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Water-storage capacity controls energy partitioning and water use in karst ecosystems on the Edwards Plateau, Texas

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ABSTRACT

Woody plants are encroaching into grasslands and savannas of the karst Edwards Plateau, but their impacts on climate and hydrology are unclear because of high variability in soil depth and uncertainties about the contribution of water in fractured limestone to the water available to trees. Water use is controlled by available energy (*AE*) and its partitioning between latent (λE) and sensible (*H*) heat fluxes. We hypothesized that the partitioning of *AE* depends on soil depth, with greater depth leading to more λE and less *H*. We compared energy fluxes of a deep soil savanna with ~50% woody cover dominated by Ashe juniper (*Juniperus ashei*) and a shallow soil woodland dominated by live oak (*Quercus virginiana*) and juniper over a 5-year period, which included periods of unusually high rainfall and severe drought. Although *AE* was 7% higher in the woodland, λE was about 2% higher at the savanna over the 5-year study. Site differences in evapotranspiration were maximal during dry periods between rainfall events, suggesting greater storage of water at the savanna site. During periods of high rainfall, the impact of water storage limitations was minimal, and site differences in evapotranspiration were controlled mainly by *AE* and its partitioning into *H*. Both sites were characterized by rapid reductions in λE and reciprocal increases in *H* during drying cycles following rainfall, indicating that neither of these ecosystems had access to easily utilized sources of deep water. Copyright © 2012 John Wiley & Sons, Ltd.

KEY WORDS evapotranspiration; energy balance; available energy; woody encroachment; karst

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INTRODUCTION

Quantifying evapotranspiration (ET) and its variation across landscapes is critical for improving the accuracy of climate change and ecohydrological models, assessing the impact of land use change on local and regional water balances, and managing water resources, especially in areas where water is limiting. Many water-limited regions are experiencing increases in density and cover of woody plants (woody encroachment), which adds to spatial and temporal uncertainties in ET. Some studies have shown an increase in ET with woody cover (Dugas *et al*., 1998; Zhang *et al*., 2001; Baldocchi *et al*., 2004), whereas others have shown little effect (Dugas *et al*., 1996; Kurc and Small, 2004). Whether or not woody species increase ET depends on linkages among climate, vegetation structure, and edaphic factors as outlined in frameworks presented by Huxman *et al*. (2005) and Moore and Heilman (2011). Edaphic constraints are particularly important in semiarid to subhumid regions that have shallow soils with limited water storage capacity underlain by substrates that impede water retention and root growth (Milly, 1994).

Uncertainties about the hydrological impact of woody encroachment are especially large in karst landscapes. This is worrisome because karst aquifers provide 25% of freshwater for human consumption worldwide and 40% in the USA (White *et al*., 1995). Karst is formed by dissolution of soluble rock, mainly limestone and dolomite, and solution enlarged fissures allow rapid transport of surface water to groundwater. Soils are generally shallow, rocks occupy a large fraction of the soil volume, and the underlying bedrock restricts vertical root growth depending upon the degree of fracture in the rock (Katsura *et al*., 2009; Grigg *et al*., 2010). Highly weathered limestone products such as marl that are sometimes sandwiched between layers of rock can store high quantities of water, up to $0{\cdot}5\,m^3\,m^{-3}$ (Querejeta *et al*., 2006). However, fast, preferential flow through wide fissures and shafts can also lead to water bypassing the root zone (Dasgupta *et al*., 2006; Arbel *et al*., 2010; Canton *et al*., 2010). The contribution of the epikarst (the soil to bedrock transition zone) to ET remains uncertain (Querejeta *et al*., 2006; Rong *et al*., 2011).

It is widely assumed that increases in woody cover cause parallel increases in ET because deep tree roots continue to take up water at times when more shallow-rooted grasses have run out (Tennesen, 2008). However, evidence shows that this assumption is not universally valid (Bosch and

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Hewlett, 1982; Hibbert, 1983; Kerkhoff *et al.*, 2004; Afinowicz *et al.*, 2005; Huxman *et al.*, 2005; Heilman *et al.*, 2009). Differences in rainfall patterns, in the water storage capacity of the root zone, and in the rooting patterns and hydrologic niches of woody plant species all influence the response of tree transpiration to declining availability of water in the root zone (Jackson *et al.*, 1999; Seyfried and Wilcox, 2006; McCole and Stern, 2007; McDowell *et al.*, 2008; Schwinning, 2008; McDowell, 2011). In addition, the water use of an ecosystem may be maximized far below 100% woody cover as individual trees use more water at lower density (Wu *et al.*, 2001).

In arid and semiarid ecosystems, ET is almost always limited by precipitation, but in regions where annual precipitation is closer to potential ET, temporal dynamics of ET are jointly controlled by available energy (*AE*) and available water, which together govern the partitioning between latent and sensible heat (Milly, 1994). Woody ecosystems typically have more *AE* for ET, in large part because albedos are reduced because of multiple reflection and scattering of solar radiation by the canopy (Kessler and Jaeger, 1999; Baldocchi *et al.*, 2004; Rost and Mayer, 2006). The amount of *AE* that is partitioned into latent heat is linked to plant-available water in the root zone. If water storage capacity is restricted, less water is stored during periods of high rainfall for later use by plants during dry periods (Milly, 1994). Limited storage capacity makes the partitioning of *AE* between latent heat and sensible heat fluxes highly responsive to rainfall (Heilman *et al.*, 2009) and therefore not that fundamentally different from the pulse dynamics of more arid systems or herbaceous grasslands (Kurc and Small, 2007; Nagler *et al.*, 2007).

The focus of our study is the Texas Hill Country, a deeply dissected karst ecoregion in south and west central Texas on the eastern edge of the 93 000 km^2 Edwards Plateau from which it was eroded. The region contains the Edwards-Trinity and Edwards-Balcones Fault Zone aquifers, which are sources of drinking water for over two million people living in the Austin-San Antonio corridor. Chronic overgrazing and suppression of wildfires have allowed woody species such as Ashe juniper and honey mesquite to expand into grasslands and savannas so that large portions of the Plateau are now dominated by dense thickets of woody plants. Removal of woody plants has become a widely accepted practice for increasing water availability, despite a lack of quantitative information on how water use is affected by plant species composition, rainfall variability, and local geology.

In this paper, we compare energy and water fluxes over a 5-year period in two ecosystems – a savanna with ~50% woody cover, mainly Ashe juniper (*Juniperus ashei*), on a deep soil, and a ~90% woody cover live oak (*Quercus fusiformis*) – Ashe juniper woodland on shallow soil. The study period included a year with unusually high rainfall and a 2-year period with severe drought. We examine seasonal and interannual variations in energy and water vapour fluxes, and responses of fluxes to rainfall and water deficits, with a focus on evaluating how precipitation and edaphic constraints interact to control energy exchanges and ecosystem water use. Although we expected the woodland to have more energy potentially available to support evaporation, we hypothesized that long-term loss of water through ET would be higher in the savanna site, which had the higher storage capacity for water in the soil. However, we also expected this relationship to change in periods with high amounts of rainfall, with less need for water storage and greater control by *AE* over ecosystem ET.

METHODOLOGY

Site description

Energy and water vapour flux measurements were made at a woodland and a savanna on the Freeman Ranch, a 1700 ha research area operated by Texas State University-San Marcos on the eastern edge of the Edwards Plateau (Figure 1). Measurements at the woodland were managed by Texas A&M University and at the savanna by the University of New Mexico. Both sites are on the Edwards Aquifer recharge zone, characterized by highly faulted and fractured limestone, some of which outcrops at the surface.

The woodland (29°56·50′N, 97°59·49′W) contained mainly live oak (*Quercus virginiana*) and Ashe juniper (*J. ashei* Buckholtz). Tree densities for juniper were 1015 ha^{-1} and 850 ha^{-1} for oak. Most of the Ashe juniper was multi-stemmed, and the trees had self-pruned so the leaves were concentrated in a narrow band at the top of the tree canopies. The soil in the woodland is Comfort stony clay (Clayey-skeletal, mixed, superactive, thermic Lithic Argiustolls), with a ~20-cm deep A horizon overlying fractured indurated limestone bedrock (R horizon). The water storage capacity of the A horizon, excluding the effect of rock outcrops, was estimated to be 70 mm, on the basis of capacitance measurements. Excavations showed that both oak and juniper formed dense root mats above the bedrock (Figure 2), but some roots penetrated the rock through cracks and fissures.

