential ($\Psi_p$) measurements, initially every 2 weeks and then every 2 days after a large rain event. One hour before dawn on each of the ten sampling dates, two fully developed mesquite and oak leaves and two juniper twigs were taken from each of the marked sap flow trees at the savanna sites and analysed within 2 h using a model 670 leaf pressure chamber instrument (PMS Inc., Corvallis, OR). At FOR, five samples per species were taken from trees located next to access towers <10 m from the sap flow trees, because the sap flow tree canopies were above reach.

Data analysis
To determine if there was a significant difference among species in transpiration and water availability, we carried out a repeated-measures mixed-model analysis of pre-dawn leaf water potential ($\Psi_p$) and sap flux measurements using the analytical software SPS 17.0. The $\Psi_p$ repeated-measures mixed model was multilevel. Sampled replicates were nested within sampled tree and were both considered random factors. The date of sampling was considered the repeated effect, and the species and site were both considered to be fixed factors. Site differences, species differences and species × site interactions for each site and species combination were tested to examine whether site or species affect $\Psi_p$ and whether the difference between species depends on the site. An additional repeated-measures mixed-model analysis was conducted on data isolated from the two driest days (day 105, April 14, and day 133, May 12) to see if the same trends were observed during the driest conditions.

The sap flux data were divided into two main periods between rain events to see if there were species-specific responses to the dry-down. The two clusters between major rain events (day 71, 55 mm; day 85, 9 mm; day 107, 4–11 mm; day 117, 49–52 mm; and day 136, 49–66 mm) were days 85–107 (Mar 28–Apr 17) and days 119–135 (Apr 29–May 15). Data were available from all three sites at these times, and for clarity, we refer to them as the first and second dry-down periods, respectively. The date of sampling was considered the repeated effect, and the species and site were both considered to be fixed factors. Site differences, species differences and species × site interactions for each site and species combination were tested to examine whether site or species affect $\Psi_p$ and whether the difference between species depends on the site. An additional repeated-measures mixed-model analysis was conducted on data isolated from the two driest days (day 105, April 14, and day 133, May 12) to see if the same trends were observed during the driest conditions.

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Modelling species-specific plant water use
A vertical soil–plant–atmosphere water transfer model, 1DWTB (Rebel et al., 2005), was parameterized to simulate the exchange of water in the soil–plant–atmosphere interface on the Edwards Plateau, for days 1–150 of 2009 (January to May). Input data included atmospheric data collected from (or near) each site, e.g. precipitation, net radiation, ambient temperature, humidity and wind speed. Potential evapotranspiration ($PET$) was calculated by using the Penman–Monteith equation. Model parameters include basic soil parameters such as saturated water content ($SAT$), field capacity ($FC$), permanent wilting point ($PWP$), drainage coefficient ($SWCON$) and soil depth, as well as number of layers and vegetation parameters such as rooting depth, root distribution, LAI and extinction coefficient.

A capacitance approach was used to simulate the soil water movement and storage through a series of layers in the vertical soil column. Water is transferred downward if water content exceeds $FC$, with the rate of downward movement depending on the $SWCON$. Root densities in each layer partition the transpiration demand in the soil profile. However, when the transpirational demand in one layer cannot be met, the demand will be transferred to a deeper layer, up to the last layer where roots are present. When the plant-available water (defined as current water content – $PWP$) for the root profile is less than the transpirational demand, the potential transpiration will be limited to actual transpiration (Butler and Riha, 1992).

To partition $PET$ into potential transpiration and potential evaporation, we used the fraction of solar radiation intercepted by the canopy (Landsberg, 1986; Norman and Campbell, 1989), which is a function of the measured LAI and light extinction coefficient ($k$), resulting in a dimensionless vegetation factor ($VegFac$, Equation (2)).

\[
VegFac = 1 - e^{-k\text{LAI}}
\]  

Rebel et al. (2005) performed a model sensitivity analysis and found that VegFac had the greatest influence on the simulated soil water content, followed by the parameter $FC$. The model was least sensitive to the soil hydraulic conductivity and $PWP$.

