

Small-scale variability in water storage and plant available water in shallow, rocky soils

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Abstract

Background and aims We quantified spatial variability in water storage and plant access to water in the rocky soils of a karst savanna dominated by Ashe juniper (*Juniperus ashei*) and honey mesquite (*Prosopis glandulosa*).

Methods In a 25×25 m grid with 5-m node spacing, water content and bulk density profiles were measured to a depth of 1.6 m by a combination of time domain reflectometry, neutron thermalization and gamma ray densitometry. Changes in water content were used to infer recharge and plant uptake of soil water. Predawn water potentials of trees were sampled periodically to evaluate individual differences in water access.

Results Pore volume and maximum water storage varied between 0.24 and 0.42 m³ m⁻³, and 198 to 431 mm, respectively, across the 36 individual profiles. Porosity

accounted for 19 and 20 % and depth for 35 and 61 % of the variation in uptake and recharge, respectively. Predawn water potentials were consistently different among individual trees over multiple dry seasons.

Conclusions Unequal water status among trees was consistent with the variability of recharge and uptake in the rooting zone, suggesting that trees cannot fully compensate for spatial variability in soil properties by roots foraging for water.

Keywords Karst · Soil water storage capacity · Root distribution · Root water access

Introduction

The capacity of an ecosystem to store plant-available water is a primary regulator of ecohydrological processes and pivotal for evaluating the potential impact of land use changes on local and regional water balances and water resource management (Laio et al. 2001; Seyfried and Wilcox 2006). The term available water capacity (AWC) refers to the difference in root zone water content between permanent wilting point and field capacity, equivalent to an upper limit to the amount of stored water useful to plants (Federer et al. 2003). In semi-arid to sub-humid systems, where annual precipitation approximately equals annual potential ET, AWC has substantial control over the fractions of precipitation partitioned into ET and deep drainage (Milly and Dunne 1994).

In reality, AWC is an abstraction of complex water transfer and uptake processes near the soil surface and

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not easy to quantify (Guswa et al. 2002). The AWC concept assumes that there is a spatially uniform storage “bucket” of invariant size to which plant roots have access. Inaccuracies stemming from the bucket representation of the rhizosphere have been discussed at length in the literature and include uncertainties in determining the maximal effective rooting depth of plants and setting realistic values for field capacity and the water extraction limit for plants (Federer et al. 2003). In a sensitivity analysis of ET for nine locations in North America, Federer et al. (2003) ranked the magnitude of error associated with uncertainty in AWC third, less serious only than uncertainty in climate and cover type, and more serious than uncertainties associated with infiltration patterns and hydraulic redistribution.

The bucket representation of AWC is particularly problematic and untested in landscapes characterized by shallow, rocky soils. This condition is frequently found in, but not limited to, karst terrain. Karst is formed by dissolution of soluble rock, mainly limestone and dolomite. The scarcity of soil compared to rock in such landscapes limits water retention (Fiés et al. 2002) and affects permeability (Sauer and Logsdon 2002). Soil grades into fractured rock, and fractured rock into bedrock in such environments, with scattered rocks and boulders embedded within soil layers, and soil pockets scattered within rock layers (Estrada-Medina et al. 2013). Conditions in these heterogeneous structured soils are conducive to non-uniform flow, causing irregular wetting of the soil profile (Gerke 2006).

The problem of non-uniform flow in unsaturated soils and fractured rock is well known to hydrology, but investigated chiefly in relation to groundwater recharge and contaminant transport (Bazan et al. 2013). To our knowledge, what these conditions imply for root development and the water relations of the resident vegetation has not received much attention.

Roots in rock typically grow much deeper than in uniform soils (Schenk 2008), tens of meters instead of just meters, but deep roots are also scarce (Katsura et al. 2009; Grigg et al. 2010; Estrada-Medina et al. 2013). The main water source used by woody plants in karst, besides the shallow soil, is associated with soil pockets or clay layers that occur within a few meters of the surface (Estrada-Medina et al. 2013; Querejeta et al. 2006). Consequently, large fractions of the rooting zone may be unusable to plants or simply unused for

lack of access. How such heterogeneity in the water storage capacity of different materials, coupled with orders of magnitude difference in root density, translate into an average effective AWC remains an open question.

We examined this question using two complementary approaches. At a site known for its high rock content and shallow bedrock layer, we took periodic measurement of predawn water potentials on two dominant tree species over 2.5 years. We hypothesized that individual trees would express unequal access to stored water by showing consistent differences in the minimum observed water potentials over successive dry periods. Secondly, we took periodic measurements of soil water content across 36 vertical profiles within a 25 by 25 m plot area to measure spatial variation in water content and dynamics at a scale relevant to individual root systems. We hypothesized that we would find a wide range of values for maximal water content, depletion and recharge, and that this variation would only be partially correlated with differences in porosity, due to non-uniform flow of soil water and heterogeneous root densities. The site was also instrumented with a weather station and eddy flux tower, so that the spatially-averaged precipitation input and evapotranspiration output could be compared to observed changes in water content at the plot scale.

Materials and methods

Site description

The research site (29.9495° N, 97.9962° W) is a savanna on the Freeman Ranch, a 1,700 ha research area near San Marcos, Texas, USA. It contains clusters of Ashe juniper and mesquite (*Prosopis glandulosa* Torr.) interspersed among grassland dominated by King Ranch bluestem (*Bothriochloa ischaemum* (L.) Keng) and Texas wintergrass (*Nassella leucotricha* (Trin. & Rupr.) Pohl). Areal densities of juniper and mesquite were 340 ha⁻¹ and 300 ha⁻¹, respectively. Seasonal maximum leaf area indices were 1.81 m² m⁻² for juniper and 0.65 m² m⁻² for mesquite (Elkington et al. 2012). The soil is a Rumble gravelly clay loam (clayey-skeletal, mixed, active, thermic Typic Argiustolls, 1 % slope) with chert fragments occupying ~50 % of the volume between depths of 0.2 and 1.0 m. Limestone residuum occurs at depths of 1 to 1.5 m.