The savanna (29°56·97′N, 97°59·77′W) consisted of clusters of Ashe juniper and honey mesquite (*Prosopis glandulosa* Torr.) interspersed among intermittently grazed grassland dominated by King Ranch bluestem (*Bothriochloa ischaemum* (L.) Keng.), an introduced C_4 species that has become invasive on the Plateau, and Texas wintergrass [*Nassella leucotricha* (Trin. & Rupr.) Pohl], a C_3 species. Tree densities of juniper were 336 ha^{-1} and 304 ha^{-1} for mesquite. Unlike in the woodland, juniper in the savanna had full crowns that reached to the ground. The savanna soil is a Rumple gravelly clay loam (Clayey-skeletal, mixed, active, thermic Typic Argiustoll), with an R horizon at depths of ~1·5 m (Figure 2). The A horizon is ~20 cm thick and overlies a ~40 cm thick Bt horizon. Approximately 50% of the soil volume was occupied by rock fragments, mainly chert. The water storage capacity of the soil above the R horizon was estimated to be 350 mm, on the basis of neutron probe measurements made

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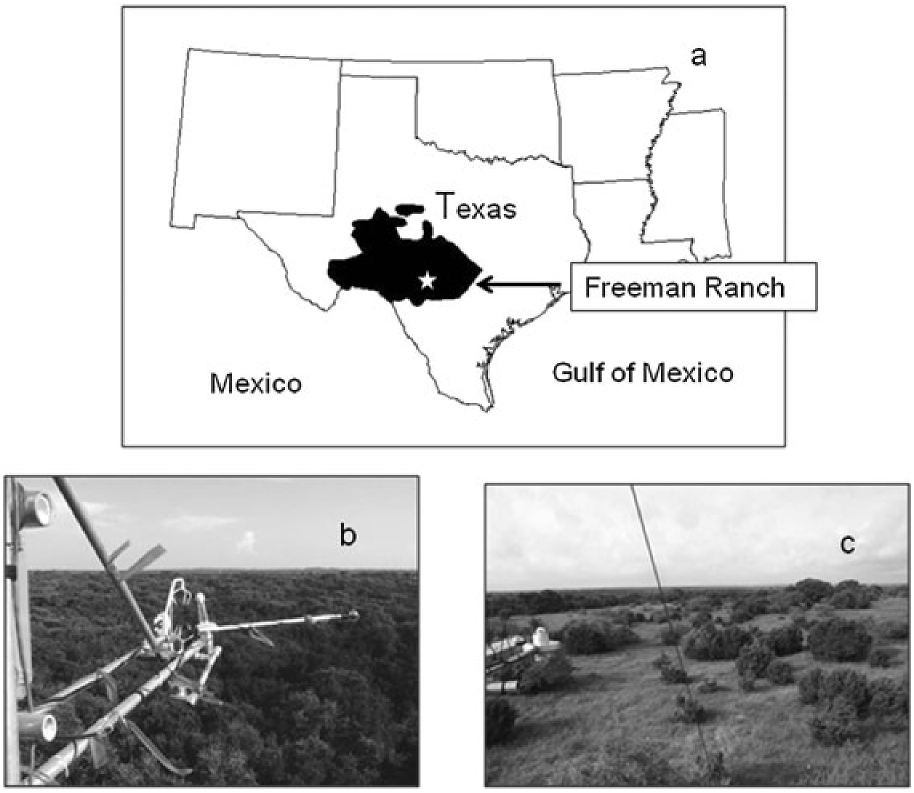

Figure 1. (a) Location of the Edwards Plateau (shaded) and Freeman Ranch (star) and photographs of (b) woodland and (c) savanna sites.

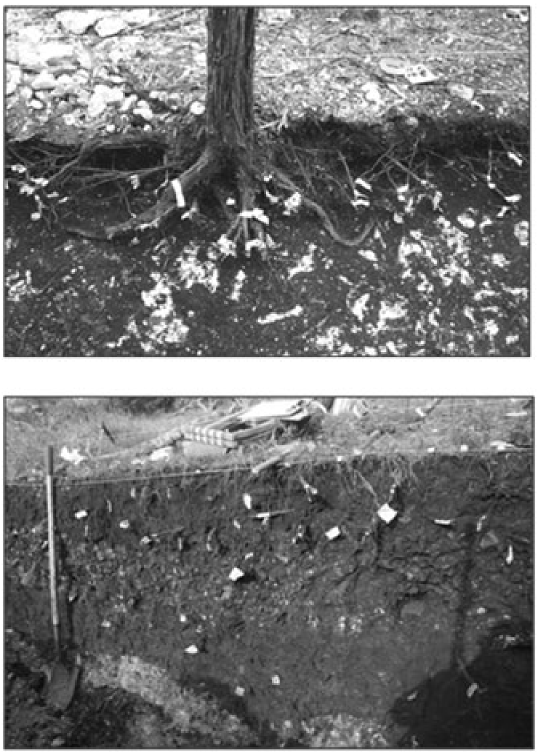

Figure 2. Photographs of excavations showing the 20 cm deep soil layer and rooting patterns above the bedrock (top) and the 1·5 m deep soil at the savanna (bottom).

in early 2010. According to a study conducted in 2006, an estimated 90% of juniper roots in the top 2 m of the soil were in the upper 70 cm, whereas 90% of mesquite roots were in the top 100 cm. These estimates were based on observations in a 5·4-m long, 2-m deep trench that was excavated over a width of 2 m. All tree roots with diameters ≥3 mm were counted in 10 cm × 10 cm × 10 cm soil volume increments.

Energy balance measurements

The surface energy balance can be described by the equation

$$R_n - G - S = \lambda E + H \quad (1)$$

where R_n is net radiation, G is soil heat flux, S is the temporal rate of change in the areal density of heat stored in the biomass and air between the soil surface at the height at which turbulent fluxes are measured, λE is latent heat flux, and H is sensible heat flux. Energy fluxes in Equation (1) have units of W m^{-2}. Collectively, the three terms to the left of the equal sign represent the AE, the net amount of energy on hand for partitioning between the turbulent fluxes of λE and H.

Net radiation is the difference between incoming and outgoing solar and longwave radiation, and can be described by the equation

$$R_n = R_s - aR_s + R\downarrow - R\uparrow \quad (2)$$

where R_s is solar radiation, a is albedo, $R\downarrow$ is atmospheric longwave radiation, and R↑ is longwave radiation emitted by the surface, a function of surface temperature. From 2005 through 2007, net radiation was measured at heights of 15 m at the woodland and 6 m at the savanna by model Q7·1 net radiometers (REBS, Seattle, WA) calibrated with

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a Kipp & Zonen CRN1 net radiometer (Kipp & Zonen Corp., Delft, Netherlands). In 2008, all Q7·1 radiometers were replaced with CRN1 radiometers. The Q7·1 were single channel devices that gave a measure of R_n whereas the CRN1 provide independent measurements of all four terms on the right hand side of Equation (2).

Soil heat flux (G) was measured by heat flux plates (three per site at depths of 5 cm) adjusted for heat storage above the plates using the calorimetric method (Liebethal *et al.*, 2005). The rate of heat storage S in the woodland was calculated as described in Heilman *et al.* (2009), but it was ignored for the savanna because it was expected to be inconsequential, given the structure and mass of canopies at that site (Garai *et al.*, 2010).

Sensible and latent heat fluxes were determined by eddy covariance using the equations

$$H = \rho c_p \overline{w' T'_a} \tag{3}$$

and

$$\lambda E = \lambda \overline{w' \rho'_v} \tag{4}$$

where ρ is density of air, c_p is specific heat of air, w is vertical wind speed, T_a is air temperature, and ρ_v is vapour density. The primes in Equations (3) and (4) denote the fluctuations from a temporal average and the overbars time averages, from 30 min intervals in our case. Vertical wind speed and air temperature were measured using CSAT-3 sonic anemometers (Campbell Scientific Inc., Logan, UT), and vapour density by LI-7500 open path infrared gas analyzers (LI-COR Inc., Lincoln, NE). Anemometers and gas analyzers were at the same heights as the net radiometers, and the outputs were sampled and recorded at 10 Hz. Gas analyzers were calibrated periodically using a tank gas of known CO_2 concentration and air of known humidity produced from a LI-COR model LI-610 dewpoint generator.

