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## *Woody Plant Rooting Depth and Ecosystem Function of Savannas: A Case Study from the Edwards Plateau Karst, Texas*

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### Introduction

Savannas are characterized by the co-dominance of grasses and deep rooted shrubs or trees (e.g., Walter, 1971) in seasonally dry environments with a limited and fluctuating water supply. The two dominant plant functional types have contrasting strategies of drought avoidance, which determine the ecosystem-wide responses of savannas to precipitation variability. Grasses typically avoid drought by focusing their physiological activity in periods when soil water availability is high and become dormant as soon as the shallow soil, the sole source of their water supply, dries out. Shrubs and trees typically avoid drought by switching to deeper water sources, below the root zone of the grasses. Although this pattern has been observed in savannas, there are also variations on the theme, depending on two key factors: rooting depth and water availability in the lower root zone of the trees.

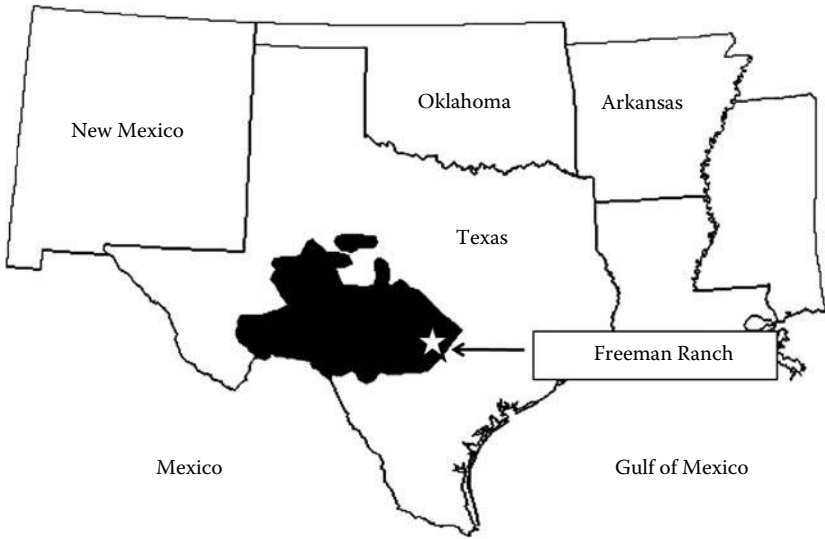
Rooting depth is a trait that can vary greatly among tree species; for example, the genera of mesquite, tamarix, and eucalypt (Stromberg et al., 2007; Scott

et al., 2006; Mitchell et al., 2009) have some of the most deeply rooted species known. These species are often called *phreatophytes*, implying access to groundwater, though in many cases the phreatophytic life style is “facultative” (Smith et al., 1997), and trees do well even without groundwater (Potts et al., 2008; Brunel, 2009). On the other end of the spectrum, many gymnosperms, including juniper, are described as having an extensive shallow root system rather than a deep root system (e.g., Hall, 1952; Dealy, 1990).

Rooting depth is also affected by soil condition and geology. For example, roots in sandy soils tend to grow deeper, due, in part, to the greater infiltration depth of water in sandy soil and also because of less mechanical resistance to root growth (Collins and Bras, 2007). Then there are systems, including many savanna systems, in which the soil is shallow and underlain by fractured bedrock. Based on a global analysis of rooting depths, Schenk (2008) concluded that the rooting depths of trees in these systems can far exceed those of trees in deep soils (7.9 m vs. 2.2 m in geometric mean rooting depth). Some observations appear to support this generalization. For example, Jackson et al. (1999), working in the eastern Edwards Plateau, found oak roots (*Quercus fusiformis*) in caves 20 m below ground; and in one frequently cited anecdote, a mesquite root (*Prosopis velutina*) was found at 60 m depth in an Arizona mine. However, there are also examples to the contrary. For example, roots of eastern white cedar on cliff faces extended only 30 cm into the bedrock (Matthes-Sears, 1995); and in the limestone karst of the Yucatan Peninsula, Mexico, roots of a shrub community penetrated only 3 m into a fractured limestone matrix (Querejeta et al., 2006, 2007), even though a permanent water table was available at 9–20 m. Clearly, bedrock is not a uniform medium for root proliferation, in some cases providing enhanced opportunities for deep root development and in others prohibiting the formation of deep roots.

Rooting depth, whether due to genetic differences or imposed by the environment, affects the function of savannas and woodlands in important ways. Where roots are deep, they are likely to tap into more permanent water sources (e.g., groundwater or perched water tables), as seen in the study by Jackson et al. (1999). This should buffer gross primary production to precipitation variability and support the carbon sequestration potential of wooded ecosystems, albeit potentially at the cost of reduced groundwater recharge, stream flow, and a receding water table (Jackson et al., 2005). Where deep root proliferation is blocked or where no water subsidy is available at depth, we would expect ecosystem fluxes to be more tightly coupled to precipitation, and persistent droughts would cause a severe decrease in primary production. Accordingly, we would also not expect trees in such systems to inordinately impact regional water balance.

Here we present tower-based measurements of net ecosystem exchange from three study sites on the eastern Edwards Plateau, a karst region in central Texas (Figure 6.1). Our goal is to examine whether groundwater significantly subsidizes the water consumption of trees in the region, a reasonable hypothesis given that the hydrology of karst areas is complex and frequently



**FIGURE 6.1**  
Location of the Edwards Plateau (shaded) and the Freeman Ranch.

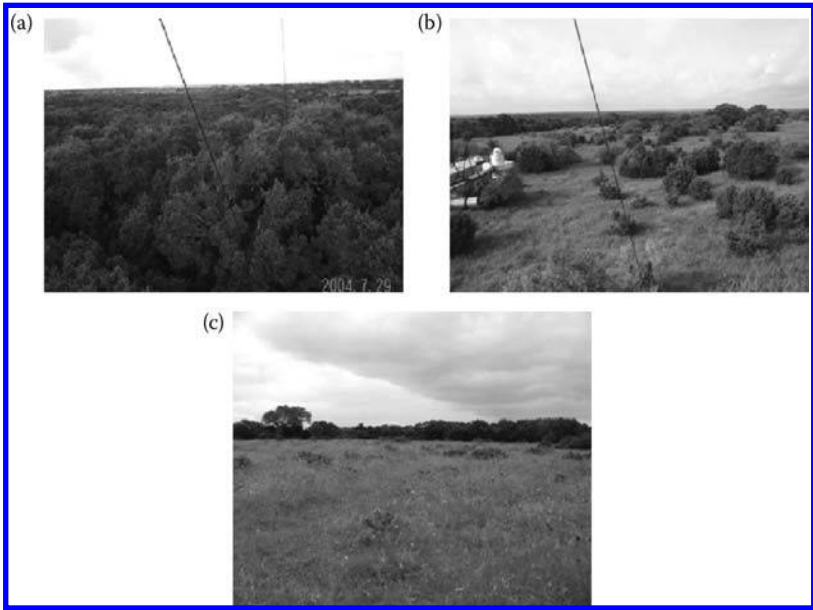
involves perched water tables, springs, and underground streams. The study site was not far (approximately 50 km) from the cave sites where Jackson et al. (1999) and McElrone et al. (2004, 2007) conducted their examination of roots in caves. Both sites have similar overstory composition, dominated by Ashe juniper (*Juniperus ashei*) and Plateau live oak (*Quercus fusiformis*). One important difference is, however, that our study site has no known caves.