In 2006, we dug a 5.4-m long, 1.5 to 2-m deep trench near two mature mesquite and juniper trees at a location 80 m north of the instrumented plot to map root distribution. Working towards the tree trunks, all roots of diameters ≥ 3 mm were counted in $10 \times 10 \times 10$ cm soil volume increments, over a maximal width of 2 m. By tracing the roots back to the central root, we distinguished between juniper and mesquite roots. Lumping root counts in 10 cm depth increments showed that the root densities of both species peaked between 0.3 and 0.4 m and were much lower below 0.8-m depth (Fig. 1). Nevertheless we did see isolated roots of both species disappear into the bedrock at 1.5 to 2-m depth.

Predawn water potentials

Predawn water potentials were monitored between June 2009 and August 2011 on juniper and mesquite trees in and near the water content measurement grid (within an approximately 25-m radius). Terminal branches from 6 trees of each species were clipped and stored in sealed plastic bags until water potentials were measured with a Scholander pressure chamber (PMS Instruments, Albany, OR, USA), at most within an hour after clipping. The same trees were repeatedly sampled. Our experience with water potential measurements indicates that the method we used does not create high variability, especially compared to seasonal variability or variability among individuals.

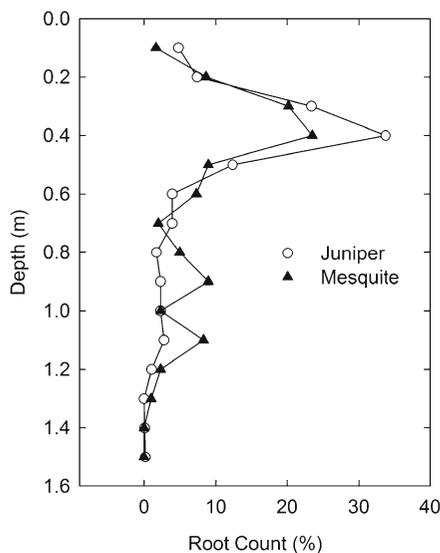


Fig. 1 Root count profiles for a juniper and a mesquite mapped in a trench excavated near the water content measurement grid