Supporting measurements

Several other meteorological and soil measurements were made in support of the energy balance measurements. Global irradiance (R_s) was measured with pyranometers (LI-200, LI-COR) whereas temperature and humidity profiles were measured using ventilated HMP45C probes (Vaisala, Woburn, MA). Rainfall was measured with tipping-bucket rain gauges (Texas Electronics, Inc., Dallas, TX, USA). Volumetric water contents at depths of 2·5, 10 and 20 cm were automatically measured using EC-10 capacitance sensors (Decagon, Inc., Pullman, WA, USA) from 2005 to 2007, and by 5TM capacitance sensors (Decagon) in 2008 and 2009, with three sensors installed horizontally at each depth. Installation of water content sensors below 20 cm was hindered by rocks at both sites. All soil sensors were installed within a few metres of the flux towers. At the savanna, sensors were installed inside an electric fence to prevent damage by grazing cattle. Grazing was not an issue at the woodland.

Data processing and gap filling

All fluxes were calculated as 30-min averages. Eddy covariance calculations included spike (large amplitude fluctuations) removal, 'natural wind' coordinate rotation (Lee *et al.*, 2004), adjustments for variations in air density due to water vapour (Webb *et al.*, 1980; Ham and Heilman, 2003), corrections for frequency response (Massman, 2000), and a humidity correction for sonic anemometer-derived H (Schotanus *et al.*, 1983). A friction velocity (u^*) filter was used to reject data obtained when wind speed and turbulence were low ($u^* < 0{\cdot}15\ \mathrm{m\,s^{-1}}$ for both sites). The filter was determined as the value above which further increases in u^* had little effect on λE (Hastings *et al.*, 2005). Gaps in meteorological data and turbulent fluxes were filled using the on-line tools of Reichstein (http://gaia.agraria.unitus.it/database/eddyproc/EddyInputForm.html).

Energy balance closure

The sum of λE and H should equal the sum of all other energy sources and sinks, but energy balance closure is seldom achieved with eddy covariance because of systematic underestimation of the turbulent fluxes by as much as 20–30% with respect to AE (Wilson *et al.*, 2002). In our case, the closure fraction (ratio of $\lambda E + H$ to AE) averaged 0·91 for the woodland and 0·84 for the savanna, on the basis of the daily totals of the energy fluxes. The energy imbalance creates a systematic error in calculation of long term sums of turbulent fluxes and ET that must be addressed when doing comparative studies among ecosystems (Scott, 2010; Barr *et al.*, 2011). Typically, this imbalance is addressed by forcing the energy balance to close (Wohlfahrt *et al.*, 2010).

We forced closure with the Bowen ratio conservation approach discussed by Twine *et al.* (2000) and used by Oliphant *et al.* (2004), Scott *et al.* (2004), Barr *et al.* (2006), Barr *et al.* (2011), Steinwand *et al.* (2006), Kosugi *et al.* (2007), and Wohlfahrt *et al.* (2010). We multiplied daily totals of λE and H by $AE/(\lambda E + H)$, thus preserving the Bowen ratio ($H/\lambda E$) measured by eddy covariance without favouring sensible or latent heat in the apportionment of the missing energy (Steinwand *et al.*, 2006). Wolf *et al.* (2008) showed that eddy covariance estimates of the Bowen ratio agreed with gradient-based estimates, when all corrections we used (density, frequency response, etc.) were applied to the eddy covariance data.

RESULTS

Environmental conditions and vegetation dynamics

Microclimatic conditions at the savanna from 2005 through 2009 are shown in Figure 3, and the seasonal variability shown there is representative of what occurred at the woodland. Weather variability between sites was generally not an issue because the sites were in close proximity (0·9 km apart). The sites received between 5·9 and

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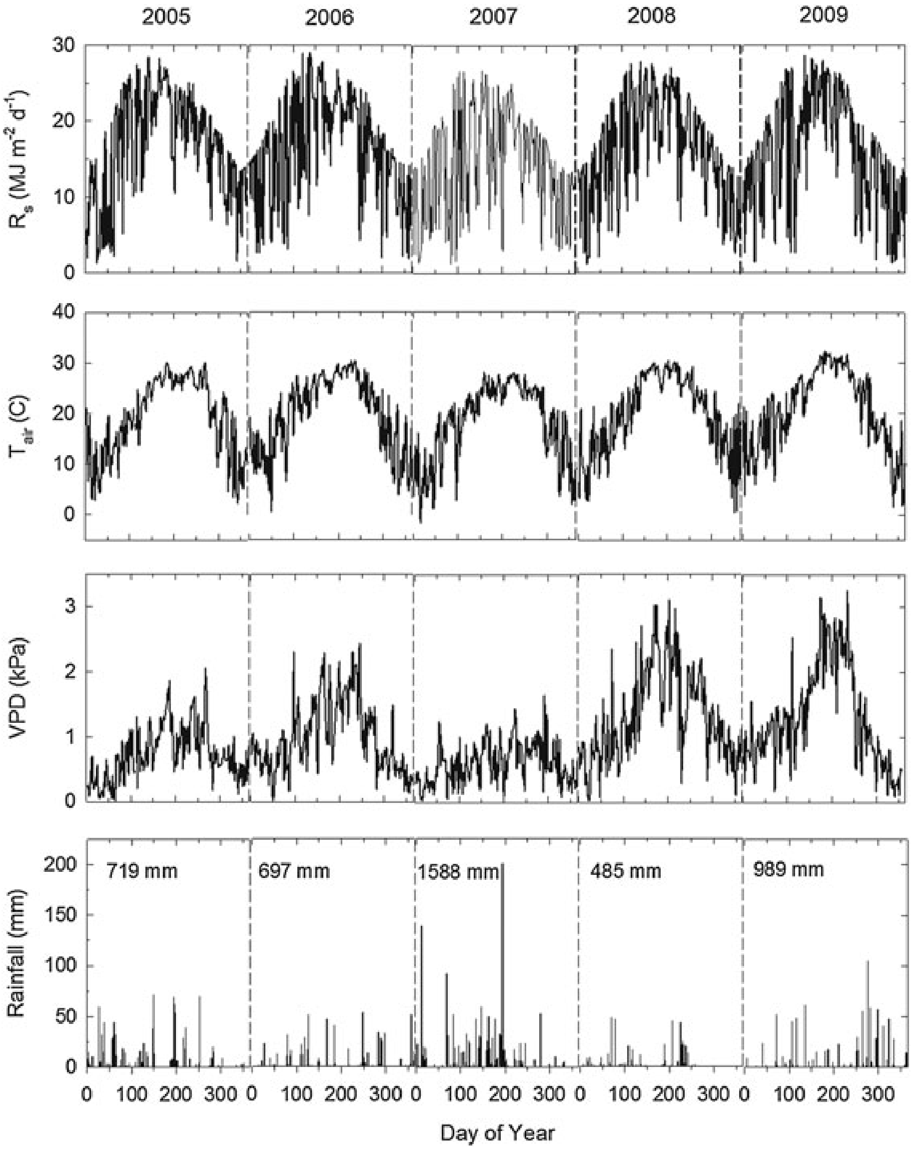

Figure 3. Seasonal variation in global irradiances (R_s), average daily air temperature (T_{air}), vapour pressure deficit, and rainfall at the savanna from 2005 to 2009. Numbers in the rainfall panel are annual totals.

6·1 GJ m^{-2} of solar radiation (R_s) in four of the 5 years. The exception was 2007, a year with high rainfall and cloud cover, where R_s decreased to 5·3 GJ m^{-2} because of greater cloud cover.

Total rainfall in 2005 and 2006 was 719 mm and 697 mm, respectively, below the annual mean of 878 mm. Rainfall during the last 3 months of 2004 was 425 mm, 225 mm above the annual mean for those months, so that water storage was high going into 2005. In addition, 273 mm of rain fell during the first 3 months of 2005. In contrast, total rainfall during the last 3 months of 2005 was only 44 mm, resulting in low root zone water content at the beginning of 2006. There were several extended periods with limited rainfall during the first 2 years, the most severe of which occurred between days 154 (3 June) and 194 (13 July) in 2005, and days 186 (5 July) and 243 (31 August) in 2006. The year 2007 was unusually wet, with a total rainfall of 1588 mm, including a 16-day period in July during which, 361 mm of rain fell with 201 mm on just 1 day (13 July). An extended period with low rainfall began in September 2007, and it resulted in a severe drought that continued through August 2009. Total rainfall in 2009 was actually higher than the 30-year mean, but 60% of the annual total occurred in the last 4 months of the year (Figure 3).

Mean annual air temperature and vapour pressure deficits varied from 18·1 °C and 0·51 kPa, respectively, in 2007 to 20·6 °C and 1·3 kPa in 2009. Reference (potential) ET (ETo), calculated using the method of Allen *et al.* (1994), ranged from 1002 mm in 2007 to 1554 mm in 2009 (Table I).