We examine a 3-year continuous record (2005–2007) of eddy covariance measurements of carbon, water, and energy fluxes across three study sites with varying degrees of woody cover (grassland, savanna, and woodland) (Figure 6.2) to focus on estimating the role that woody species play in regulating carbon, water, and energy exchange and to assess whether and how the presence of woody plants changes sensitivity to precipitation. The 3 years span a wide range of moisture conditions, with annual precipitation in 2 consecutive years of the study being 13 and 19% below the 100 year mean of 913 mm, whereas precipitation in the third year was 66% above the mean and it was one of the wettest years on record (see Figure 6.3).

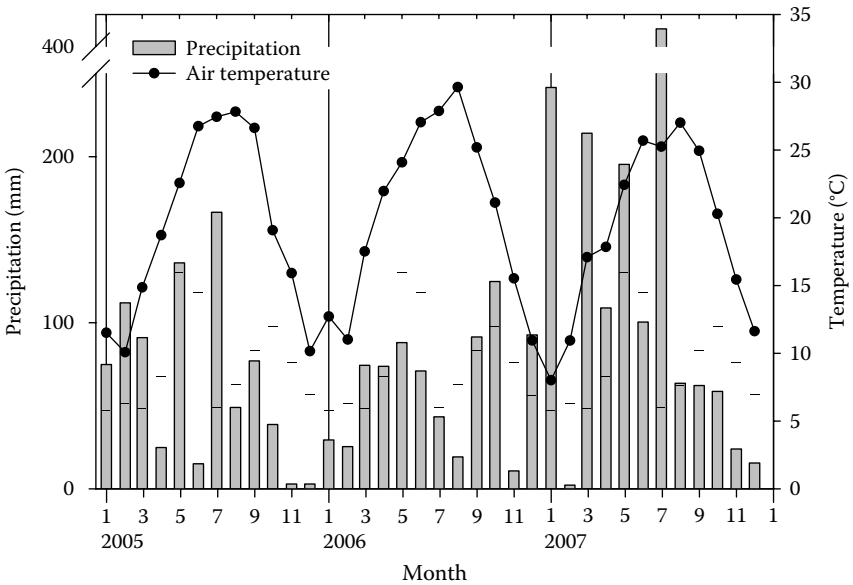
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## Site Descriptions

The three sites, located within 2.5 km of each other, include a grassland, a live oak-Ashe juniper forest, and a juniper or honey mesquite (*Prosopis glandulosa*) savanna on the Freeman Ranch, a 1701-ha research area on the eastern edge of the Edwards Plateau just north of San Marcos, Texas, owned



**FIGURE 6.2** (See color insert following page 320.) (a) View from the top of the woodland flux tower. (b) View from the top of the savanna flux tower. (c) Grassland tower pasture.



**FIGURE 6.3** Monthly precipitation totals and mean daily temperatures for 2005–2007. Dashes represent the historical mean precipitation for each month.

by Texas State University, San Marcos. The entire ranch is in the Edwards Aquifer recharge zone. Extensive portions of the Plateau are dominated by live oak (*Quercus virginiana*)-Ashe juniper (*Juniperus asheii*) savannas interspersed with perennial, mixed C<sub>3</sub>/C<sub>4</sub> grasslands. In the last 150 years, both Ashe juniper and honey mesquite have expanded rapidly into grasslands and savannas in this region mainly due to suppression of wildfires and introduction of livestock (Archer et al., 1995; Van Auken, 2009). Soils on the Plateau are shallow and rocky on slopes but deeper in broad valleys and flats. The limestone bedrock is fractured, and imbedded in the limestone are clay lenses and layers of marl and caliche, where water can be stored. *J. asheii* is primarily associated with the rocky and shallow soils of the limestone karst on the eastern edge of the Plateau. Mesquite is excluded or reduced to a shrub-like habit where soils are  $\leq 1.5$  m thick. In general, mesquite is not very common on the eastern Edwards Plateau, and it is more abundant in the deep prairie soils to the east and south of this region.

The grassland site is an intermittently grazed, perennial C<sub>3</sub>/C<sub>4</sub> pasture with widely interspersed, small (shrublike) honey mesquite trees inside the opening of an oak-juniper savanna (Table 6.1, Figure 6.2). The soil at the site is a Comfort stony clay (clayey-skeletal, mixed, superactive, thermic Lithic Argiustoll) with an approximately 20-cm deep A horizon overlying an approximately 20-cm thick Bt1 horizon containing chert fragments. A Bt2

**TABLE 6.1**

Location, Vegetation, and Soil Characteristics of Each Tower Site

Site	Location	Elevation (m)	Dominant Species	Soils	LAI (m <sup>2</sup> m <sup>-2</sup> )
Grassland	29°55.80'N, 98°0.60'W	230	<i>Bothriochloa ischaemum</i> (C4) <i>Stipa leucotricha</i> (C3)	Comfort stony clay (~40 cm)	0.5
Savanna	29°56.97'N, 97°59.77'W	272	<i>Juniperus asheii</i> <i>Prosopis glandulosa</i> <i>Bothriochloa ischaemum</i> (C4) <i>Stipa leucotricha</i> (C3)	Rumple-Comfort dominated by Rumple gravelly clay loam (1.5–2.0 m)	1.1
Woodland	29°56.40'N, 97°59.40'W	232	<i>Juniperus asheii</i> <i>Quercus virginiana</i>	Comfort stony clay (~10–20 cm)	2.0

Source: Adapted from ORNL DAAC (Oak Ridge National Laboratory Distributed Active Archive Center). 2009. MODIS subsetted land products. Collection 5. Available on-line (<http://www.daac.ornl.gov/MODIS/modis.html>) from ORNL DAAC, Oak Ridge, Tennessee. Accessed May 1, 2009.