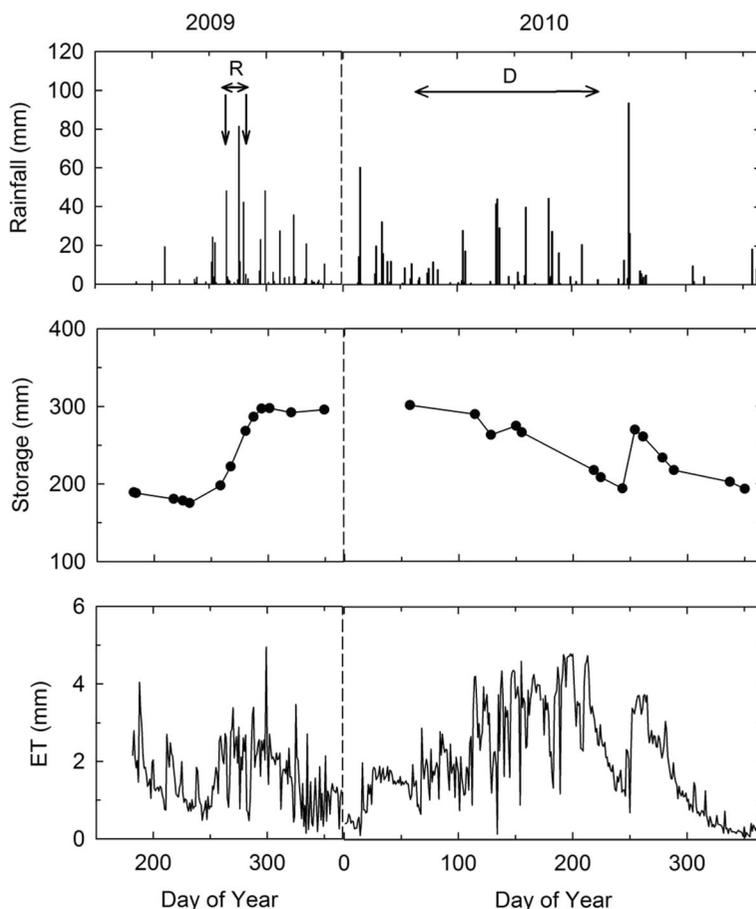
Water content measurements

In the summer of 2009, 36 aluminum access tubes (5.1-cm diam.) were installed in a 25×25 m grid (5 m node spacing) for neutron probe measurements of volumetric soil water content θ . The measurement grid was located in the fetch footprint of an eddy covariance flux tower (AmeriFlux site US-FR2). Bore holes were drilled to a depth of 1.6 m using a 8.9-cm diam. screw auger attached to a truck-mounted drill rig (CME 75, Central Mine Equipment Co., St. Louis, MO), and access tubes inserted and sealed with expandable polyurethane foam (Poly-Set, Utility Structural Systems, Arlington, TX) as described by Tokumoto et al. (2011). At some locations, the drill encountered impenetrable rock. In these cases, the drill was repositioned near the original location, usually within 0.5 m, a new hole was bored and the access tube inserted. However, at eight locations, rock was still encountered at depths of 1 to 1.4 m, despite multiple repositioning of the drill. Insertion of access tubes at these locations was restricted to depths at which rock was hit. Water content profiles were measured at 0.2-m depth intervals, beginning at 0.2 m below the soil surface, using a CPN Model 503DR neutron moisture gauge (Instrotek, Inc., Raleigh, CA). Neutron probe measurement intervals ranged from days to weeks depending on amount and frequency of rainfall. Water content in the upper 0.15 m was measured by time domain reflectometry (TDR) with probes installed near the access tubes. Wet bulk density (ρ_{wet}) profiles were measured through each access tube using a model CPN 501DR density probe (Campbell Pacific Nuclear Corp.). Neutron and density probes were calibrated in a 190 L drum with known volumes of soil, rock, and water (Tokumoto et al. 2012). Dry bulk density (ρ_b) was estimated by subtracting the product of the density of water and volumetric water content from ρ_{wet} . TDR measurements were recorded every 6 h by a model CR1000 datalogger (Campbell Scientific, Logan, UT). Porosity was calculated as $1 - \rho_b / \rho_s$ where ρ_s is particle density (2.6 Mg m^{-3} for the clay loam and rock) (Tokumoto et al. 2012).

Evapotranspiration measurements

Evapotranspiration (ET) was measured for comparison with changes in soil water content at the plot scale. Flux density of water vapor from the surface to the

Fig. 2 Seasonal variation of rainfall, mean storage over the plot area from 0 to 1.4 m and evapotranspiration (ET) over the observation interval of the plot experiment. The intervals labeled R and D mark the periods over which recharge and depletion were quantified, respectively



atmosphere F_v ($\text{m}^3 \text{m}^{-2} \text{s}^{-1}$) was determined by eddy covariance using the equation

$$F_v = \frac{\overline{w' \rho_v'}}{\rho_w} \quad (1)$$

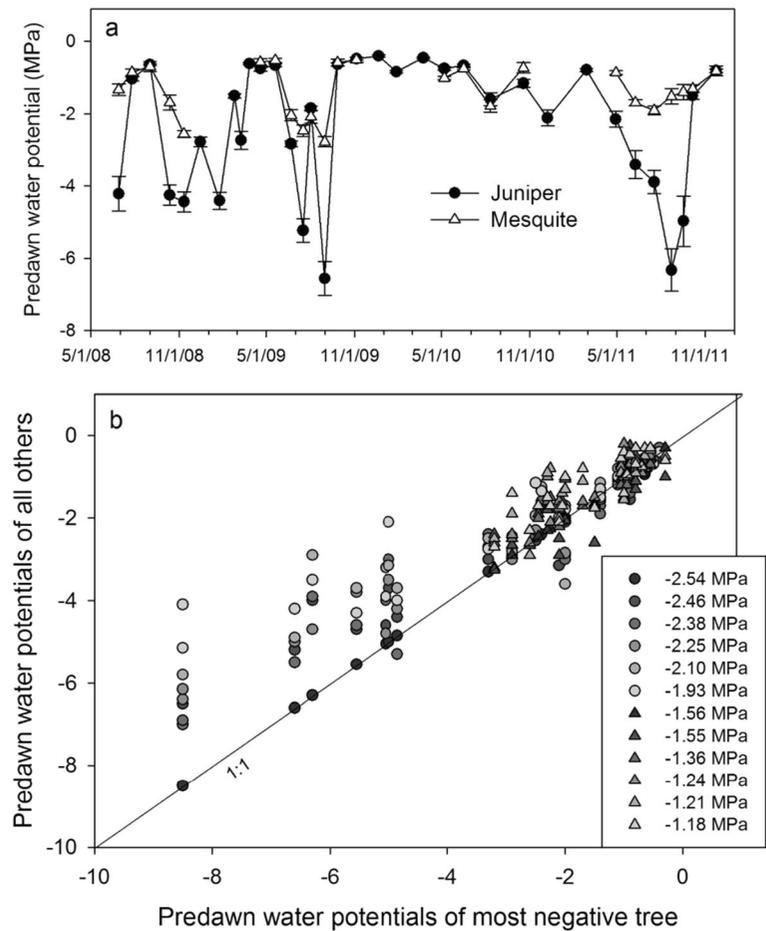
where w (m s^{-1}) is vertical wind speed, ρ_v (kg m^{-3}) is water vapor density, ρ_w (kg m^{-3}) is density of water, ' denotes fluctuation about a mean value, and the overbar indicates a 30-min temporal average. Vertical wind speed and vapor density were measured by a sonic anemometer (CSAT3, Campbell Scientific) and open-path gas analyzer (LI-6262, Li-COR, Lincoln, NE), respectively, mounted at a height of 10 m above the surface on a tower that was 66 m downwind of the soil water content measurement grid. Processing of eddy covariance measurements included spike removal, "natural wind" coordinate rotation (Lee et al. 2004), adjustments for variations in air density due to water vapor

(Webb et al. 1980), corrections for frequency response (Massman 2000), and corrections for energy balance closure (Twine et al. 2000). Data collected during low turbulence (friction velocity $< 0.15 \text{ m s}^{-1}$) were rejected. Data gaps created by low turbulence and instrument malfunctions were filled using the on-line tools of Reichstein (<http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/upload.php>).