Model parameterization and calibration. The model was parameterized to simulate soil water content ($\theta$) and tree transpiration fluxes at each of the sites for each plant species. All model simulations contained 12 soil layers, which increased in thickness with soil depth to a total depth of 1 m. Measured $\theta$ values were used to parameterize $SAT$, $FC$, $PWP$, $SWCON$ and root distribution. Rooting depth was then parameterized using $\Psi_p$ measurements. The $\theta$ sensors were each considered separately for each dominant species present at the location to account for the vegetation effect and differing sensor depths in the soil column at $SAV_{shallow}$ and $SAV_{deep}$. It was not possible at the FOR site to separate the species because the vegetation and therefore the roots are mixed and inseparable. Woody plant LAI was measured directly, whereas $k$’s were taken from the literature and the VegFac was calculated according to Equation (2) (Table II).

A sensitivity analysis of the model (Rebel et al., 2005) has shown that $SAT$ is a very unsensitive parameter. We have parameterized $SAT$ using the highest measured $\theta$ data from each sensor. Higher values of $SAT$ did not change the model behaviour. $PWP$ was parameterized using $\theta$ data from each sensor when the soil was driest. $FC$ was parameterized using $\theta$ data from each sensor several days after large precipitation.
events, for each soil depth and site. Root distribution was estimated by inverse modelling the soil water dynamics in dry periods, when sensitivity of soil water dynamics to root water uptake is largest (Musters and Bouten, 1999; Dekker et al., 2000), whereas the drainage factor (SWCON) was estimated by inverse modelling the soil water dynamics in wet periods, when sensitivity of soil water dynamics to water drainage is largest. We first assumed root distributions to decline exponentially with depth and root depth to be equal to the estimated average soil depth. We then adjusted these parameters, first from a visual assessment to account for the temporal behaviour in the different layers. Afterwards, the optimal parameters were determined iteratively using the minimal bias objective function between modelled and measured \( \theta \) (bias = \( \Sigma (\theta_{\text{obs}} - \theta_{\text{mean}}) \times (\theta_{\text{mean}})^{-1} \)). Lastly, we estimated rooting depth for each of the three species by evaluating plant water stress, measured as \( \Psi_p \) and simulated as an index of actual transpiration divided by potential transpiration. These parameterization steps were iterated until optimization for the parameters FC, SWCON, root distribution and rooting depth was achieved. The parameters SAT, PWP, LAI and \( k \) were kept constant.

The model was verified by visually evaluating the simulated transpiration flux against the measured daily sap flux records, both scaled between 0 and 1 (max modelled and measured) to match the transpiration dynamics. Because the soil water use by juniper and oak trees could not be separated under the closed canopy at FOR, the predicted transpiration rates at this site were compared with the combined sap flux of juniper and oak per square metre of ground cover. At the savanna sites, however, each species was considered separately, and predicted transpiration was compared with sap flux per square metre of the projected canopy area.

As mentioned in the section on Modelling Species-specific Plant Water Use, the most sensitive model parameters were Vegfac and FC (Rebel et al., 2005). Changing the dimensionless vegetation parameter (Vegfac) from 0.5 to 0.95 altered the model efficiency (the ratio of evapotranspiration to transpiration based on LAI and \( k \); Rebel et al., 2005) by 30%, whereas a 20% change in FC resulted in a 10% change in model efficiency. Vegfac, which represents the fraction of solar radiation intercepted by the canopy, was calculated using LAI and \( k \). A positive change in LAI or \( k \) results in a positive change in the Vegfac and subsequently a positive change in the amount of PET partitioned into potential transpiration. An increase in potential transpiration would be limited only by the plant-available soil water, resulting in potentially higher and/or faster plant water use and drier soils and/or faster drying out of the soils after rain events. However, because LAI is measured directly for each tree at each site and \( k \)'s were taken from the literature for each species, we feel confident in the accuracy of this parameter. Further, spatial variability in soil moisture is not accounted for because we only incorporated one sensor under each tree type, at each depth and site. We therefore focus on dynamics rather than specific values to reduce the importance of spatial variability in soil moisture.

**RESULTS**

**Site and species comparison**

As mentioned in the Climate section, although spring was not particularly dry, the winter leading up to our first measurements was very dry and may have impacted on the plants as described in the discussion.