Note: Leaf area index (LAI) for each site is the average of the maximum value for years 2005–2007. Leaf area index at the grassland site was estimated from replicate clipped samples. The herbaceous component of LAI at the savanna site was estimated from replicate clipped samples. Juniper LAI was based on allometric equations of Hicks and Dugas (1998). Mesquite LAI was estimated from destructive sampling following Ansley et al. (1998). Leaf area index at the woodland site is from the subset MODIS Land Product from Oak Ridge National Laboratory Distributed Active Archive Center.

horizon starting at a depth of approximately 50 cm contains chert slabs with cracks and gaps between slabs filled with soil. Grasses are dominated by King Ranch bluestem [*Bothriochloa ischaemum* (L. Keng.), an introduced C<sub>4</sub> species that has become invasive throughout the Plateau, and Texas wintergrass (*Stipa leucotricha* Trin. & Rupr.)], a C<sub>3</sub> species. The vegetation also includes a high percentage of forbs, which is typical of Plateau grasslands.

The savanna site consists of clusters of Ashe juniper and honey mesquite interspersed among intermittently grazed grassland that is similar to that at the grassland site (Table 6.1, Figure 6.2). This site is typical of Plateau grasslands with deeper soils undergoing encroachment (Eggemeier and Schwinning, 2009). In 2006, woody cover was estimated as 48% based on lidar measurements. Both *J. ashei* and *P. glandulosa* have been increasing at this site since 1970, and there are numerous juvenile trees of both species. The soil is a Rumble-Comfort association dominated by Rumble gravelly clay loam (clayey-skeletal, mixed, active, thermic Typic Argiustoll), and it is deeper than at the other two sites, about 1.5–2.0 m.

The woodland site is a continuous closed canopy of live oak and Ashe juniper that is typical of ecosystems occupying intermittent drainages and upland slopes on the Plateau (Table 6.1, Figure 6.2). Mean diameter at breast height (DBH) and basal area (BA) of live oak are 0.17 m and 23.5 m<sup>2</sup> ha<sup>-1</sup>, respectively. Most of the Ashe juniper in the woodland is multi-trunked with an estimated density of 2850 trunks ha<sup>-1</sup>. Mean DBH and BA for juniper are 0.08 and 18.4 m<sup>2</sup> ha<sup>-1</sup>, respectively. Above ground biomass was estimated to be 5.6 kg m<sup>-2</sup> for juniper and 5.8 kg m<sup>-2</sup> for oak, based on the allometric equation of Jenkins et al. (2003). As in the grassland, the soil at the woodland site is Comfort stony clay but with only approximately 0.1 m soil cover over fractured rock. Rock outcrops occupy approximately 50% of the surface, and most of the soil is covered by oak and juniper leaf litter. The herbaceous understory consists chiefly of isolated clumps of cedar sedge (*Carex planostachys*). Historical aerial photos suggest that although *J. asheii* has been present at this site for at least the past 70 years, it has increased in density and cover over this time.

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## Methods

Identical tower-based eddy covariance systems were used to measure fluxes of CO<sub>2</sub>, sensible heat ( $H$ ), and latent heat ( $\lambda E$ ) at all three sites. Wind velocity and air temperature fluctuations were measured acoustically using CSAT-3 sonic anemometers (Campbell Scientific Inc., Logan, UT), whereas CO<sub>2</sub> and water vapor density fluctuations were measured using LI-7500 open-path infrared gas analyzers (LI-COR Inc., Lincoln, NE). Anemometers and gas analyzers were placed at 3 m at the grassland, 6 m at the savanna, and 15 m at the woodland; and outputs were sampled at 10 Hz. Gas analyzers were

calibrated periodically using a gas of known CO<sub>2</sub> concentration and a dew-point generator (LI-610, LI-COR).

The surface energy balance is described by the equation

$$R_n - G - S = H + \lambda E,$$

where  $R_n$  is net radiation,  $G$  is soil heat flux,  $S$  is heat storage in aboveground biomass and in the canopy air space,  $H$  is sensible heat flux, and  $\lambda E$  is latent heat flux. Collectively, the three terms to the left of the equal sign represent the available energy, the net amount of energy on hand for partitioning between the turbulent fluxes of  $H$  and  $\lambda E$ . Net radiation was measured with model Q7.1 net radiometers (REBS, Seattle, WA) placed at the same elevations as the anemometers and gas analyzers. Soil heat flux was determined by soil heat flux plates and calorimetry (Liebethal et al., 2005). Sensible and latent heat fluxes were obtained from eddy covariance. In the woodland, heat storage in aboveground biomass and in the canopy air space was calculated using temperature and humidity profiles (Heilman et al., 2009). Storage fluxes in savanna and grassland biomass were ignored.

All fluxes were calculated as 30-min averages. Eddy covariance calculations 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; Ham and Heilman, 2003), and corrections for frequency response (Massman, 2000). We forced energy balance closure with the Bowen ratio conservation approach discussed by Twine et al. (2000) to facilitate comparison of evapotranspiration (ET) between the three land covers. The Bowen ratio conservation method (Twine et al., 2000) is a widely used method of forcing closure, and it has been extensively used in woodland ecosystems (Oliphant et al., 2004; Scott et al., 2004; Barr et al., 2006; Steinwand et al., 2006; Kosugi et al., 2007). The principal assumption of this method is that eddy covariance correctly measures the Bowen ratio, allowing it to be used to partition the missing energy between sensible and latent heat fluxes. Wolf et al. (2008) showed that eddy covariance estimates of the Bowen ratio were accurate, based on comparisons with traditional, gradient-based estimates, when all relevant corrections (density, frequency response, etc.) were applied to the eddy covariance data. Data rejected during a filtering process for each site include during precipitation events, when wind direction was from behind the tower, if friction velocity ( $u^*$ ) was below specific thresholds determined for each site (Reichstein et al., 2005) or for high deviation in stationarity tests. Three profiles of soil water content (Decagon ECHO probes) and soil temperature (Type T thermocouples) were measured in each site (at 0–5 cm, 5–10 cm, 10–20 cm depth). Additional measurements at each site include precipitation (Texas Electronics tipping bucket TE-525), air temperature and relative humidity profiles (Vaisala HMP 45C), and photosynthetically active radiation (Licor SI-190). Gaps in meteorological data and turbulent fluxes were filled, and net ecosystem exchange of carbon was partitioned into the components gross ecosystem production and ecosystem respiration using

the online tools of Reichstein (<http://www.bgc-jena.mpg.de/bgc-mdi/html/eddyproc/index.html>).