Water balance

We used a water balance analysis to examine recharge and plant water uptake. Two periods were singled out for this analysis. Recharge was calculated as the difference in water storage between 15 September and 7 October 2009, the time span labelled R in Fig. 2. Total rainfall during this period was 152 mm, of which 92 mm occurred on 3 and 4 October alone. Depletion was calculated as the difference in water storage between

Fig. 3 Predawn water potentials measured in and around the plot area between June 2008 and November 2011. In the *bottom panel*, the individual water potentials are plotted against the water potentials of the individual (juniper or mesquite) with the most negative average potentials. The line is the 1:1 line. The *numbers* in the legend show the average predawn water potentials over time of individual trees



26 February 2010 and 12 August 2010, the time span labelled D in Fig. 2. This was a period of sporadic rainfall during which there was a general decline in water storage.

The change in water storage in each layer of thickness Δz , at depth d , over time interval Δt was calculated as

$$\Delta S_d = S_{d,t} - S_{d,t+\Delta t} = (\theta_{d,t} - \theta_{d,t+\Delta t}) \Delta Z_d \quad (2)$$

where S is storage, θ is volumetric water content, Δz is thickness of the layer (0.1 m for the surface layer and 0.2 m for the remainder), and d and t denote depth and time. Changes in storage at each depth were calculated for every grid point ($n=36$). At grid points where insertion of access tubes was restricted by rock, we assumed that the remainder of the profile beneath the depth of insertion was occupied by rock, which is reasonable given that the horizontal extent of the rock was at least 0.5 m, based on multiple attempts to bore holes at those locations. Rock at these locations was assumed to have a

density of 2.6 Mg m^{-3} and a volumetric water content of $0.01 \text{ m}^3 \text{ m}^{-3}$ based on measurements by Tokumoto et al. (2012).

The maximum observed storage at every grid point within a layer at a given depth $S_{d,max}$ was calculated as

$$S_{d,max} = \theta_{d,max} \Delta z_d \quad (3)$$

where $\theta_{d,max}$ is maximum observed water content of the layer at each grid point over the course of the study. Cumulative values of $S_{d,max}$ and ΔS_d at a grid point were calculated as the sum of the values of each layer in the profile.

Statistical analysis

Water content measurements were analyzed for spatial autocorrelation with Moran's I using a rook neighborhood with binary weights. No spatial autocorrelation was detected at the scale of our measurements, allowing

measurements from each grid point to be treated as independent data points. To examine the effect of fixed physical soil characteristics (porosity and depth) on soil water dynamics, we conducted variance analysis (36 horizontal points \times 7 depths). Specifically, we used ANCOVA to test the effects of depth (as random effect) and porosity (as covariate) on soil water recharge observed between 15 September and 7 October 2009 and on soil water depletion ($\Delta S_{d,i}$) between 26 February and 12 August 2010. We used SPSS Version 21 (IBM Corporation, New York).

Results

Predawn water potentials

Predawn water potentials of individual trees varied between -0.3 and -8.5 MPa over the 30-month observation period. With 6 individual trees per species, there were 15 possible tree pairs for which water potential fluctuations could be compared (e.g., tree numbers 1&2, 1&3, ... 5&6). Of the 15 pairs per species, 7 juniper and 4 mesquite pairs had significantly different ($p=0.05$) average water potentials over time. The same trees were consistently most and least water-stressed in successive dry periods (Fig. 3). Individual differences increased with drought severity up to a 4.4 MPa one-time difference observed between two juniper trees on 23 August, 2011 (Fig. 3b). The maximal difference observed between two mesquite trees on the same day was 1.4 MPa. These differences are indicative of unequal access to water.

Variability in porosity, recharge, and depletion

To identify causes for this heterogeneity in water access, we examined variability of porosity and soil water dynamics in the measurement grid over an 18-month period (1 July 2009 through 31 December 2010), a period that included very dry conditions at the end of a severe 2-year drought, as well as a high rainfall period from September 2009 to February 2010 (Fig. 2). Total rainfall during the study was 1,258 mm and exceeded total ET by 234 mm.

Bulk porosity of the rock and soil mixture averaged $0.35 \text{ m}^3 \text{ m}^{-3}$ (equivalent to an areal volume density of $0.56 \text{ m}^3 \text{ m}^{-2}$ or 560 mm for the soil profile) which is much lower than the estimated porosity of $0.54 \text{ m}^3 \text{ m}^{-3}$ of the soil fraction (Tokumoto et al. 2012). Average

maximum water storage S_{max} , integrated over the 1.6 m depth was 313 mm ($\theta=0.2 \text{ m}^3 \text{ m}^{-3}$), and average minimum storage S_{min} was 175 mm ($\theta=0.11 \text{ m}^3 \text{ m}^{-3}$). The difference between the two, 138 mm, is an approximation of average AWC. This was only 25 % of the entire estimated pore volume, while S_{max} was about 60 % of pore volume. Maximum storage ranged from 198 to 431 mm, and AWC from 49 to 174 mm.

Rocks in the soil generated variation in porosity across soil layers and between grid points, and these variations in porosity explained an appreciable amount of the variation in S_{max} ($r^2=0.63$). We expect that there was a small amount of induced correlation in this estimate based on Lenahan et al. (2011), because porosity was calculated from ρ_{wet} , then corrected for water content. Rock fraction increased with depth so that layer porosity generally declined from the top down (Figs. 4a, 5a), as did S_{max} (Figs. 4b, 5b). The upper 0.6 m of the profile, where most roots were located (Fig. 1), was a region of relatively uniform porosity averaging $0.4 \text{ m}^3 \text{ m}^{-3}$. Average porosity then declined to $0.25 \text{ m}^3 \text{ m}^{-3}$ at 1.4 m and also became noticeably more variable among grid points. Figure 4 illustrates qualitatively that porosity, S_{max} and depletion were not always highly correlated as one might expect. For example, at a depth of 1 m, there was a band of high porosity and S_{max} along the left side of the plot (Fig. 4a,b), but within this region there was only one spot of substantial depletion (Fig. 4c).

