

Ecohydrological impacts of woody-plant encroachment: seasonal patterns of water and carbon dioxide exchange within a semiarid riparian environment

RUSSELL L. SCOTT*, TRAVIS E. HUXMAN†, DAVID G. WILLIAMS‡ and DAVID C. GOODRICH*

*Southwest Watershed Research Center, USDA-ARS, 2000 E. Allen Road, Tucson, AZ 85719, USA, †Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA, ‡Department of Renewable Resources and Botany, University of Wyoming, Laramie, WY 82071, USA

Abstract

Across many dryland regions, historically grass-dominated ecosystems have been encroached upon by woody-plant species. In this paper, we compare ecosystem water and carbon dioxide (CO₂) fluxes over a grassland, a grassland–shrubland mosaic, and a fully developed woodland to evaluate potential consequences of woody-plant encroachment on important ecosystem processes. All three sites were located in the riparian corridor of a river in the southwest US. As such, plants in these ecosystems may have access to moisture at the capillary fringe of the near-surface water table. Using fluxes measured by eddy covariance in 2003 we found that ecosystem evapotranspiration (ET) and net ecosystem exchange of carbon dioxide (NEE) increased with increasing woody-plant dominance. Growing season ET totals were 407, 450, and 639 mm in the grassland, shrubland, and woodland, respectively, and in excess of precipitation by 227, 265, and 473 mm. This excess was derived from groundwater, especially during the extremely dry premonsoon period when this was the only source of moisture available to plants. Access to groundwater by the deep-rooted woody plants apparently decouples ecosystem ET from gross ecosystem production (GEP) with respect to precipitation. Compared with grasses, the woody plants were better able to use the stable groundwater source and had an increased net CO₂ gain during the dry periods. This enhanced plant activity resulted in substantial accumulation of leaf litter on the soil surface that, during rainy periods, may lead to high microbial respiration rates that offset these photosynthetic fluxes. March–December (primary growing season) totals of NEE were –63, –212, and –233 g C m⁻² in the grassland, shrubland, and woodland, respectively. Thus, there was a greater disparity between ecosystem water use and the strength of the CO₂ sink as woody plants increased across the encroachment gradient. Despite a higher density of woody plants and a greater plant productivity in the woodland than in the shrubland, the woodland produced a larger respiration response to rainfall that largely offset its higher photosynthetic potential. These data suggest that the capacity for woody plants to exploit water resources in riparian areas results in enhanced carbon sequestration at the expense of increased groundwater use under current climate conditions, but the potential does not scale specifically as a function of woody-plant abundance. These results highlight the important roles of water sources and ecosystem structure on the control of water and carbon balances in dryland areas.

Keywords: carbon dioxide exchange, carbon sequestration, ecohydrology, eddy covariance, evapotranspiration, mesquite (*Prosopis velutina*), riparian, woody-plant encroachment

Received 11 January 2005; revised version received 18 July 2005 and accepted 25 August 2005

Introduction

The global, wide-spread invasion of woody plants into grasslands (Mayeux *et al.*, 1991) has potentially large biogeochemical consequences (Archer, 1994; McPherson, 1997; Hibbard *et al.*, 2001; McCulley *et al.*, 2004; Smith & Johnson, 2004). Woody-plant encroachment has been attributed to land use changes (e.g. domestic livestock introduction, fire suppression, native herbivore elimination) acting alone or in concert with changes in atmospheric boundary conditions (e.g. air temperature, precipitation, or [CO₂]) (Archer *et al.*, 1995). The debate on the causal mechanism for this phenomenon continues, while considerably less is known about consequences of this change on energy, water, and nutrient cycles in ecosystems.

In the southwestern US, precipitation is often the dominant control on biological activity (Noy-Meir, 1973). Altered depth-duration frequency distributions of precipitation events, combined with shifts in vegetation (e.g. woody-plant encroachment of grasslands, nonnative species invasions, encroachment by phreatophytes in riparian areas) may alter biological activity across a landscape in quite unpredictable ways (Huxman *et al.*, 2005). Woody-plant encroachment has been hypothesized to be an important component of the changing North American carbon cycle (Archer *et al.*, 2001; Pacala *et al.*, 2001), although there is uncertainty as to site-specific characteristics of this vegetation change impact (Goodale & Davidson, 2002; Jackson *et al.*, 2002). Additionally, woody-plant encroachment likely alters the hydrological characteristics at both the local and regional scales (Wilcox, 2002; Huxman *et al.*, 2005), yet there are few empirical studies clearly demonstrating these effects.