## Results and Discussion

### Energy Balance

Available energy ( $R_n - G - S$ ) was highest in the woodland site, due to greater absorption of shortwave radiation, reduced emission of longwave radiation by the forest canopy, and lower soil heat flux. Partitioning of available energy between  $H$  and  $\lambda E$  was controlled by water availability and turbulence. Bowen ratios in the savanna were generally lower than those at the other sites, perhaps due to greater water storage or retention in the root zone consistent with deeper soils at this site relative to the other two sites. Sensible heat flux is controlled by aerodynamic conductance, which increases with turbulence, whereas  $\lambda E$  is controlled mainly by canopy (stomatal) conductance, especially when water becomes limiting (Rost and Mayer, 2006). In absolute terms, the woodland generated 20% more  $H$  than the grassland or savanna in 2005, 22% more in 2006, and 29–47% more in 2007 (Table 6.2).

### Carbon and Water Balance

In terms of carbon balance, the presence of woody species increased the ability of these savannas to sequester carbon. Over the entire 3-year record, cumulative carbon gain in the grassland was 308 g C m<sup>-2</sup>, compared with 893

**TABLE 6.2**

Annual Totals of Available Energy ( $R_n - G - S$ ), Latent Heat Flux ( $\lambda E$ ), and Sensible Heat Flux ( $H$ ) for the Grassland, Savanna, and Woodland in 2005–2007

Year	Site	$R_n - G - S$ (GJ m <sup>-2</sup> year <sup>-1</sup> )	$\lambda E$ (GJ m <sup>-2</sup> year <sup>-1</sup> )	$H$ (GJ m <sup>-2</sup> year <sup>-1</sup> )	$\lambda E / (R_n - G - S)$	$H / (R_n - G - S)$
2005	Grassland	3.58	1.79	1.79	0.50	0.50
	Savanna	3.73	2.01	1.72	0.54	0.46
	Woodland	4.03	1.98	2.15	0.49	0.51
2006	Grassland	3.51	1.44	2.07	0.41	0.59
	Savanna	3.66	1.57	2.09	0.43	0.57
	Woodland	4.04	1.50	2.54	0.37	0.63
2007	Grassland	3.20	2.05	1.15	0.64	0.36
	Savanna	3.56	2.25	1.31	0.63	0.37
	Woodland	3.82	2.13	1.69	0.56	0.44

Source: Adapted from Twine, T. E. et al. 2000. *Agricultural and Forest Meteorology* 103, 279–300.

Note:  $\lambda E$  and  $H$  are the fractions of available energy. Energy balance closure was forced here using the procedure of Twine, et al. (2000).



and 978 g C m<sup>-2</sup> in the savanna and woodland, respectively. The sites with woody species are also slightly more resilient to drought and less responsive to variability in precipitation. In the grassland, NEP was very sensitive to differences in annual precipitation (Table 6.3), as expected of an ecosystem dominated by shallow-rooted herbaceous species. The overall carbon sink in the grassland (NEP) decreased by 22% from 2005 to 2006 as precipitation inputs decreased by 50 mm; then, it quadrupled in 2007 as precipitation doubled. Most of the increase in carbon gain can be explained by an increase in total carbon uptake through photosynthesis (GPP) (Table 6.3). In the woodland site, NEP was more similar across years and actually slightly less in the wet year compared with the two dry years, as respiration (R) in the woodland increased disproportionately more than total carbon uptake (GPP) in 2007 (Table 6.3). The savanna sink was similar to the woodland sink, except in 2006, the second year of the drought, when NEP was about halfway between that of the grassland and woodland sites. One interpretation is that in 2005, the savanna was able to utilize stored water carried over from the previous year, thus inflating carbon gain with regard to the grassland. In 2006, this reserve was likely depleted, and the intermediate value of NEP between that of the forest and the grassland mirrored the intermediate functional type composition of the savanna. The savanna sink increased by 80% from 2006 to 2007, in response to the large increase in precipitation in 2007.

There is very little evidence to support a permanent deep source of water for the woody species in our savanna and woodland. In 2006 and 2007, annual ET did not exceed precipitation inputs in any of the sites (Table 6.3). Although

**TABLE 6.3**

Annual Totals of Net Ecosystem Production (NEP), Gross Primary Production (GPP), Ecosystem Respiration (R), and Evapotranspiration (ET) for the Grassland, Savanna, and Woodland in 2005, 2006, and 2007

Year	Site	NEP (g C m <sup>-2</sup> y <sup>-1</sup> )	GPP (g C m <sup>-2</sup> y <sup>-1</sup> )	R (g C m <sup>-2</sup> y <sup>-1</sup> )	R/GPP	ET (mm y <sup>-1</sup> )	Precip (mm y <sup>-1</sup> )
2005	Grassland	-64	719	655	0.92	732	790
	Savanna	-389	1285	896	0.70	820	
	Woodland	-337	1529	1192	0.78	806	
2006	Grassland	-50	569	520	0.91	587	741
	Savanna	-183	978	795	0.81	638	
	Woodland	-353	1282	929	0.72	610	
2007	Grassland	-194	1291	1097	0.85	816	1536
	Savanna	-326	1643	1316	0.81	861	
	Woodland	-289	1576	1287	0.82	849	

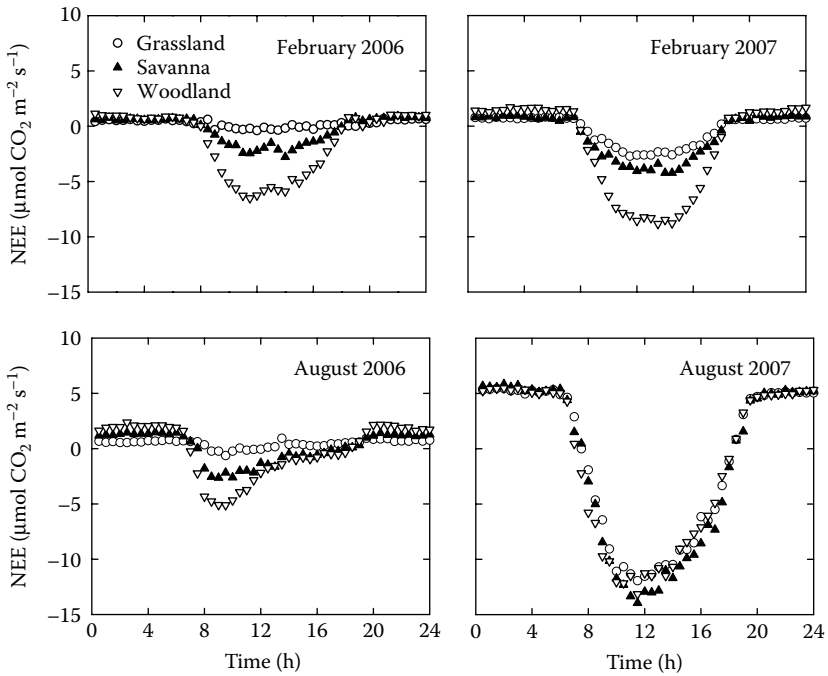
*Note:* We used the standard sign convention for NEE with NEE > 0, indicating a net loss of CO<sub>2</sub> to the atmosphere (source) and NEE < 0 indicating net CO<sub>2</sub> uptake by the ecosystem (sink). R and GPP are always positive. Also shown is the fraction of total carbon lost as respiration per total carbon gained through photosynthesis (R/GPP).