To quantify how recharge and depletion tracked fixed physical constraints of the soil, specifically depth and porosity, we performed ANCOVA on individual grid points. The effect of variation in porosity was highly significant and by itself, explained 19 and 20 % of the variance in depletion and recharge, respectively (Table 1). The effect of depth was also highly significant and explained 35 and 61 % of the variation in depletion and recharge, respectively. Overall, 16 % of the variation in depletion and 12 % of the variation in recharge were unaccounted for by porosity and depth.

During the time interval in which we evaluated recharge (R in Fig. 2), rainfall exceeded cumulative ET by 104 mm. The instrumented portion of the plot, down to a depth of 1.6 m, absorbed a spatial average of 70 mm, leaving 34 mm of precipitation unaccounted for. Average layer recharge peaked at 0.6 m depth (Fig. 5b), but individual profiles had recharge peaks at depths anywhere between 0.4 and 1 m (data not shown). Very few profiles had substantial recharge below 1 m, the profile of maximal recharge shown in Fig. 5c being an exception.

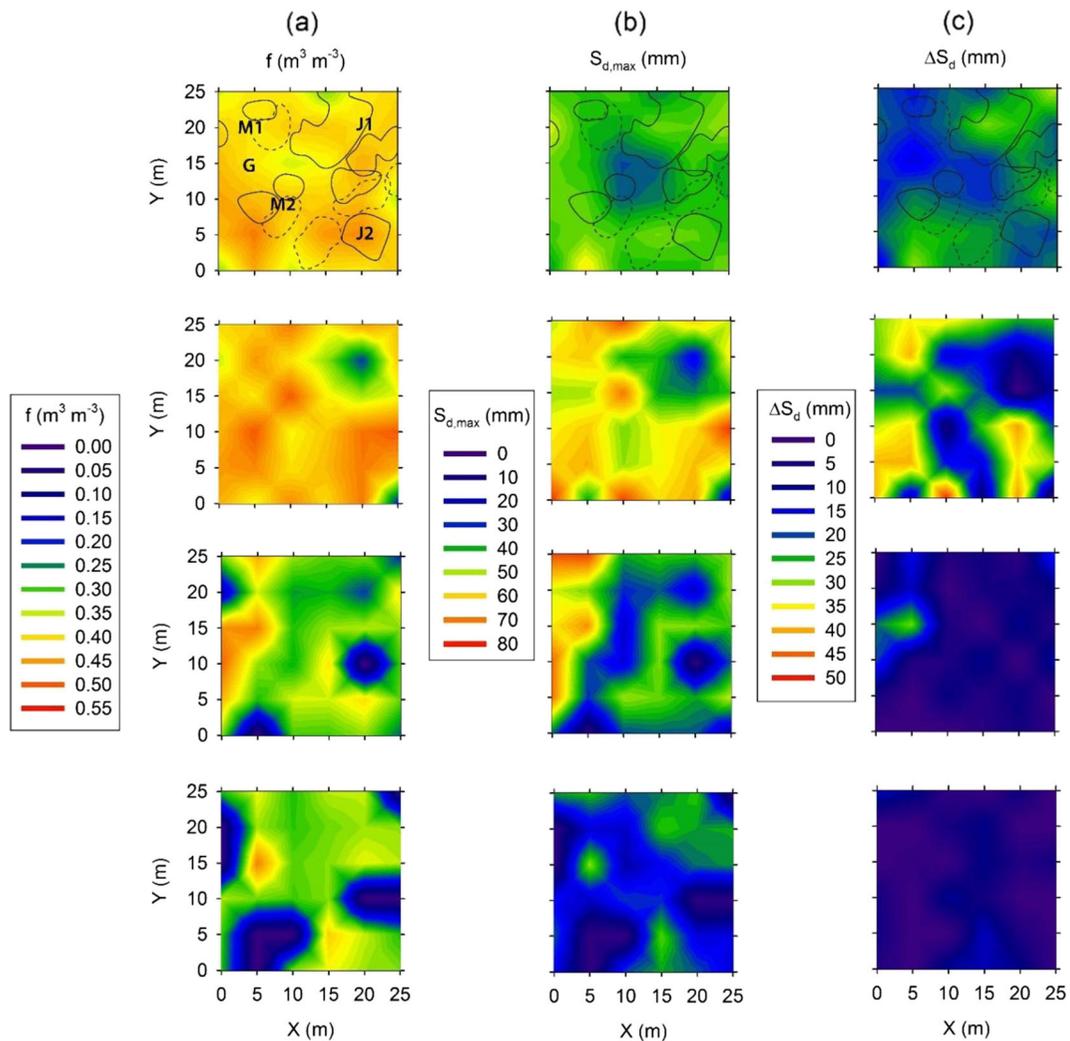


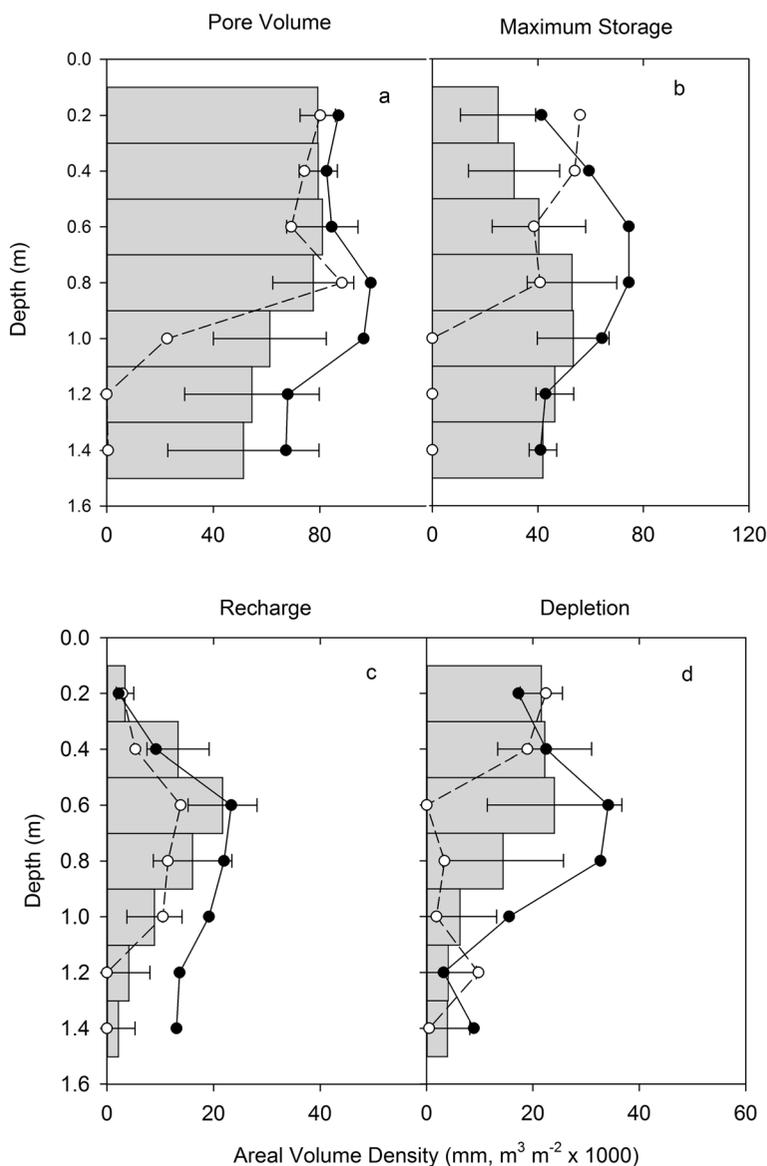
Fig. 4 Spatial variability in porosity (a), maximum water storage (b) and soil water depletion between 26 February 2010 and 12 August 2010 (c). The depths are from top to bottom: 0.2, 0.6, 1.0 and 1.4 m. *Solid and dashed lines* in the top panels show the boundaries of juniper and mesquite tree canopies, respectively.

During the time interval in which we evaluated depletion (D in Fig. 2), average depletion was nearly constant from 0.2 to 0.6 m depths, then declined between 0.6 and 1.0 m depths (Fig. 5c). Variability in depletion was highest at 0.6 and 0.8 m depth, just below the bulk of the root system (Fig. 1). On average, cumulative ET during rain-free periods was 10 % higher than spatially-averaged depletion in the top 1.6 m. This suggests uptake from below the depth of our measurements, consistent with our observations of roots growing into the bedrock.

The letter labels identify grid locations most-closely associated with juniper trees (J1, J2), mesquite trees (M1, M2) and a grass opening without tree cover (G). Contour plots were created using SigmaPlot 12.5 (Systat Software, Inc.)