**Site comparisons.** Patterns in juniper sap flux differed between the forest and savanna sites earlier in the season but converged later in the season as fluxes at FOR declined (Figure 5a). Juniper sap flux during the first dry-down period, depicted as grey in Figure 5a between days 85 and 107, was much greater at FOR than at both savanna sites (repeated-measures analysis for the first dry-down period: \( \text{SAV}_{\text{shallow}} P = 0.008 \) and \( \text{SAV}_{\text{deep}} P = 0.009 \)). This difference was however not observed during the second dry-down period, between days 119 and 135 (\( P = 0.05 \)). Not only did Juniper at FOR had higher transpiration rates per sapwood area during this first dry-down period but water potentials also responded more strongly to the first rain event compared with later in the season (Figure 5b). Figure 5b also shows that juniper \( \Psi_p \) decreases faster at FOR after the first spring rain event, to a point just before the next rain event around day 105, when these trees were more stressed than trees at the savanna sites (second to fourth measurements). Water potentials did not drop as fast in the second dry-down in conjunction with lower transpiration rates. Juniper sap flow rates converged later in the season among sites and were generally lower at FOR and \( \text{SAV}_{\text{shallow}} \) compared with earlier in the season, despite following a series of rain events around days 117–120. During this wetter period, junipers at \( \text{SAV}_{\text{deep}} \) were transpiring significantly more per sapwood area than at \( \text{SAV}_{\text{shallow}} \) (pairwise comparison, \( P = 0.098 \)).

Mesquite trees had similar access to soil water at the two savanna sites (Figure 5c, d). No significant differences were observed in \( \Psi_p \) or the sap flux (repeated-measures analysis, \( P > 0.05 \)). Although mean sap flux appeared to be higher at \( \text{SAV}_{\text{shallow}} \), during the first dry-down, very high sensor-to-sensor variability rendered differences undetectable. Interestingly, fluxes were more dynamic at \( \text{SAV}_{\text{shallow}} \) where maximum LAI was highest (Figure 5c).

The \( \Psi_p \) and sap flux rates of oak trees at the two sites during the dry-down periods were not found to differ (repeated-measures analysis, \( P > 0.05 \)). Therefore, the oak trees at the FOR and \( \text{SAV}_{\text{deep}} \) sites apparently had similar access to soil water (Figure 5e, f). Nevertheless, oak trees at \( \text{SAV}_{\text{deep}} \) responded to the large rain event on day 70 with a greater initial increase in \( \Psi_p \) than those at FOR (Figure 5f), but then \( \Psi_p \) declined after 2 weeks without significant rainfall. Unfortunately, sap flux data were missing from \( \text{SAV}_{\text{deep}} \) during this event.

**Species comparisons.** The greatest differences among species were observed at FOR (Figure 5) where juniper transpired more per sapwood area than oak during the first dry-down period (repeated-measures mixed-model analysis, \( P = 0.024 \)). Juniper sap flux declined sharply during this time, and the difference was no longer observed during the second
Both juniper and oak responded strongly to the first large rain event at day 70, increasing rapidly in transpiration shortly afterwards. Interestingly, juniper $\Psi_p$ increased the most in response to that event, but then $\Psi_p$ steadily declined, whereas oaks at FOR appear to steadily increase their $\Psi_p$ during this time. No differences in transpiration per sapwood area or $\Psi_p$ were observed among species at SAVshallow or SAVdeep (repeated-measures analysis, $P > 0.05$). This suggests that all species responded similarly to water stress in these sites with deeper soils than FOR.

Site and species interactions. The magnitude of difference in sap flux between juniper and oak depended on the site (repeated-measures mixed-model analysis, $P = 0.02$). Clearly, the two species differed the most at FOR during the first dry-down period. However, the sap flux response of juniper and mesquite to soil moisture decline did not differ between the two savanna sites (repeated-measures mixed-model analysis of species or site $\times$ species, $P > 0.05$).

Neither site nor species had a significant effect on $\Psi_p$ (repeated-measures mixed-model analysis, $P > 0.05$). However, when the two driest periods were isolated (days 105 and 133; Figure 6), species differences accounted for the most variation in $\Psi_p$ ($P = 0.03$), and the magnitude of difference depended on the site (site $\times$ species, $P = 0.03$). Table III shows that $\Psi_p$ was significantly lower during dry periods in juniper than in oaks. Mesquite and oaks had similar $\Psi_p$ at the savanna site. This may indicate the
Soil moisture dynamics. The optimized soil and vegetation parameters are shown in Table IV and Figure 7, and the accompanying best fit θ for the FOR and SAV shallow sites are shown in Figure 8. SAV deep had too few θ measurements to confidently parameterize the model. At the SAV shallow site, soils under juniper dried out more between rain events than soils under mesquite, and soils under mesquite dried out more between rain events than soils under juniper, and soils under mesquite dried out faster later in the season than in the early season as LAI increased (Figure 4). At SAV shallow, a divergence between modelled and actual θ is only seen when smaller rain events are not registered by shallow θ sensors under the juniper or mesquite trees (Figure 8). At FOR, the peak in θ that was expected after the rain event at day 70 was not recorded by the 10-cm-deep θ sensor (Figure 8). These small discrepancies could be accounted for by the processes of canopy interception (the small rainfall events at SAV shallow) and surface run off (the larger rain event on day 70 at FOR).