annual ET is slightly higher than precipitation inputs in the woodland and savanna in 2005 (Table 6.3), these values of ET were likely inflated relative to precipitation inputs, as the trees utilized stored water carried over from the previous year. In 2004, total precipitation was approximately 30% higher than the historical average, particularly toward the end of the year (where 560 mm fell in October and November alone). Further, woodland ET exceeded grassland ET by only 10%, 4%, and 4% in 2005, 2006, and 2007, respectively (Table 6.3), far less than the upward of 60%, which is typically observed when trees have access to groundwater (e.g., Engel et al., 2005; Scott et al., 2006; Paco et al., 2009). Differences in ecosystem ET were, in part, related to differences in available energy, which was greatest in the woodland (Table 6.2), and second, due to likely differences in the amount of water retained in the root zone after rainfall. Proportionally more available energy was partitioned into ET at the savanna site, the ecosystem with the deepest soil (~2 m of relatively clay-rich soils compared with thin soil over fractured bedrock at the woodland site, Table 6.1), and, thus, highest water storage capacity in the root zone.

Nevertheless, both the savanna and woodland had access, at least intermittently, to water sources in either the soil (deeper soils at the savanna site) or bedrock (at the woodland site in the rooting zone of the trees) that was not available to the grasses at the grassland site. During the very dry months of February and August in 2006 after months of below-average precipitation, the woodland and, to a lesser extent, the savanna were taking up carbon, whereas the grassland was largely dormant (Figure 6.4). In 2007, when precipitation inputs were large, net carbon uptake patterns were nearly identical among the three sites (Figure 6.4). Overall, the patterns we see in carbon and water balance over the 3-year period suggest that woody species increase the ability of Edwards Plateau landscapes to sequester carbon, but not necessarily at the expense of increased water use.

### Sensitivity to Precipitation Pulses and Drying Cycles

In all three land covers, ecosystem fluxes of carbon and water were highly sensitive to precipitation pulses and subsequent drying cycles throughout the year. Focusing specifically on a 100-day period in 2005, both NEE of CO<sub>2</sub> and ET or ETo declined rapidly at all sites during drying cycles (Figure 6.5), regardless of the amount of woody cover. The response shown in Figure 6.5 is typical of what occurred during most drying cycles, with the Bowen ratio ( $\beta = H/\lambda E$ ), approaching 5 at the grassland and woodland. However, during severe dry periods,  $\beta$  of both the savanna and woodland exceeded that of the grassland, reaching values greater than 20, due to higher turbulence at those sites. Characteristic of all three sites were large reductions in  $\lambda E$  when the soil dried between rainfall events, accompanied by large increases in  $H$ . This response suggests that all three land covers relied primarily on water from recent rainfall events and a limited amount of stored water rather than on a permanent water source at depth.

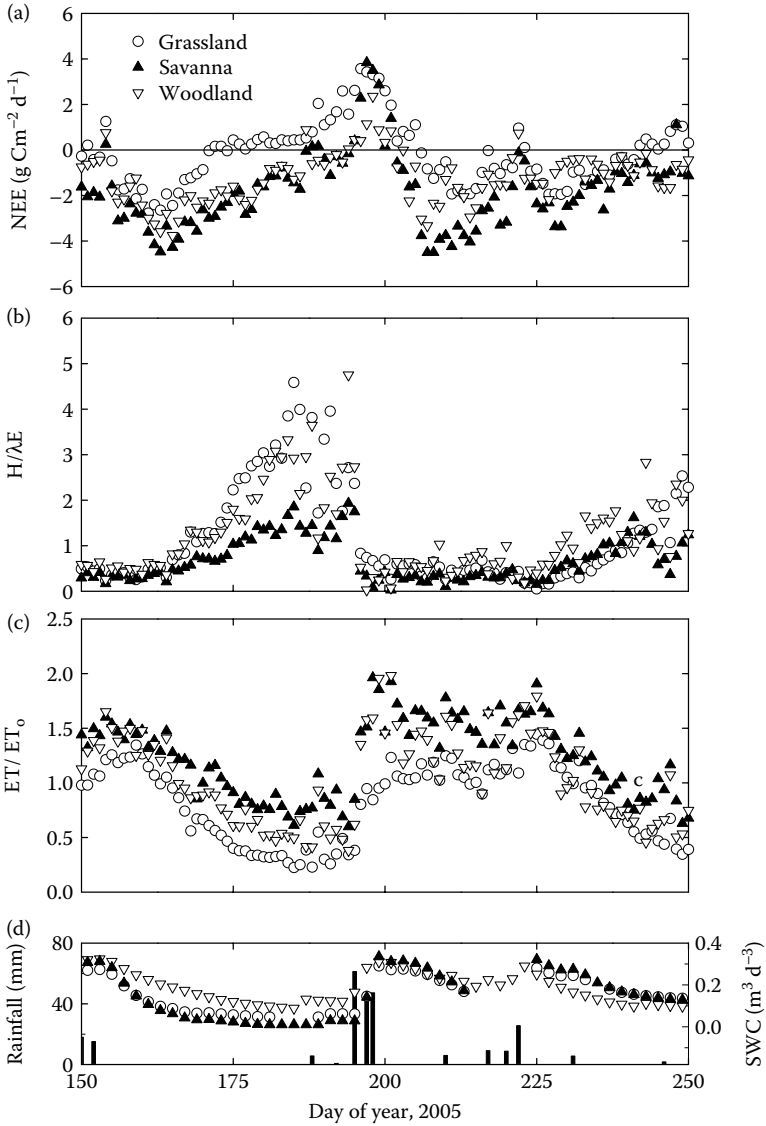
**FIGURE 6.4**

Mean monthly diurnal NEE for grassland, savanna, and woodland for February and August 2006 and 2007. Numbers represent means  $\pm 1$  SE.