Seasonal trends in leaf area index (LAI), obtained from MODIS satellite estimates for the pixels containing the flux towers, are shown in Figure 4. In general, LAI was higher at the woodland than at the savanna, although differences in averages and seasonal trends were overall small. LAIs were highest in 2007 and lowest in 2008, reflecting differences in rainfall among years.

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Table I. Annual totals of available energy, latent heat flux, sensible heat flux, for and evapotranspiration for the woodland and savanna for 2005 to 2009, along with ratios of λE and H to AE, annual rainfall, and reference ET (ETo).

Year	Site	*AE*	λE	*H*	$\lambda E/AE$	H/AE	ET	Rainfall	ETo
			($GJ\,m^{-2}$)				(mm)	(mm)	(mm)
2005	Woodland	4·02	1·98	2·04	0·49	0·51	806	719	1195
	Savanna	3·73	2·01	1·72	0·54	0·46	824	—	—
2006	Woodland	3·94	1·44	2·50	0·37	0·63	587	697	1276
	Savanna	3·75	1·59	2·16	0·42	0·58	649	—	—
2007	Woodland	3·61	2·23	1·38	0·62	0·38	908	1588	1002
	Savanna	3·56	2·25	1·31	0·63	0·37	918	—	—
2008	Woodland	3·88	1·29	2·59	0·33	0·67	526	485	1483
	Savanna	3·68	1·38	2·30	0·38	0·62	563	—	—
2009	Woodland	3·82	1·37	2·45	0·36	0·64	559	989	1554
	Savanna	3·60	1·38	2·22	0·38	0·62	563	—	—

AE, available energy; λE, latent heat flux; *H*, sensible heat flux; ET, evapotranspiration.

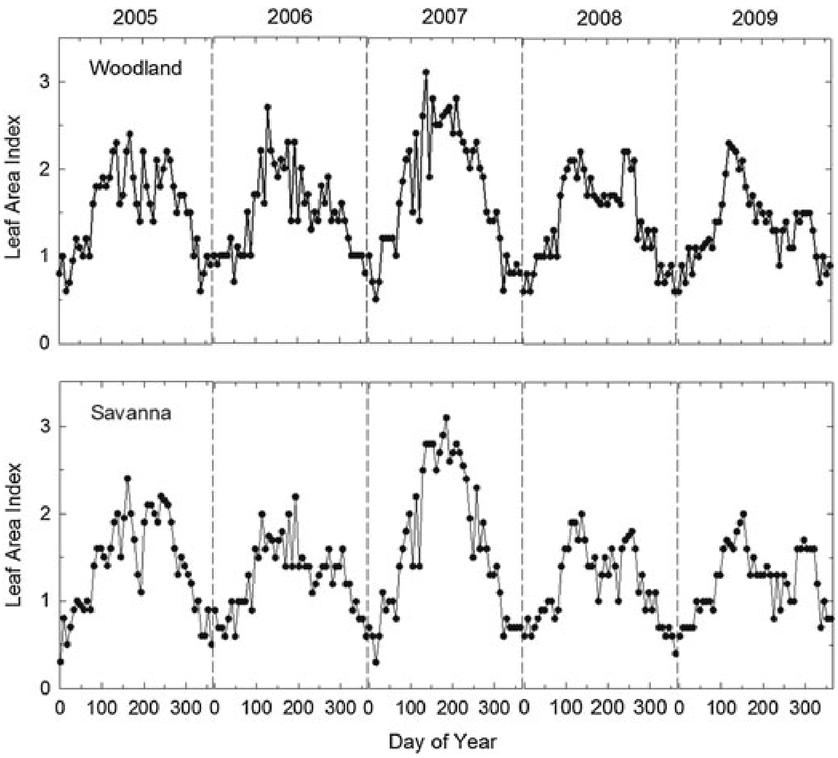

Figure 4. MODIS estimates of leaf area index of the woodland and savanna for 2005–2009.

Available energy

Seasonal variations in available energy ($AE = R_n - G - S$), shown in Figures 5(a) and 6(a), followed closely by those of R_s (Figure 3). Overall, more energy was available at the woodland than at the savanna (Table I) due mainly to higher R_n. Annual totals of R_n averaged 3·85 $GJ\,m^{-2}$ (66% of R_s) at the woodland and 3·61 $GJ\,m^{-2}$ (62% of R_s) at the savanna. Maximum R_n reached 21 $MJ\,m^{-2}\,d^{1}$ at the woodland and 19 $MJ\,m^{-2}\,d^{-1}$ at the savanna. Higher R_n at the woodland was due principally to a lower albedo (Figure 7), resulting in greater absorption of solar radiation. In general, the woodland also emitted less longwave radiation ($R\uparrow$) than the savanna, which contributed to higher R_n (Figure 7).

Daily totals of storage heat flux ($G + S$) ranged from $-2{\cdot}2$ $MJ\,m^{-2}\,d^{-1}$ to 1·3 $MJ\,m^{-2}\,d^{-1}$ in the woodland, and from -1·3 $MJ\,m^{-2}\,d^{-1}$ to 0·8 $MJ\,m^{-2-}d^{-1}$ in the savanna. Storage heat flux generally accounted for <5% of daily *AE*. Heat storage reached its minimum in early spring and maximum in late summer, 1/4 cycle out of phase with solar radiation. Annual totals were near zero at both sites. Diurnal fluctuations of *G* and *S* in the woodland were of similar magnitude, but peak gains in *G* lagged those in *S* by 4–6 h, as reported by Heilman *et al*. (2009).

Latent and sensible heat fluxes and evapotranspiration

Seasonal changes in λE (or ET) and *H* tracked changes in *AE* and available water. There were large fluctuations in λE

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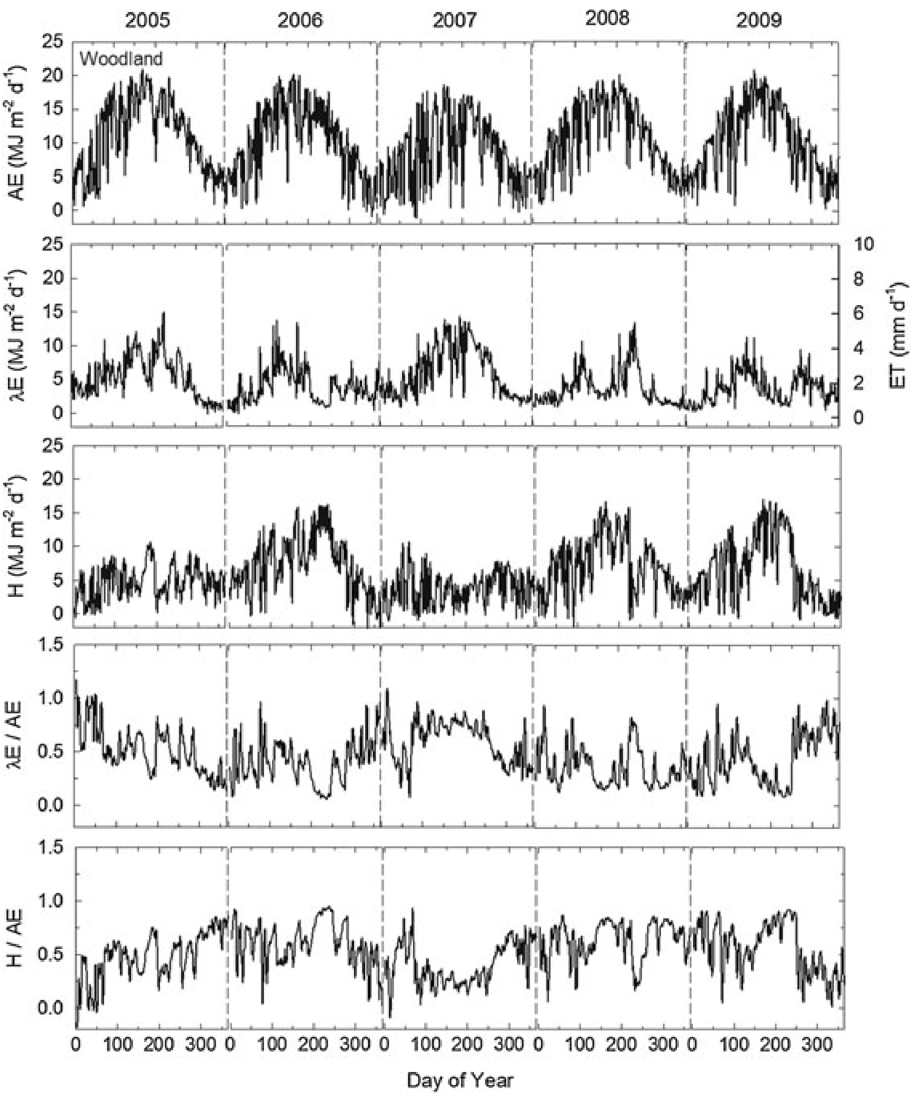

Figure 5. Seasonal variations in available energy (*AE*), latent heat flux (*λE*), evapotranspiration (ET), and sensible heat flux (*H*) at the woodland along with 5-d running averages of ratios of *λE* and *H* to *AE*.

and *H* in response to rainfall and water deficits in every year but 2007, with reductions in λE accompanied by increases in *H* as the root zone dried between rainfall events. In general, responses to rainfall at the two sites were in synchrony (Figures 5, 6 and 8), indicating that both sites relied heavily on water from recent rainfall events, rather than antecedent water.