In Fig. 6, we examined five specific soil profiles that were most closely associated with two juniper trees, two mesquite trees and a grassy opening. The two trees of each species were of apparently similar age. Underneath Juniper 1 was a region of low porosity (most likely a large rock), which limited uptake from 0.6 to 1.0 m depth. At this location, most water was taken up at 0.2 and at 1.2 m for a total of 74 mm. The root system of Juniper 2 was relatively unobstructed by rock, and water uptake occurred chiefly between 0.2 and 0.6 m, with 86 mm in total. At Mesquite 1, equally unobstructed by rock, 111 mm of water were extracted all the way from 0.2 to

Fig. 5 Vertical profiles of pore volume (a), maximum storage (b), recharge (c) and depletion (d). Error bars indicate ± 1 standard deviation among sampling points. Line plots indicate profiles at locations with greatest (filled circles) and least (open circles) total pore volume, storage, recharge and depletion. Values of volume density are for 0.2-m depth increments



1.0 m. Mesquite 2 met with a region of low porosity at 1 m and had highest water uptake at 0.2, 0.4 and 1.4 m for a total of 77 mm. At the grass location, porosity was among the highest in the measurement grid, especially at depths below 0.8 m, nevertheless, uptake occurred only in the upper 1.0 m and amounted to 89 mm.

Discussion

The bucket approximation of AWC assumes horizontally uniform recharge and access to stored water for plants, with both recharge and depletion decreasing

from the top down, the former due to infiltration dynamics and the latter due to attenuating root densities. These vertical patterns were also evident as statistically significant trends in our data set, but there was substantial variation around this trend. This variation was observed at the grid scale of 5 m, thus at a scale that should generate significant variation in the water supply to individual trees. The fact that we did observe temporally consistent differences in the predawn water potentials of trees is independent support of the notion that individual trees experience a wide range of effective AWCs.

One source of variability was the rockiness of the soil, which caused variation in local porosity (Figs. 4, 5).