The response of both NEE and  $ET/ET_0$  to precipitation pulses in the savanna and woodland sites typically outpaced the response in grassland sites (Figure 6.5). This suggests that the trees at our sites, unlike the grasses, remain physiologically active during drought and were able to use precipitation immediately. In addition, NEE and  $ET/ET_0$  of the wooded systems remained higher for the rest of the summer, suggesting that the series of very large rainfall events in September not only recharged the shallow soil and the grass root zone but also recharged the deeper soil or bedrock in the root zone of the trees. Rapid subsurface flow is characteristic of karst systems and distinguishes karst from systems with deep soils, where the bottom of the tree root zone receives water only through drainage from saturated soil layers above. This rapid recharge of the entire tree root zone is likely to contribute to the observed sensitivity of the karst ecosystems to precipitation, even in tree-dominated landscapes.

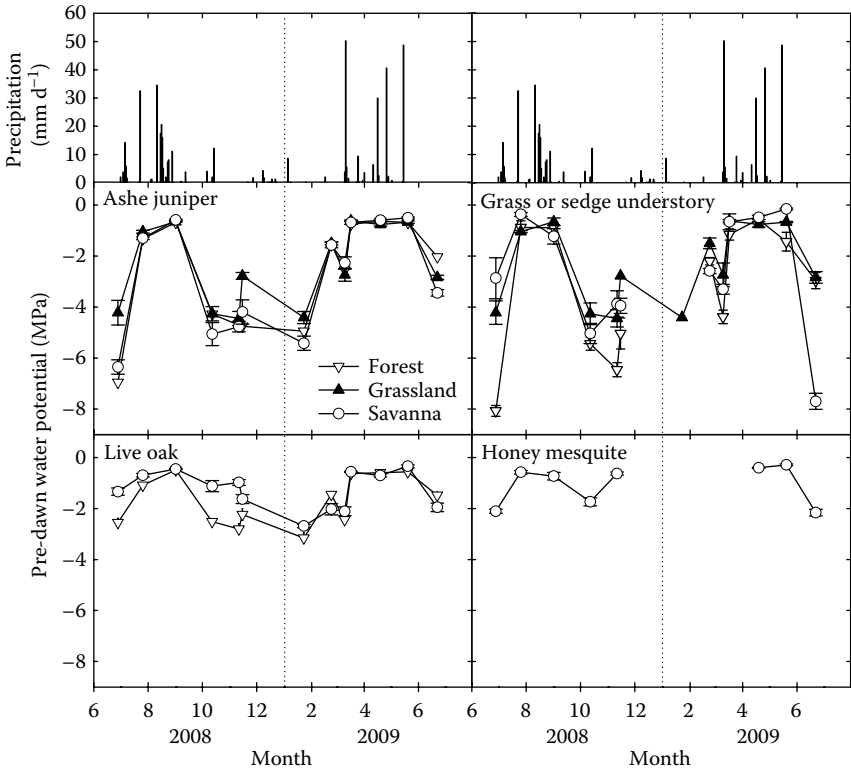
### Plant Water Status

The three dominant tree species at our study sites contrast in functional type characteristics, thus they probably contributed differentially to overall



**FIGURE 6.5**

Daily totals of (a) net ecosystem exchange of  $\text{CO}_2$ , (b) Bowen ratios ( $H/\lambda E$ ), (c) evapotranspiration (ET) normalized by reference ET ( $ET_0$ ), and (d) rainfall and soil water content for all three sites during a 100-day period in 2005. This pattern suggests that all ecosystems relied primarily on water from recent rainfall events and a limited amount of stored water rather than on a permanent water source at depth.

**FIGURE 6.6**

Water potentials taken at pre-dawn at the three eddy flux study sites from June 2008 to June 2009. Live oaks and juniper trees in the grassland site were surrounding the opening, but they were outside the fetch area of the tower. Missing points are due to unavailable samples during dormancy periods (grasses and mesquite).

ecosystem fluxes. Pre-dawn water potentials measured from June 2008 to June 2009 highlight some of these differences (Figure 6.6). This period was recognized as the worst drought since the 1950s in South Central Texas (specified as D4 exceptional drought condition by the National Weather Service) and provides further insight into the water sources available to these species and their drought tolerance.

Juniper exhibited the greatest fluctuations in pre-dawn water potentials, closely following the patterns seen in grasses and cedar sedge. This indicates that juniper did not likely have greater access to water than the understory species and is extraordinarily drought tolerant. By contrast, oaks and mesquites did exhibit pre-dawn water potentials below  $-4$  MPa. Although it is possible that the two species maintained higher water potentials because they were significantly deeper rooted than juniper and had access to less depleted water sources than the  $-6$  MPa water source of juniper trees, this is

unlikely. First, McElrone et al. (2004) have shown that (unlike juniper) live oaks lose approximately 90% of their hydraulic conductivity at  $-2$  MPa. Velvet mesquite (*Prosopis velutina*), a close relative of honey mesquite, in one study showed a 40–50% loss in stem hydraulic conductivity at  $-2$  MPa and a 60–80% loss at  $-4$  MPa (Hultine et al. 2004). Thus, a water source at  $-4$  MPa would have been of no use to oaks and of little use to mesquite. Second, other studies have shown that leaf gas exchange rates in oak are rapidly down-regulated during drought (Owens and Schreiber, 1992), more rapidly than in juniper, which is able to maintain a low but steady rate of gas exchange. This would suggest that GPP of the woodland site is increasingly carried by juniper as conditions get drier and could explain why the woodland is more water use efficient and NEP is slightly more buffered to precipitation variability than the other two sites.

At the savanna site, juniper and mesquite rooting depths were very similar. An excavation study conducted in 2006 showed that roots of mature individuals of juniper and mesquite extended to the bottom of the soil layer, at about 2 m depth although juniper root distribution was more skewed toward the surface when compared with that of mesquite (Schwinning, unpublished). In 2006, the pre-dawn water potentials of the two species at this site varied in almost perfect synchrony throughout the growing season (Eggemeyer and Schwinning, 2009), and with the exception of saplings  $<1$  m tall, which stayed above  $-2.5$  MPa in both species. After an extended dry period, large mesquite trees took up relatively more water from the deeper soil layers compared with large juniper trees, based on a comparison of stem water isotope ratios. This is consistent with the observation that mesquite had greater root allocation to deeper soil layers, but this did not prevent gas exchange rates in mesquite from decreasing to the severely low rates observed in juniper in the driest month of August. Similar to the woodland site, the contribution of juniper to savanna GPP increased with the progression of drought conditions.

Overall, tree species coexisting in the same site experienced very similar constraints of root development, even in species as dissimilar in rooting habit as Ashe juniper and honey mesquite. However, these species differed in their physiological response to variable water availability, with oaks and mesquite being more active during wet periods and juniper being more active in dry periods.