Over 5 years, the savanna consistently generated more latent heat and less sensible heat than the woodland, despite having less energy available for partitioning between the two fluxes (Table I). On average, savanna λE exceeded woodland λE by 60 MJ y^{-1}, equivalent to 24 mm of ET. The largest annual difference in ET between sites occurred in 2006, with 62 mm more ET at the savanna. The smallest annual difference occurred in 2009 when savanna ET exceeded that at the woodland by only 4 mm. Annual differences were also small in 2007, the year with unusually high rainfall, with ET at the savanna 10 mm higher than at the woodland. During the highest rainfall period in 2007, the 150 days between 10 April and 7 September, savanna and woodland ET were virtually identical (Figure 8). Total rainfall during this time was 703 mm, exceeding reference ET by 162 mm, so that water availability did not constrain ET. *AE* was higher at the woodland, but a greater fraction was partitioned into *H*, offsetting differences in *AE*. Woodlands typically generate proportionally more *H* because of higher turbulence (Rost and Mayer, 2006). In two of the years, 2005 and 2008, ET at both sites exceeded annual rainfall. These years were preceded by periods of very high rainfall, so there likely was significant carryover of antecedent rainfall.

The greatest divergence in ET between sites occurred during dry periods between rainfall events (Figure 8), indicative of differences in water availability. There were no systematic differences between sites associated with time of year or phenology. Although annual sums of ET were consistently larger at the savanna than at the woodland, differences between sites were likely within uncertainties associated with random and systematic errors in eddy covariance and energy balance measurements (Hollinger and Richardson, 2005), and gap-filling procedures.

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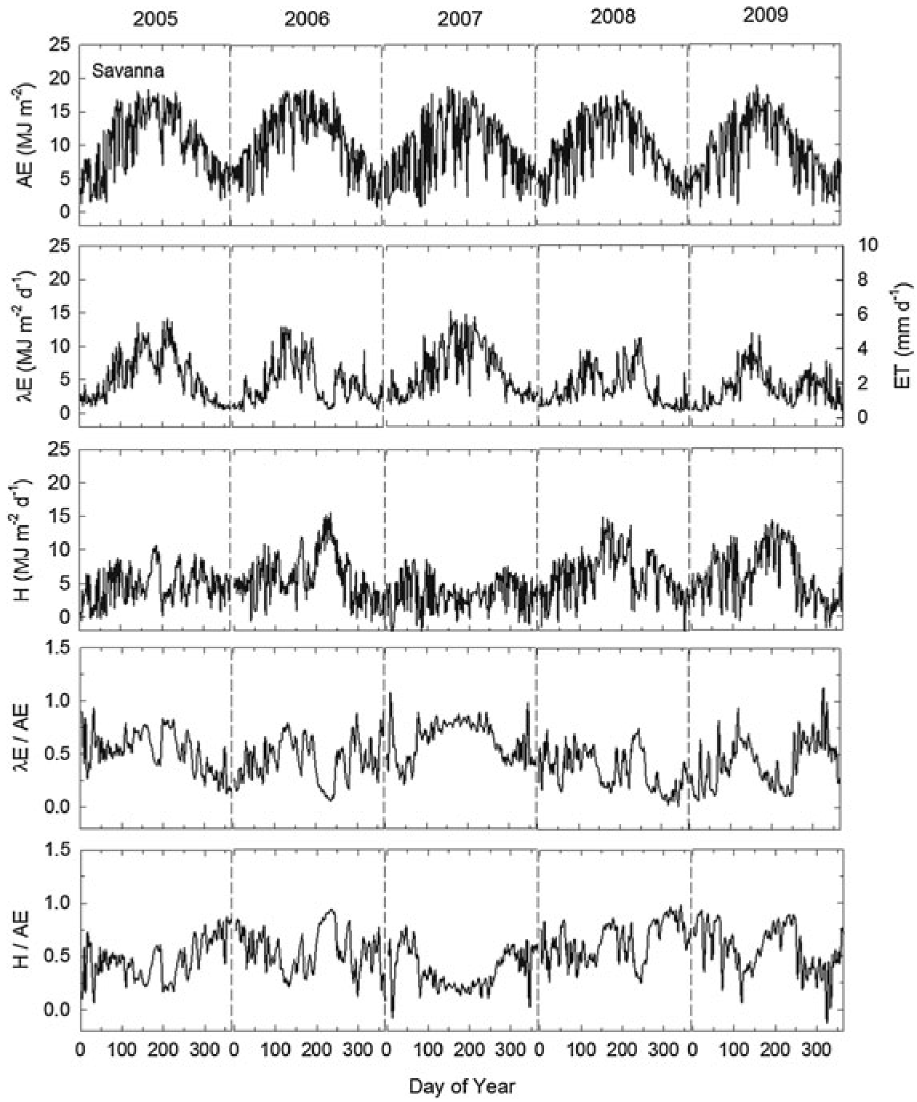

Figure 6. Seasonal variations in available energy (*AE*), latent heat flux (λE), evapotranspiration (ET), and sensible heat flux (*H*) at the savanna along with 5-d running averages of ratios of λE and *H* to *AE*.

The Bowen ratio ($\beta = H/\lambda E$) is a useful index for examining the partitioning of *AE*, because it increases when water becomes more limiting. We show one example of a drying cycle for each year of the study in Figure 9. The Bowen ratio was similar across sites at onset of each drying cycle, but diverged typically within 20 days without (or with little) rain. During most drying cycles, ET at both sites levelled off as water was depleted, and in some cases, this occurred earlier at the woodland than at the savanna site. The quicker depletion of available water in the woodland was however not the result of initially higher ET, because initial slopes of cumulative ET were nearly identical. Rather, the woodland site became water-depleted sooner because it had less stored water.

DISCUSSION

Overall, our hypothesis, that limitations in soil and subsoil water storage capacity would dominate long-term ET more so than differences in woody cover and associated differences in *AE*, was supported. ET at the savanna was higher by an average of $24\,\text{mm}\,\text{y}^{-1}$, on the basis of eddy covariance measurements, despite lower *AE*. There were periods of high rainfall for which differences in ecosystem ET were dominated by site differences in *AE*, supporting our second hypothesis. Our results illustrate how fast ET becomes water-limited in this karst ecosystem, even in sites with comparatively deep soils.

In general, ecosystem ET and the proportion of λE in *AE* increased with precipitation, whereas site differences in ET and energy partitioning decreased with precipitation. For example, in 2006, the year with the second lowest rainfall, savanna λE was 10% higher than woodland λE. Savanna and woodland λE accounted for 42% and 37%, respectively of *AE*. Similarly, in 2008, the year with the lowest rainfall, savanna λE exceeded woodland λE by 7%, and savanna and woodland λE accounted for 38% and 33%, respectively of *AE*. By contrast, in 2007, the year with highest rainfall, there was $<1\%$ difference in λE between sites, and λE accounted for 63% and 62%, respectively of *AE*.