Table III. Pairwise site and species comparisons from repeated-measures mixed-model analysis of the Ψp on the two driest days sampled during spring 2009.

<table>
<thead>
<tr>
<th>Subject</th>
<th>Comparison</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td>FOR</td>
<td></td>
</tr>
<tr>
<td>SAVshallow</td>
<td>Juniper versus live oak</td>
<td>0.000**</td>
</tr>
<tr>
<td>SAVdeep</td>
<td>Juniper versus live oak</td>
<td>0.064*</td>
</tr>
<tr>
<td>Species</td>
<td>Ashe juniper</td>
<td></td>
</tr>
<tr>
<td>FOR versus SAVshallow</td>
<td>0.823</td>
<td></td>
</tr>
<tr>
<td>FOR versus SAVdeep</td>
<td>0.287</td>
<td></td>
</tr>
<tr>
<td>SAVshallow versus SAVdeep</td>
<td>0.177</td>
<td></td>
</tr>
<tr>
<td>Honey mesquite</td>
<td>FOR versus SAVdeep</td>
<td>0.061*</td>
</tr>
<tr>
<td>Live oak</td>
<td>FOR versus SAVdeep</td>
<td>0.061*</td>
</tr>
</tbody>
</table>

*Significant at the 0.01 level.
**Significant at the 0.05 level.

following: (a) junipers were drying out soils more than oaks and/or (b) juniper and oaks were not rooted in the same place or depth.

1DWVTB model parameterization

Results from the 1DWVTB model simulations have been divided into three sections: parameterization using soil moisture (θ) dynamics, rooting distribution and depth and transpiration dynamics.

Roots. Root distributions were estimated using soil water content dynamics (dry-down), and rooting depth was estimated using measured Ψp (section on Modelling Species-specific Plant Water Use). The resulting rooting depths (Figure 7) were generally shallow compared with previously recorded rooting depths for juniper, oak and mesquite (Jackson et al., 1996); however, they are not unrealistic given the shallow soil depths at the Freeman Ranch. At the shallow-soil forest site, the estimated average soil depth was 17 cm, with 95% of the measured soil depth between 0 and 40 cm. Owing to the optimized (combined juniper and oak) root depth at the FOR site was 40 cm, we found that the tree roots at this site either extend into the cracks between rocks, although not explicitly simulated in the model, or tend to go to the deepest parts of the soil because there is significant spatial variation in soil depth (Figure 2). At SAV shallow, 95% of the measured soil depth was between 0 and 52 cm, whereas juniper was predicted to have roots going down to almost 60-cm depth; it is likely that SAV shallow has deeper soils than we physically measured because of the numerous rocks in the soil matrix.

Using the model, we found mesquite trees to have very shallow roots at SAV shallow; however, because of the discrepancies between the very low measured canopy sap fluxes (0.27 mm m⁻² day⁻¹ SAV shallow) and the amount of root water uptake that is predicted from the soil water measurements, it is likely that unknown processes were occurring with mesquite trees that were not accounted for in the model. For example, the soil water content could have gone down because of soil evaporation and/or root water uptake from other vegetation.
Modelled transpiration and water availability. Generally, the model captured the dynamics of the recorded species-specific sap flux rates, $\Psi_p$'s, and the predicted transpiration dynamics well (Figure 9). Juniper leaf water stress increased at all sites around day 105, which was reflected in the model by a reduction in the percentage of actual transpiration relative to the potential transpiration at FOR and SAVshallow. Simulated juniper transpiration dynamics fit the data well early, but not later in the spring season. Between days 110–150, the $\Psi_p$'s values do not show soil water stress, and the soil water content values (Figure 8) show no water limitation either. However, at the FOR and SAVshallow sites, measured sap fluxes decline relative to modelled values. Because the model does not simulate any soil water stress as well (Figure 9, actual transpiration divided by potential transpiration), the model over-predicts transpiration later in the season.