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## Conclusion

Although an earlier study observed roots from the codominant live oak and Ashe juniper trees of the eastern Edwards Plateau to be deep enough to reach into perched water tables or underground streams (Jackson et al., 1999; McElrone et al., 2004), the trees at our site clearly had no such access. During

extended drought periods, these species frequently reached their limits of drought tolerance and drastically reduced gas exchange. This occurred although at least two of the dominant tree species at the site, live oak and mesquite, are understood to have the capacity to form deep roots (Jackson et al., 1999). Edaphic constraints, in the form of largely unbroken limestone layers, prohibited the development of deep tap roots. This suggests a strong control of karst geology over the water sources available to plants. Contrary to the earlier study (Jackson et al., 1999; McElrone et al., 2004), which showed local geology facilitating access to a deep permanent water source, at our site, local geology constrained deep root development and limited access to water.

Questions of water access by trees are extremely sensitive. The general public often sees the water demands of municipalities threatened by tree encroachment (see Tenneson, 2008). The fix on the Edwards Plateau is seen in clear-cutting, which is encouraged by government subsidies without regard to local geology and the likelihood that trees have access to groundwater at a given site. Several studies to date have shown that the relationships between woody cover and stream flow or groundwater levels are complex and case dependent (Wilcox et al., 2005; Wilcox and Thurow, 2006; Wilcox et al., 2008). Huxman et al. (2005) wrote an insightful review of ecohydrological consequences of woody encroachment and developed general rules to evaluate circumstances in which woody encroachment is likely to impact water yield and those in which it is not. Large portions of the Edwards Plateau, even those described as being in the "recharge zone" of the Edwards Aquifer, as our study site, do not appear to provide much opportunity for water theft (Tenneson, 2008); and the large amount of public funds allocated to support brush control may not have the desired effect on groundwater recharge, but rather, at least temporarily, reduce rates of carbon sequestration.

Another indication that water sources for trees on the Edwards Plateau are quite limited is the conspicuous switch in savanna composition between the Blackland Prairie, where mesquite is common and juniper uncommon, and the Edwards Plateau, where juniper and mesquite abundances are reversed (Eggemeyer and Schwinning, 2009). The karst landscape appears to select shallow-rooted, drought-tolerant tree species and is against deep-rooted phreatophytes, contrary to what would be expected if access to groundwater was truly made easier by the karst geology. Querejeta et al. (2006, 2007) obtained similar results in the karst of the Yucatan Peninsula, showing that shrubs and trees were predominantly rooted in the top 1 m of the bedrock.

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## References

- Anslley, R. J., B. A. Trevno, and P. W. Jacoby. 1998. Interspecific competition in honey mesquite: Leaf and whole plant response. *Journal of Range Management* 51, 345–352.

- Archer, S. R., D. S. Schimel, and E. H. Holland. 1995. Mechanisms of shrubland expansion: Land use, climate or CO<sub>2</sub>. *Climate Change* 29, 91–99.
- Barr, A. G., K. Morgenstern, T. A. Black, J. N. McCaughey, and Z. Nezcic. 2006. Surface energy balance closure by the eddy-covariance method above three boreal forest stands and implications for the measurement of the CO<sub>2</sub> flux. *Agricultural and Forest Meteorology* 140, 322–337.
- Brunel, J. P. 2009. Sources of water used by natural mesquite vegetation in a semi-arid region of northern Mexico. *Hydrological Sciences Journal-Journal Des Sciences Hydrologiques* 54(2): 375–381.
- Collins, D. B. G., and R. L. Bras. 2007. Plant rooting strategies in water-limited ecosystems. *Water Resources Research* 43, ARTN W06407, doi:10.1029/2006WR005541.
- Dealy, J. E., 1990. Western juniper. In *Silvics of North America, U. S. Department of Agriculture Handbook 654, Vol. 1, Conifers*, eds. R. M. Burns and B. H. Honkala (Technical Coordinators). U.S. Government Printing Office, Washington, DC; 113.
- Eggemeyer, K. D. and S. Schwinning. 2009. Biogeography of woody encroachment: Why is mesquite excluded from shallow soils? *Ecohydrology* 2(1), 81–87.
- Engel, V., E. G. Jobbagy, M. Stieglitz, M. Williams, and R. B. Jackson. 2005. Hydrological consequences of eucalyptus afforestation in the argentine pampas. *Water Resources Research* 41, W10409.
- Hall, M. T. 1952. Variation and hybridization in *Juniperus*. *Annals of the Missouri Botanical Garden* 39, 1–64.
- Ham, J. M. and J. L. Heilman. 2003. Experimental test of density and energy-balance corrections on CO<sub>2</sub> flux as measured using open-path eddy covariance. *Agronomy Journal* 95, 1393–1403.
- Heilman, J. L., K. J. McInnes, J. F. Kjelgaard, M. K. Owens, and S. Schwinning. 2009. Energy balance and water use in a subtropical karst woodland on the Edwards Plateau, Texas. *Journal of Hydrology* 373, 426–435.
- Hicks, R. A. and W. A. Dugas. 1998. Estimating ashe juniper leaf area from tree and stem characteristics. *Journal of Range Management* 51, 633–637.
- Hultine, K. R., R. L. Scott, W. L. Cable, and D. G. Williams. 2004. Hydraulic redistribution by a dominant, warm desert phreatophyte: seasonal patterns and response to precipitation pulses. *Functional Ecology* 18, 530–538.
- Huxman, T. E., B. P. Wilcox, D. D. Breshears, et al. 2005. Ecohydrological implications of woody plant encroachment. *Ecology* 86, 308–319.
- Jackson, R. B., E. G. Jobbagy, R. Avissar, et al. 2005. Trading water for carbon with biological sequestration. *Science* 310 (5756), 1944–1947.
- Jackson, R. B., L. A. Moore, W. A. Hoffman, W. T. Pockman, and C. R. Linder. 1999. Ecosystem rooting depth determined with caves and DNA. *Proceedings of the National Academy of Sciences of the United States of America* 96(20), 11387–11392.
- Jenkins, J. C., D. C. Chojacky, L. S. Heath, and R. A. Birdsey. 2003. National-scale biomass estimators for United States tree species. *Forest Science* 49, 12–35.
- Kosugi, Y., S. Takahashi, H. Tanaka, et al. 2007. Evapotranspiration over a Japanese cypress forest. I. Eddy covariance fluxes and surface conductance characteristics for 3 years. *Journal of Hydrology* 337, 269–283.
- Lee, X., J. Finnigan, and U. K. T. Paw. 2004. Coordinate systems and flux bias error. In *Handbook of Micrometeorology A Guide for Surface Flux Measurement and Analysis*, ed. X. Lee, W. Massman, and B. Law, Kluwer Academic Publishers, pp. 33–66.
- Liebethal, C., B. Huwe, and T. Foken. 2005. Sensitivity analysis for two ground heat flux calculation approaches. *Agricultural and Forest Meteorology* 132, 253–262.