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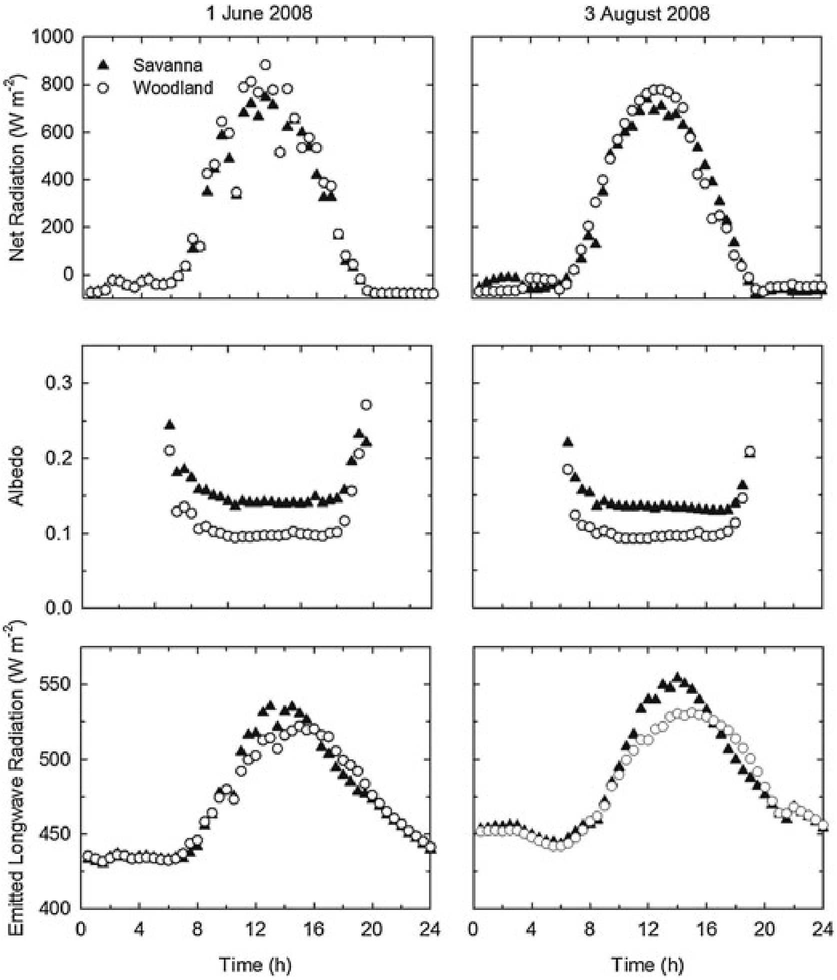

Figure 7. Net radiation, albedo, and emitted longwave radiation for the savanna and woodland on 1 June and 3 August 2008.

The last year of the study, 2009, appears to fall outside this general trend. With an annual precipitation of 989 mm, this was the second wettest year in this study, but ET was comparatively low and site differences in annual totals of λE and ET were minimal (Table I). What these annual comparisons do not show is that 2009 was an exceptional drought year up to September, followed by a long rainy period (Figure 3). In fact, 60% of the annual total precipitation of 2009 occurred in the last 4 months of the year. During the 8 months of drought, savanna ET exceeded woodland ET by 32 mm, whereas during the 4 months of heavy rainfall, savanna ET was 28 mm lower than at the woodland.

It may seem contradictory that the energy fluxes in these ecosystems became water-limited only days after the last rainfall (Figure 9), even though the ecosystems also seem to have the capacity to use water that must have been stored for months and perhaps years. We think this may be related to the complexity of the soil/epikarst system, which has several very different storage components. Soil depth at the woodland was ~20 cm and had high root density and an estimated storage capacity of at most 70 mm, whereas the savanna soil was much deeper (~1·5 m) with an estimated storage capacity of 350 mm. We know that the epikarst below must have contributed to the water supply of trees at the woodland because cumulative ET during some drying cycles exceeded soil water storage capacity, and because excavations showed that some roots grew beyond the soil zone into the epikarst.

Soil on top and soil pockets in the rock are likely to recharge and deplete quickly, thus producing highly pulsed ET dynamics, reminiscent of drier ecosystems (Heilman *et al*., 2009). But there could be much larger volumes of water stored in fractured rock or clay layers below the soil that are slow to recharge and deplete. A recent study by Estrada-Medina *et al*. (2012) in the limestone karst of Yucatan, Mexico, showed that roots were highly concentrated in the overtopping soil layers and in soil enclosures within the rock. Here, fluctuations in water content were large and rapid. However, a larger amount of water was stored in the rock, to which root access was restricted, and which gave up water more slowly.

Differences among species in plant response to water deficits also contribute to differences in energy balance partitioning, and they may interact with heterogeneities in the water storage components in the soil/epikarst system. A steep decline in ET early in the drying cycle is expected of savannas, as herbaceous species are more shallow

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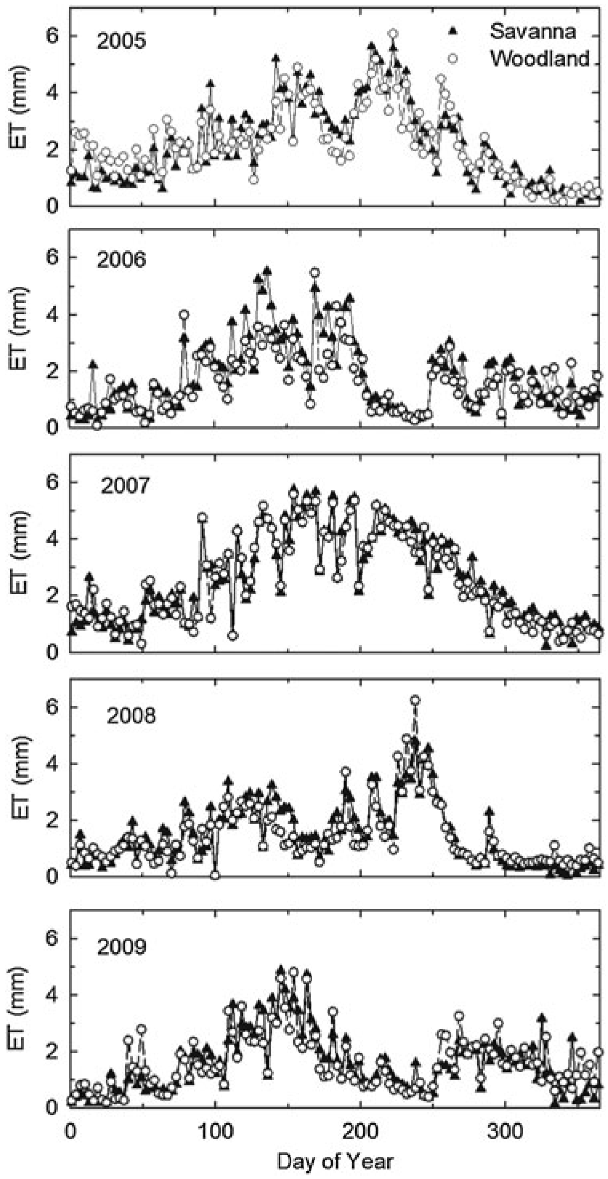

Figure 8. Comparison of daily evapotranspiration at the savanna and woodland from 2005 to 2009.

rooted and run out of extractable water sooner. However, the oak-juniper woodland site in this study showed very similar dynamics, in spite of having a negligible herbaceous component. Measurements of plant water potentials over 3 years (Schwinning, unpublished data) suggest that live oak maintains higher water potentials during drought than Ashe juniper, presumably by regulating transpiration via stomatal closure and leaf abscission (McDowell *et al.*, 2008; McDowell, 2011). Ashe juniper tolerates much lower water potentials presumably to maintain gas exchange when hydraulic conductance becomes highly limiting. Accordingly, oak must have a greater percentage decrease in transpiration during dry periods than juniper (Bendevis *et al.*, 2010). Juniper may therefore be primarily responsible for extracting water from non-soil substrates at the woodland site when soil water has become depleted. This would explain juniper dominance on sites with especially thin soils, for example, on steep slopes.

CONCLUSION

Our study shows that increases in density of woody plants on the Edwards Plateau do not necessarily lead to increased water consumption, due at least in part to constraints imposed by shallow soils with limited water storage capacity. Because soil depth on the Plateau is highly variable, the impact of woody plants on water use will be highly dependent on local geology, as well as on rainfall. During extended periods of high rainfall, the impact of water storage limitations will be minimal, and ecosystems will generally consume water in proportion to the amount of *AE* and the fraction of *AE* partitioned into sensible heat, both of which are higher for woodlands. However, when rainfall is limited or intermittent, which is the usual situation on the Edwards Plateau, woody ecosystems on deeper soils will use more water than those on shallow soils. There is a caveat to this, however. If roots have access to stable sources of water at depth such as perched water tables and water in caves, constraints imposed by soil depth will be reduced. Although this can occur where these features exist (Jackson *et al.*, 2000; Doody and Benyon, 2011), it is not the norm (Schwinning, 2008). Over time, the rain-limited Edwards Plateau ecosystems will likely consume all of the available water in their root zones, regardless of plant density, species composition, and physiological response to water deficits. Therefore, a more critical question for estimating the ET of karst ecosystems is to improve understanding of the structure and capacity of the epikarst and the proportion of precipitation lost by drainage through preferential flow pathways.