A similar trend was found in mesquite trees growing at SAVshallow. The model and the data do not predict that mesquite experiences any soil water stress (Figure 9), but we do find a reduction in measured sap flux later in the season. This mismatch between the model and the data later in the season was not as severe at SAVshallow as FOR (Figure 9), but it appears that all the trees were experiencing some late-spring water stress at SAVshallow and FOR. At SAVdeep, we do not see the same declining temporal behaviour in measured sap fluxes of juniper, mesquite or oak.

DISCUSSION

We have found some evidence that plant-available water was greater at SAVdeep and SAVshallow than at FOR where the soils were shallowest, which we expected because of higher soil water storage. The predicted root depths were also slightly less, and we observed the most rapid decline in transpiration at the FOR site compared with that at the SAVdeep or SAVshallow. In particular, juniper was more sensitive to site differences than mesquite or oak. The decline in transpiration over time was not as severe at SAVshallow and was minimal at SAVdeep, suggesting that the depth of the soil at each site limits the plant-available water. Because direct soil moisture stress is not clear (Figure 8), it is possible that these trees did not have sufficient time to recover from embolism that occurred during the preceding dry winter, rendering them more susceptible to increasing vapour pressure deficits. During the second dry-down period around early May, temperatures heated up, and likewise, the vapour pressure deficit increased and was likely a significant source of stress. However, the transpiration rates may also be less than we expect later in the season at FOR because the available soil water is declining faster than at the savanna sites because of the larger density of sapwood (Figure 4), which contributes to a larger total transpiration demand.

Mesquite transpiration during the second dry-down period had the same behaviour as juniper, shutting down at SAVshallow and not at SAVdeep, which further supports our
hypothesis that plant-available water was higher in deeper soils. Given the rapid increase in mesquite LAI throughout our study period, we were surprised to find that mesquite did not increase transpiration over time. It is likely that the reduction in mesquite sap flux at SAV\textsubscript{shallow} later in the season without obvious signs of leaf stress is an adaptive feature of this species. Wan and Sosebee (1991) found that the stomatal conductance of mesquite is very responsive to soil water availability and dryness of the air and is less responsive to internal water status. Dugas et al. (1992) found that when moisture was limited, mesquite trees decreased transpiration rates by 35–75%. Eggemeyer and Schwinning (2009) also reported that during summer drought, mesquite was not more water stressed compared with juniper but that their photosynthetic rate was minimized to levels below that of juniper. Interestingly, we did not see the same reduction in transpiration at the deeper-soil SAV\textsubscript{deep}. SAV\textsubscript{deep} trees performed consistently better and more even in their sap fluxes in the second dry-down period, when it was wetter (Figure 5), whereas SAV\textsubscript{shallow} trees were much more dynamic and responsive to rain, suggesting that the mesquite trees were more stressed at SAV\textsubscript{shallow}. However, the mesquite trees at SAV\textsubscript{shallow} were on average larger and accumulated more leaf area than trees at SAV\textsubscript{deep}.

In contrast to juniper and mesquite, oak sap fluxes and $\Psi_p$ between FOR and SAV\textsubscript{deep} suggests that there is no difference in the soil water available to the oak trees at both sites. Thus, we did not find evidence to support our hypothesis that the increased soil water storage in the deeper soils would facilitate higher transpiration rates of oaks.

Differences between sites were not necessarily driven by differences in rooting depth. We found strong indications that plants used less water as the season progressed than the model predicted, which indicates that mechanisms outside the model’s parameters are being employed in response to water stress, for example in the form of stomatal regulation of leaf gas exchange. We found no evidence that any species gained access to deep moisture sources via deep roots, as for instance shown by Philips (1963). Instead, the rooting depth appears to be primarily constrained by the apparent soil depth of the sites.
This is consistent with Schwinning (2008) who found that juniper and oak trees likely only reduce water storage in the uppermost layers. Our model predictions of shallow-root distributions at FOR concur with a physical survey of the root distribution at this site (Heilman et al., 2009), which found that most roots concentrated in the top 20 cm of soil, above a rock layer, and that relatively few roots were below this point in rock cracks and fissures. Live oak and juniper were both predicted to have only modestly deeper root distributions in the savannas. Nevertheless, the model is a representation of the measured soil moisture dynamics of one specific sensor at each depth under each vegetation type. For us to have upscaled results, it would be useful to have multiple sensors at multiple depths for each vegetation type to account for spatial variation.