- Massman, W. J. 2000. A simple method for estimating frequency response corrections for eddy covariance systems. *Agricultural and Forest Meteorology* 104, 185–198.
- Matthes-Sears, U. and D. W. Larson. 1995. Rooting characteristics of trees in rock—a study of *Thuja-occidentalis* on cliff faces. *International Journal of Plant Sciences* 156(5), 679–686.
- McElrone, A. J., W. T. Pockman, J. Martinez-Vilalta, and R. B. Jackson. 2004. Variation in xylem structure and function in stems and roots of trees to 20 m depth. *New Phytologist* 163(3), 507–517.
- McElrone, A. J., J. Bichler, W. T. Pockman, C. R. Linder, R. N. Addington, and R. B. Jackson. 2007. Aquaporin-mediated changes in hydraulic conductivity of deep tree roots accessed via caves. *Plant Cell and Environment* 30(11), 1411–1421.
- Mitchell P. J., E. J. Veneklaas, H. Lambers, and S. S. O. Burgess. 2009. Partitioning of evapotranspiration in a semi-arid eucalypt woodland in south-western Australia. *Agricultural Meteorology* 149, 25–37.
- Oliphant, A. J., C. S. B. Grimmond, H. N. Zutter, et al. 2004. Heat storage and energy balance fluxes for a temperate deciduous woodland. *Agricultural and Forest Meteorology* 126, 185–201.
- ORNL DAAC (Oak Ridge National Laboratory Distributed Active Archive Center). 2009. MODIS subsetted land products. Collection 5. Available on-line (<http://www.daac.ornl.gov/MODIS/modis.html>) from ORNL DAAC, Oak Ridge, Tennessee. Accessed 2005–2007.
- Owens, M. K. and M. C. Schreiber. 1992. Seasonal gas-exchange characteristics of two evergreen trees in a semi-arid environment. *Photosynthetica* 26(3), 389–398.
- Paco, T. A., T. S. David, M. O. Henriques, et al. 2009. Evapotranspiration from a Mediterranean evergreen oak savannah: The role of trees and pasture. *Journal of Hydrology* 369, 98–106.
- Potts, D. L., R. L. Scott, J. M. Cable, T. E. Huxman, and D. G. Williams. 2008. Sensitivity of mesquite shrubland CO<sub>2</sub> exchange to precipitation in contrasting landscape settings. *Ecology* 89(10), 2900–2910.
- Querejeta, J. I., L. M. Egerton-Warburton, and M. F. Allen. 2007. Hydraulic lift may buffer rhizosphere hyphae against the negative effects of severe soil drying in a California Oak savanna. *Soil Biology & Biochemistry* 39(2), 409–417.
- Querejeta, J. I., H. Estrada-Medina, M. F. Allen, J. Jiménez, and R. Ruenas. 2006. Utilization of bedrock water by *Brosimum alicastrum* trees growing on shallow soil atop limestone in a dry tropical climate. *Plant and Soil* 287 (1–2), 187–197.
- Reichstein, M., E. Falge, D. Baldocchi, et al. 2005. On the separation of net ecosystem exchange into assimilation and ecosystem respiration: Review and improved algorithm. *Global Change Biology* 11, 1424–1439.
- Rost, J. and H. Mayer. 2006. Comparative analysis of albedo and surface energy balance of a grassland site and an adjacent Scots pine forest. *Climate Research* 30, 227–237.
- Schenk, H. J. 2008. Soil depth, plant rooting strategies and species' niches. *New Phytologist* 178(2), 223–225.
- Schwinning, S. 2008. The water relations of two evergreen tree species in a karst savanna. *Oecologia* 158(3), 373–383.
- Scott, R. L., E. A. Edwards, W. J. Shuttleworth, T. E. Huxman, C. Watts, and D. C. Goodrich. 2004. Interannual and seasonal variation in fluxes of water and carbon dioxide from a riparian woodland ecosystem. *Agricultural and Forest Meteorology* 122, 65–84.

- Scott, R. L., T. E. Huxman, D. G. Williams, and D. C. Goodrich. 2006. Ecohydrological impacts of woody-plant encroachment: Seasonal patterns of water and carbon dioxide exchange within a semiarid riparian environment. *Global Change Biology* 12, 311–324.
- Smith, S. D., R. K. Monson, and J. E. Anderson. 1997. *Physiological Ecology of North American Desert Plants*. Springer-Verlag, Berlin.
- Steinwand, A. L., R. F. Harrington, and D. Or. 2006. Water balance for Great Basin phreatophytes derived from eddy covariance, soil water, and water table measurements. *Journal of Hydrology* 329, 595–605.
- Stromberg, J. C., S. J. Lite, R. Marler, et al. 2007. Altered stream-flow regimes and invasive plant species: The Tamarix case. *Global Ecology and Biogeography* 16, 381–393.
- Tenneson, M. 2008. When juniper and woody plants invade, water may retreat. *Science* 322, 1630–1631.
- Twine, T. E., W. P. Kustas, J. M. Norman, et al. 2000. Correcting eddy-covariance flux underestimates over a grassland. *Agricultural and Forest Meteorology* 103, 279–300.
- Van Auken, O. W. 2009. Causes and consequences of woody plant encroachment into western North American grasslands. *Journal of Environmental Management* 90, 2931–2942.
- Walter, H. 1971. Natural savannas as a transition to the arid zone. In: *Ecology of Tropical and Subtropical Vegetation*. Oliver and Boyd, Edinburgh, pp. 238–265.
- Webb, E. K., G. I. Pearman, and R. Leuning. 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.
- Wilcox, B. P., M. K. Owens, R. W. Knight, and R. K. Lyons. 2005. Do woody plants affect streamflow on semiarid karst rangelands? *Ecological Applications* 15, 127–136.
- Wilcox, B. P. and T. L. Thurow. 2006. Emerging issues in rangeland ecohydrology: Vegetation change and the water cycle. *Rangeland Ecology & Management* 59, 220–224.
- Wilcox, B. P., P. I. Taucer, C. L. Munster, M. K. Owens, B. P. Mohanty, J. R. Sorenson, and R. Bazan. 2008. Subsurface stormflow is important in semiarid karst shrublands. *Geophysical Research Letters* 35 L10403, doi:10.1029/2008GL033696.
- Wolf, A., N. Saliendra, K. Akshalov, D. A. Johnson, and E. Laca. 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.