Implications of our results go beyond the Edwards Plateau because large portions of terrestrial landscapes have shallow soils overlying substrates that impede water movement and root growth (Schwinning, 2010). The response to these ecosystems to climate change is largely unknown. Although the frequently experienced drought conditions may make these ecosystems pre-adapted to a drier climate, we do not know to what extent they depend on large, but slowly extracted stored water in subsoil substrates. If they do, the prediction of extended, more severe droughts may reverse the trend of woody encroachment on the Edwards Plateau and similar ecosystems worldwide. We may have seen evidence for this in the Texas Drought of 2011, when according to estimates of the Texas Forest Service, 2–10% of the estimated 4·9 billion trees in the state died, including the highly drought resilient species Ashe juniper.

It is critical that global vegetation models account for variation in the edaphic structure and associated constraints on water storage and ET. A global effort is underway to produce digital soil maps for predicting soil properties at ~100 m resolution (http://GlobalSoilMap.net), and this information will be useful for improving the modelling of water dynamics in the root zone, although it does not resolve how much water may be available for plant use in subsoil layers.

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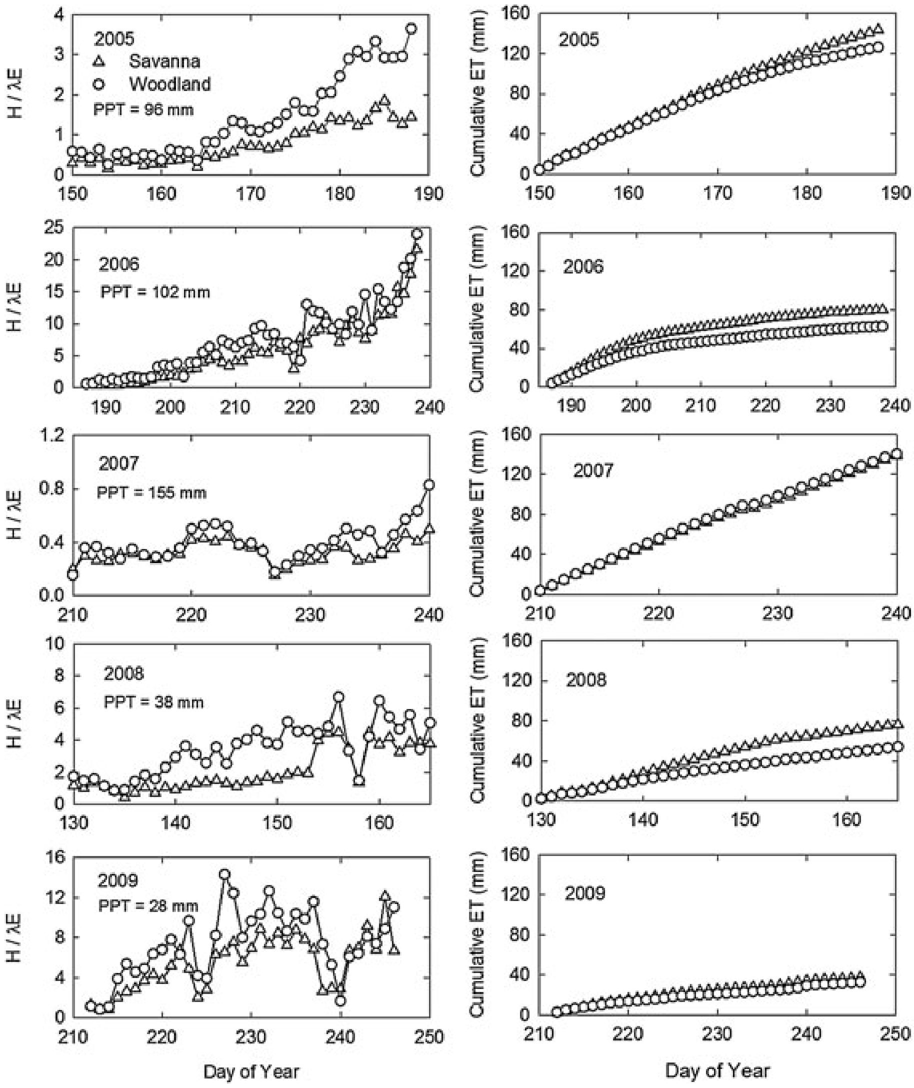

Figure 9. Bowen ratios (*H/λE*) and cumulative evapotranspiration at the savanna and woodland during dying cycles in 2005–2009. Also shown is total rainfall in the 3 weeks preceding the drying cycles.

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REFERENCES

Afinowicz JD, Munster CL, Wilcox BP. 2005. Modeling effects of brush management on the rangeland water budget: Edwards Plateau, Texas. *Journal of the American Water Resources Association* **41**: 181–193.

Allen RG, Smith M, Perrier A, Pereira LS. 1994. An update for the calculation of reverence evapotranspiration. *ICID Bulletin* **43**: 35–92.

Arbel Y, Greenbaum N, Lange J, Inbar M. 2010. Infiltration processes and flow rates in developed karst vadose zone using tracers in cave drips. *Earth Surface Processes and Landforms* **35**: 1682–1693.

Baldocchi DD, Xu L, Kiang N. 2004. How plant functional-type, weather, seasonal drought, and soil physical properties alter water and energy fluxes of an oak-grass savanna and an annual grassland. *Agricultural and Forest Meteorology* **123**: 13–39.

Barr AG, Morgenstern K, Black TA, McCaughey JN, Nezic Z. 2006. Surface energy balance closure by the eddy-covariance method above three boreal forest stands and implications for the measurement of the CO_2 flux. *Agricultural and Forest Meteorology* **140**: 322–337.

Barr AG, Van der Kamp G, Black TA, McCaughey JH, Nesic Z. 2011. Energy balance closure at the BERMS flux towers in relation to the water balance of the White Gull Creek watershed 1999-2009. *Agricultural and Forest Meteorology*. DOI: 10.1016/ j.agrformet. 2011.05.017

Bendevis MA, Owens MK, Heilman JL, McInnes KJ. 2010. Carbon exchange and water loss from two evergreen trees in a semiarid woodland. *Ecohydrology* **3**: 107–115.

Bosch JM, Hewlett JD. 1982. A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. *Journal of Hydrology* **55**: 3–23.

Canton Y, Villagarcia L, Moro MJ, Serrano-Ortiz P, Were A, Alcala FJ, Kowalski AS, Sole-Benet A, Lazaro R, Domingo F. 2010. Temporal dynamics of soil water balance components in a karst range in southeastern Spain: estimation of potential recharge. *Hydrological Sciences Journal-Journal Des Sciences Hydrologiques* **55**: 737–753.

Dasgupta S, Mohanty BP, Koehne JM. 2006. Impacts of juniper vegetation and karst geology on subsurface flow processes in the Edwards Plateau, Texas. *Vadose Zone Journal* **5**: 1076–1085.

Doody TM, Benyon RG. 2011. Direct measurement of groundwater uptake through tree roots in a cave. *Ecohydrology* **4**: 644–649.

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Dugas WA, Hicks RA, Gibbens RP. 1996. Structure and function of C3 and C4 chihuahuan desert plant communities: energy balance components. *Journal of Arid Environments* **34**: 63–79.

Dugas WA, Hicks RA, Wright P. 1998. Effect of removal of *Juniperus ashei* on evapotranspiration and runoff in the Seco Creek watershed. *Water Resources Research* **34**: 1499–1506.

Estrada-Medina H, Graham RC, Allen MF, Jiménez-Osornio JJ, Robles-Casolco S. 2012. The importance of limestone bedrock and dissolution karst features on tree root distribution in northern Yucatán, México. *Plant and Soil*. DOI. 10.1007/s11104-012-1175-x

Garai A, Kleissl J, Llewellyn Smith SG. 2010. Estimation of biomass heat storage using thermal infrared imagery: application to a walnut orchard. *Boundary-Layer Meteorology* **137**: 333–342.

Grigg AM, Lambers H, Veneklaas EJ. 2010. Changes in water relations for Acacia ancistrocarpa on natural and mine-rehabilitation sites in response to an experimental wetting pulse in the Great Sandy Desert. *Plant and Soil* **326**: 75–96.

Ham JM, Heilman JL. 2003. Experimental test of density and energy-balance corrections on CO_2 flux as measured using open-path eddy covariance. *Agronomy Journal* **95**: 1393–1403.