Contrary to expectations, we observed very little species-specific differentiation in access to water stored in the bedrock. Instead, all three species were probably shallow rooted because they responded similarly to surface soil moisture dynamics. Minor differences in $\Psi_p$ between species were more pronounced during dry periods, when juniper had lower $\Psi_p$ than oak and some mesquite trees (Table III). This supports the earlier findings that juniper has high resistance to xylem embolism (Fonteyn et al., 1985; Willson and Jackson, 2006; Willson et al., 2008) and, therefore, an ability to withstand low soil water potentials. At FOR, juniper responded more to early spring rain events despite having an apparent higher water stress during dry periods. These findings of a competitive advantage of juniper are consistent with Schwinning (2008) who found that live oak trees always had higher pre-dawn water potentials than Ashe juniper during drought and that live oaks are less capable of maintaining gas exchange at low water potentials. The reduced capacity of live oak trees to respond to the initial rain at the beginning of 2009, after an extended period without rain, could be due to cavitation.

Live oak has much larger conduit diameters than Ashe juniper (McElrone et al., 2004), a fact that partly explains why oaks are more vulnerable to embolism than junipers. Oaks generally avoid embolism through stomatal regulation (Tyree and Cochard, 1996). In the event that embolism does occur, embolized conduits can possibly be refilled by dissolution of the bubble, which can take place at moderately negative xylem pressures, and recover their function. However, there is some evidence that embolized conduits with larger diameters, such as those in oak, are more difficult to refi ll (Sperry, 1995). This reduced ability to recover from cavitation may explain why the oaks in this study were not responding strongly to rain events after the very dry winter period. This is contrary to expectations that live oak, with large diameter vessels that maximizes conductance, would be more responsive to precipitation pulses than juniper in terms of leaf gas exchange, as found by Bendevi s et al. (2010).

Juniper roots on the other hand appear to tolerate the high soil moisture stress found in shallow soils during dry periods and are, therefore, more readily able to respond to precipitation, a fact that Owens and Schreiber (1992) found as the likely reason that juniper can outcompete live oak and may explain why junipers could take more water from the soil than oak at FOR earlier in the season. The lower and less responsive oak sap fluxes throughout the rest of the season may also indicate that oak trees were stressed much earlier than juniper trees.

In contrast to FOR, our study found no significant differences between the transpiration of juniper and oak at a relatively deep-soil savanna site. At this site, juniper did not even respond noticeably more to precipitation events relative to other species, highlighting the importance of site characteristics on the competitive advantage and water usage of juniper. Variations in rooting depth are often known to complement differences in drought tolerance and temporal resource demand (Davis and Mooney, 1986; Schenk and Jackson, 2002). However, our data show no evidence for differentiation between the root profiles at $SAV_{deep}$ and FOR.

**CONCLUSIONS**

We found that the dominant trees at our study site on the Edwards Plateau, Ashe juniper, live oak and honey mesquite, have similar water use behaviour at two relatively deep-soil savanna sites. However, water use of Ashe juniper, a species that has increased dramatically in abundance in the Edwards Plateau savannas over the past century, is sensitive to site-specific soil differences. At the Ashe juniper–live oak forest site with shallow soils, juniper trees had higher transpiration rates after early spring rain, compared with live oak trees at the same location. After the harsh dry winter preceding this study, juniper was able to take more advantage of the first major spring rain event on these very shallow soils, compared with the other woody vegetation. Later in the season, all the woody vegetation responded less to rain, indicating that the trees were stressed, maybe in relation to the rising vapour pressure deficit.

Using the 1DWTB model, we predict that roots do not typically extend below the rock layer into cracks but were mostly constrained by the apparent soil depth of the sites. We conclude that the woody encroachers do not have access to perennially stable water supplies and are in fact accessing very similar water resources as the live oak trees. These results provide new evidence that these species perform similarly on shallow soils and that their water use is restricted by soil depth. The only species-specific water use strategy found important in determining transpiration losses was that of the encroacher juniper, who was able to withstand low soil water potentials and transpire more after rain events after a long dry period in very shallow soils. We find therefore that Juniper is likely to have a long-term advantage over live oak on very shallow soils but is not likely to deplete deep-water storages.

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