Table 1 ANCOVA result for soil moisture depletion and recharge

	Sums of squares	df	<i>F</i>	<i>p</i> -value	Partial η^2 ^a
Water depletion					
Corr. model	20,688	7	53.7	<0.001	0.61
Intercept	2	1	0.035	0.852	0.00
Porosity	3,200	1	58.1	<0.001	0.19
Depth	7,074	6	21.4	<0.001	0.35
Error	13,426	244			
Total	82,111	252			
Water recharge					
Corr. Model	12,994	7	87.5	<0.001	0.72
Intercept	31	1	1.5	0.225	0.01
Porosity	1,295	1	61.1	<0.001	0.20
Depth	7,999	6	62.9	<0.001	0.61
Error	5,176	244			
Total	43,086	252			

^aThe partial η^2 is a measure of effect size after controlling for all other effects in the design and is calculated as $SS_{\text{Eff}}/(SS_{\text{Eff}} + SS_{\text{Error}})$

Clearly, a region of soil occupied by solid rock cannot recharge or become depleted. Variation in local porosity played a sizeable but secondary part in explaining recharge and uptake variability. Porosity varied the most at depths ≥ 1 m (Figs. 4, 5), but recharge and depletion were not particularly variable at these depths, because water did not often infiltrate this deep and there were few roots to extract water. Variability in depletion was in fact highest at 0.6 and 0.8 m depth, just below the bulk of the root systems (Fig. 1). This suggests that the apparent variability in tree access to water was chiefly related to uneven recharge and root distribution between 0.6 and 1 m depth.

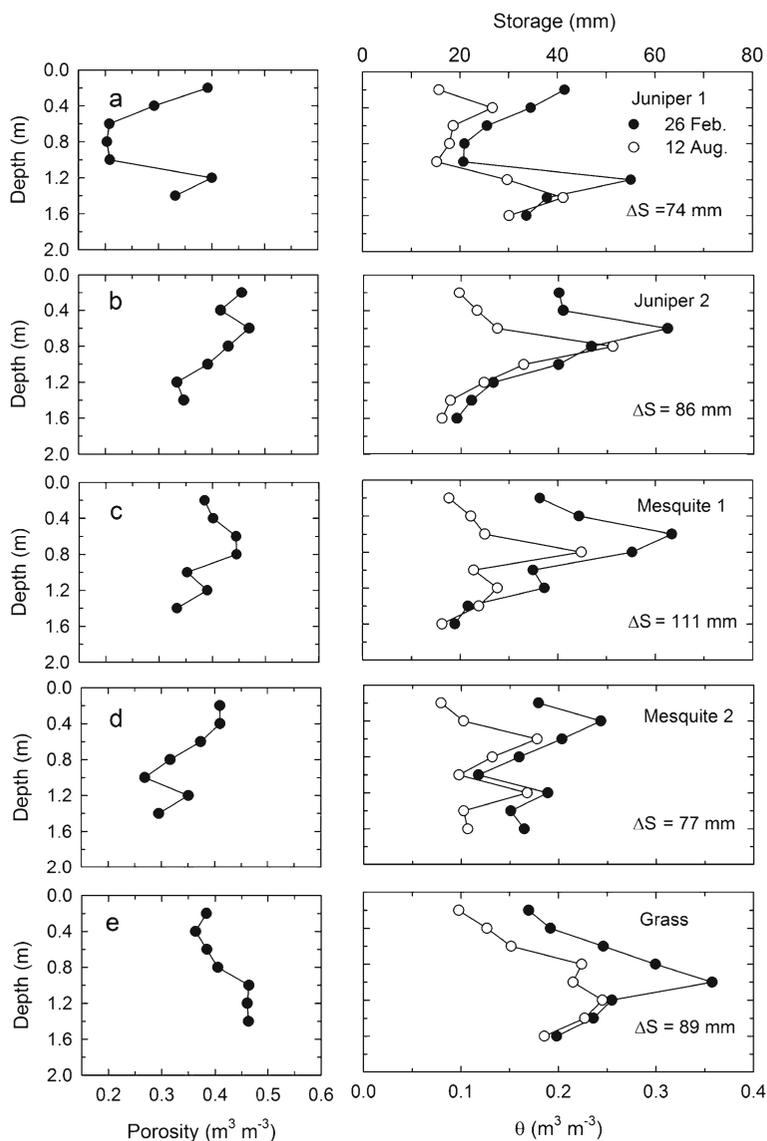
From the water potential measurements we know that individual trees have variable access to water, but we do not know the corresponding range of effective AWC for individual trees. Profiles underneath individual grid points varied in recharge between 44 and 103 mm and in depletion between 57 and 134 mm. This variation is substantial but overestimates the variation experienced by whole root systems, as their zones of influence are likely to span a random collection of profiles. We determined by bootstrapping (Efron 1979) that the average depletion of 1, 2, 4 or 6 randomly selected profiles had a 90 percentile range that differed by 59, 39, 27 and 22 mm, respectively. For example, if trees spanned the

equivalent of four profiles, 90 % of all trees would have an average depletion between 83 and 111 mm.

Our plot experiment was not designed to ascertain the water uptake of individual trees, but by looking at the water dynamics of grid points closest to the central roots of four trees of similar age in the plot, we attempted to gain some insight into the way in which at least parts of a root system experienced a heterogeneous soil-rock profile. We did observe a great deal of variation in profiles of water availability at the start of the depletion interval and in the amount of depletion during the interval (Fig. 6). With the caveat that these observations are by no means generalizable on statistical grounds, we did see that two trees which experienced low water availability in shallow soil layers had higher water uptake in deeper soil layers, suggestive of compensatory root growth. We also saw that water uptake near the two juniper trees did not occur below 1 m depth, while water uptake below one mesquite tree reached down to 1.4 m depth. These observations are consistent with other data suggesting that mesquite is generally deeper rooted than juniper and may further explain why mesquite trees manage to maintain higher predawn water potentials during drought, even when growing in close proximity to juniper (Fig. 3). Due to its drought tolerance, juniper has the capacity to create highly negative water potentials in its root zone, but not beyond, giving mesquite with its deeper roots a chance to avoid damagingly low soil water potentials.