Hastings SJ, Oechel WC, Muhlia-Melo A. 2005. Diurnal, seasonal and annual variation in the net ecosystem CO_2 exchange of a desert shrub community (Sarcocaulescent) in Baja California, Mexico. *Global Change Biology* **11**: 927–939.

Heilman JL, McInnes KJ, Kjelgaard JF, Owens MK, Schwinning S. 2009. Energy balance and water use in a subtropical karst woodland on the Edwards Plateau, Texas. *Journal of Hydrology* **373**: 426–435.

Hibbert AR. 1983. Water yield improvement potential by vegetation management on western rangelands. *Water Resources Bulletin* **19**: 375–381.

Hollinger DY, Richardson AD. 2005. Uncertainty in eddy covariance measurements and its application to physiological models. *Tree Physiology* **25**: 873–885.

Huxman TE, Wilcox BP, Breshears DD, Scott RL, Snyder KA, Small EE, Hultine K, Pockman WT, Jackson RB. 2005. Ecohydrological implications of woody plant encroachment. *Ecology* **86**: 308–319.

Jackson RB, Moore LA, Hoffmann WA, Pockman WT, Linder CR. 1999. Ecosystem rooting depth determined with caves and DNA. *Proceedings of the National Academy of Sciences USA* **96**: 11387–11392.

Jackson RB, Sperry JS, Dawson TE. 2000. Root water uptake and transport: using physiological processes in global predictions. *Trends in Plant Science* **5**: 482–488.

Katsura S, Kosugi K, Mizutani T, Mizuyama T. 2009. Hydraulic properties of variously weathered granitic bedrock in headwater catchments. *Vadose Zone Journal* **8**: 557–573.

Kerkhoff AJ, Martens SN, Shore GA, Milne BT. 2004. Contingent effects of water balance variation on tree cover density in semiarid woodlands. *Global Ecology and Biogeography* **13**: 237–246.

Kessler A, Jaeger L. 1999. Long-term changes in net radiation and its components above a pine forest and a grass surface in Germany. *International Journal of Climatology* **19**: 211–226.

Kosugi Y, Takanashi S, Tanaka H, Ohkubo S, Tan M, Yano M, Katayama T. 2007. Evapotranspiration over a Japanese cypress forest. I. Eddy covariance fluxes and surface conductance characteristics for 3 years. *Journal of Hydrology* **337**: 269–283.

Kurc SA, Small EE. 2004. Dynamics of evapotranspiration in semiarid grassland and shrubland ecosystems during the summer monsoon season, central New Mexico. *Water Resources Research* **40**: W09305. DOI: 10.1029/2004WR003068

Kurc SA, Small EE. 2007. Soil moisture variations and ecosystem-scale fluxes of water and carbon in semiarid grassland and shrubland. *Water Resources Research* **43**. DOI: 10.1029/2006wr005011

Lee X, Finnigan J, Paw UKT. 2004. Coordinate systems and flux bias error. In *Handbook of Micrometeorology, A Guide for Surface Flux Measurement and Analysis*, Lee X, Massman W, Law B (eds). Kluwer Academic Publ.: Dordrecht; 33–66.

Liebethal C, Huwe B, Foken T. 2005. Sensitivity analysis for two ground heat flux calculation approaches. *Agricultural and Forest Meteorology* **132**: 253–262.

Massman WJ. 2000. A simple method for estimating frequency response corrections for eddy covariance systems. *Agricultural and Forest Meteorology* **104**: 185–198.

McCole AA, Stern LA. 2007. Seasonal water use patterns of *Juniperus ashei* on the Edwards Plateau, Texas, based on stable isotopes in water. *Journal of Hydrology* **342**: 238–248.

McDowell NJ. 2011. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiology* **155**: 1051–1059.

McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG, Yepez EA. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* **178**: 719–739.

Milly PCD. 1994. Climate, soil-water storage, and the average annual water balance. *Water Resources Research* **30**: 2143–2156.

Moore GW, Heilman JL. 2011. Proposed principles governing how vegetation changes affect transpiration. *Ecohydrology* **4**: 351–358.

Nagler PL, Glenn EP, Kim H, Emmerich W, Scott RL, Huxman TE, Huete AR. 2007. Relationship between evapotranspiration and precipitation pulses in a semiarid rangeland estimated by moisture flux towers and MODIS vegetation indices. *Journal of Arid Environments* **70**: 443–462.

Oliphant AJ, Grimmond CSB, Zutter HN, Schmid HP, Su H-B, Scott SL, Offerle B, Randolph JC, Ehman J. 2004. Heat storage and energy balance fluxes for a temperate deciduous forest. *Agricultural and Forest Meteorology* **126**: 185–201.

Querejeta JI, Estrada-Medina H, Allen MF, Jimenez-Osornio JJ, Ruenes R. 2006. Utilization of bedrock water by Brosimum alicastrum trees growing on shallow soil atop limestone in a dry tropical climate. *Plant and Soil* **287**: 187–197.

Rong L, Chen X, Chen X, Wang S, Du X. 2011. Isotopic analysis of water sources of mountainous plant uptake in a karst plateau of southwest China. *Hydrological Processes* **25**: 3666–3675.

Rost J, Mayer H. 2006. Comparative analysis of albedo and surface energy balance of a grassland site and an adjacent Scots pine forest. *Climate Research* **30**: 227–237.

Schotanus P, Nieuwstadt FTM, De Bruin HAR. 1983. Temperature measurement with a sonic anemometer and its application to heat and moisture fluxes. *Boundary-Layer Meteorology* **26**: 81–93.

Schwinning S. 2008. The water relations of two evergreen tree species in a karst savanna. *Oecologia*. DOI. 10.1007/s0042-008-1147-2.

Schwinning S. 2010. The ecohydrology of roots in rocks. *Ecohydrology* **3**: 238–245.

Scott RL. 2010. Using watershed water balance to evaluate the accuracy of eddy covariance evaporation measurements for three semiarid ecosystems. *Agricultural and Forest Meteorology* **150**: 219–225.

Scott RL, Edwards EA, Shuttleworth WJ, Huxman TE, Watts C, Goodrich DC. 2004. Interannual and seasonal variation in fluxes of water and carbon dioxide from a riparian woodland ecosystem. *Agricultural and Forest Meteorology* **122**: 65–84.

Seyfried MS, Wilcox BP. 2006. Soil water storage and rooting depth: key factors controlling recharge on rangelands. *Hydrological Processes* **20**: 3261–3275.

Steinwand AL, Harrington RF, Or D. 2006. Water balance for Great Basin phreatophytes derived from eddy covariance, soil water, and water table measurements. *Journal of Hydrology* **329**: 595–605.

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

Twine TE, Kustas WP, Norman JM, Coork DR, House PR, Meyers TP, Prueger JH, Starks PJ, Wesely ML. 2000. Correcting eddy-covariance flux underestimates over a grassland. *Agricultural and Forest Meteorology* **103**: 279–300.

Webb EK, Pearman GI, Leuning R. 1980. Correction of flux measurements for density effects due to heat and water vapour transfer. *Quarterly Journal of the Royal Meteorological Society* **106**: 85–100.

White WB, Culver DC, Herman JS, Kane TC, Mylroie J. 1995. Karst lands. *American Scientist* **83**: 450–459.

Wilson K, Goldstein A, Falge E, Aubinet M, Baldocchi D, Berbigier P, Bernhofer C, Ceulemans R, Dolman H, Field C, Grelle A, Ibrom A, Law BE, Kowalski A, Meyeres T, Moncrieff J, Monson R, Oechel W, Tenhunen J, Valentini R, Verma S. 2002. Energy balance closure at FLUXNET sites. *Agricultural and Forest Meteorology* **113**: 223–243.

Wohlfahrt G, Irschick C, Thalinger B, Hörtnagl L, Obojes N, Hammerle A. 2010. Insights from independent evapotranspiration estimates for closing the energy balance: a grassland case study. *Vadose Zone Journal* **9**: 1025–1033.

Wolf A, Salliendra N, Akshalov K, Johnson DA, Laca E. 2008. Effects of different eddy covariance correction schemes on energy balance closure and comparisons with the modified Bowen ratio system. *Agricultural and Forest Meteorology* **148**: 942–952.

Wu XB, Redeker EJ, Thurow TL. 2001. Vegetation and water yield dynamics in an Edwards Plateau watershed. *Journal of Range Management* **54**: 98–105.

Zhang L, Dawes WR, Walker GR. 2001. Response of mean annual evapotranspiration to vegetation changes at catchment scale. *Water Resources Research* **37**: 701–708.

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