Tree locations did not appear to be closely associated with locations of high porosity or AWC, or uptake and neither did species identity. The average profile depletion was 96 mm but three out of four profiles beneath trees were depleted by less than the average. This suggests that there is little spatial sorting in the tree establishment phase and saplings have to adjust to local conditions as they develop into mature trees, for example by growing roots around and below rocks. The depletion profiles shown in Fig. 6 are suggestive of compensatory tree growth in the vertical dimension (i.e., where water uptake from the main root zone was blocked by a rock layer, there was more water uptake from underneath the rock layer). Over the entire grid, there was a weak but significant ($p=0.045$) negative correlation between depletion at 0.2 to 0.6 m (the main root zone) and 0.8 to 1.4 m, which was not evident in the porosity or the recharge data, and explained about 11 % of the variation (data not shown). On balance, the results of this study suggest that the root systems of trees had

Fig. 6 Profiles of porosity, water storage and volumetric water content (θ) beneath two juniper trees, two mesquite trees, and at one location beneath grass on 26 February and 12 August 2009. Locations are indicated in Fig. 4a. ΔS is the difference in water storage between the two dates



some ability to compensate for locally unfavorable conditions for water storage and uptake through plasticity in root placement, but that this ability was limited and resulted in sustained differences in water access.

The individual differences in water potential that we found among trees are remarkable and should translate into substantial differences in tree transpiration. Based on Kukowski et al. (2012), who, at a different location, collected both water potential and sap flow data in 2009, we estimate that the water potential difference between the least and most water-stressed juniper trees should correspond to a 3-fold difference in transpiration. We have no similar data for mesquite, but we

experimentally determined a $\sim 50\%$ loss of stem hydraulic conductivity for mesquite between -1 and -2 MPa (data not shown), and this is also consistent also with observations on honey mesquite's close relative velvet mesquite (*Prosopis velutina*) in Sonoran Desert uplands (Pockman and Sperry 2000). This indicates that trees in the same stand can have substantially different transpiration rates, complicating the scaling of fluxes from the level of the individual to the ecosystem. Thus, dynamics of ET decline during a dry season, captured by eddy covariance, may in reality not be interpretable based on the measured response of a representative individual, but may more accurately reflect a

decline in the number of individuals with significant transpiration.

A high degree of spatial variation in water uptake by root systems also implies more opportunity for water to bypass root systems. Significant vertical and lateral bypass flow through conduits and macropores has been observed on the Edwards Plateau, most recently by Bazan et al. (2013) and Wilcox et al. (2008). In our study, about 20 % of precipitation was unaccounted for by ET and ΔS in the top 1.6 m of the profile, and likely drained below 1.6 m. This is assuming that runoff was negligible, but given the 1 % slope at the site, there may have been some runoff. However, because the water balance did close (or nearly so) at some grid locations, we think that runoff was a minor component of the water balance. Some of the high recharge locations were beneath trees, while others were not, and some of the low recharge occurred at locations where trees were absent. This appears to rule out significant canopy interception and retention of rainwater by foliage as major contributors to the water balance. The amount of “missing” precipitation was well outside the 10 % margin of error in estimating mean water storage, and estimated uncertainty in eddy covariance measurements of ET (Scott et al. 2010). This leaves as the most plausible explanation for the fate of the “missing” water vertical and/or horizontal subsurface flow along rock surfaces and through macropores and root channels that transport water away from the zone of highest root density, as seen in other studies (Arbel et al. 2010; Dasgupta et al. 2006; Taucer et al. 2008). We cannot be sure that water became unavailable to plants after draining below 1.6 m, but we can be reasonably sure that plant uptake from these depths would have been slow and likely limited to times of acute water shortage when more shallow water sources would have been depleted.

One may ask why plants grow deep roots into regions of low average AWC at all, given that their average contributions to total water uptake must be small. Ryel et al. (2008) and (2010) proposed a conceptual model that distinguishes shallow growth pools of water from deep maintenance pools, the idea being that carbon gain for growth and reproduction is primarily controlled by readily rechargeable and extractable pools of water, but drought survival by deeper pools at relatively low water potentials. Applying this concept to the Edwards Plateau, our results imply that there may be considerable variation in the maintenance pools of individual trees in a stand, most clearly expressed in our study in the

variation of individual predawn water potentials during drought periods. A better understanding for how these maintenance pools vary across spatial scales and relative to contrasting landforms (e.g. shallow, rocky soils vs. deep homogenous soils) may be an important component of explaining the causes and patterns of drought mortality. Specifically, we believe that the presence or absence of an adequate maintenance pool played a significant role in tree survival during the Texas drought of 2011. The drought was classified as exceptional, and killed an estimated 6 % of the trees in the State, including some of the most drought-tolerant species. All regions of the State were affected, and there were areas where local mortality approached 100 %, including on the Edwards Plateau. However, trees did not die at our study site and mortality on the Freeman Ranch was limited to isolated trees, very likely those trees with the most restricted access to water.

Conclusions

It has long been known that rocky soils are edaphically drier. Here we demonstrated that rocky soils also generate a high degree of variability in AWC and large offsets in the physiological status of individual trees. Failing to acknowledge this variability may lead astray the development of mechanistic models of ecohydrology or climate change response. Incorporating spatial variability as a major aspect of ecosystem structure may clarify some of the apparent paradoxes of rock-dominated landscapes, such as a sustained capacity for deep drainage even at high tree densities, and species-independent sources of variability in the spatial patterns of tree mortality under drought conditions.

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