In this paper, we investigated the consequences of woody-plant encroachment on water and carbon dioxide (CO₂) exchange in a riparian area in southeastern Arizona, USA. Throughout this region, including areas of New Mexico, Texas, Mexico, and other warm-temperate and subtropical zones, encroachment by mesquite (*Prosopis* spp.) has been pervasive over a relatively short period (ca. 100 years). Encroachment has taken place in both upland and lowland areas and has dramatically altered ecosystem structure, and possibly function (Brown & Archer, 1989; Grover & Musick, 1990; Bahre & Shelton, 1993; Cabral *et al.*, 2003; Turner *et al.*, 2003). Velvet mesquite (*Prosopis velutina*) is a facultative riparian species native to the Sonoran and Chihuahuan Deserts. It thrives in warm semiarid environments and habitats without groundwater, but it attains maximum size and cover in riparian habitats (Campbell & Green, 1968; Stromberg *et al.*, 1993). Mesquite is a nitrogen fixer and produces abundant leaf litter with

high N concentration in riparian habitats with potentially large impacts on soil carbon cycling (Martens & McLain, 2003).

Woody-plant encroachment in riparian ecosystems of semiarid areas likely affects biodiversity and biogeochemistry (McClain *et al.*, 2003) and has the potential to alter landscape hydrology (Huxman *et al.*, 2005). In the drylands of southwestern North America, woody-plant encroachment may decouple primary productivity from summer rains because deeply rooted woody plants access stable groundwater sources unavailable to grassland species (Scott *et al.*, 2004). As such, the duration of plant activity and production potential of woody-plant-dominated systems is likely greater than the historic grassland. However, increased productivity by woody plants may be offset by larger respiratory fluxes from soil microbial communities that remain highly responsive to summer precipitation and are fueled by high-quality litter inputs from woody vegetation (McCulley *et al.*, 2004). Plant size (or age) likely influences the potential for woody plants to access deep soil water; small (young) woody plants may only have access to shallow soil moisture, similar to grasses, yet larger (older) individuals likely access groundwater. Therefore, over a gradient of woody-plant encroachment from a grassland, to a grassland–shrubland mosaic, to a well-developed woodland we can expect nonlinear responses of ecosystem gas exchange to resource availability.

Herein, we compared CO₂ and water fluxes from a grassland, an intermediate grassland–shrubland mosaic, and a successional advanced mesquite woodland, assuming that a space for time substitution adequately represents the ecosystem dynamics over the process of grassland to woodland conversion. Our eventual goal is to predict how on-going woody-plant encroachment affects ecosystem water and carbon cycling by understanding the abiotic and biotic controls on these fluxes. Accordingly, these findings represent an important first step that delineates significant differences in how the ecosystems' functioning change along the invasion gradient in a year with similar climatic forcing at each site and illuminates important future research challenges.

Methods

Description of climate and study sites

Three study sites representing a grassland, a grassland–shrubland mosaic (referred to as a 'shrubland' hereafter), and a mesquite woodland were selected on old floodplain terraces along the San Pedro River in southeastern Arizona, USA. Mesquite cover in the San Pedro

Basin increased by 410% (Kepner *et al.*, 2000) across upland and riparian habitats from 1973 to 1992 (Turner *et al.*, 2003). The climate of the river valley is semiarid with a mean maximum temperature of 26.8 °C and a mean minimum of 7.1 °C (1971–2000 averages recorded in Benson, AZ). The 1971–2000 annual precipitation amounts ranged from 313 mm in Benson, AZ to 386 mm in Sierra Vista, AZ. Rainfall in this area has a high degree of spatial and temporal variability. Winter frontal storms that may occur between November and March when dominant vegetation is dormant provide 30% of the mean annual precipitation, during periods when nighttime frosts are common. From April through June, days are typically very dry and hot. During a period from July to September, moist tropical air associated with the North American Monsoon (Adams & Comrie, 1997) combined with local surface heating generates high-intensity, short-duration convective storms, providing about 60% of the annual precipitation. Dominant riparian vegetation becomes dormant in October or November because of cold temperatures and decreased surface water availability.

The woodland study site is located on an old alluvial terrace on the east side of the San Pedro River at an elevation of 1200 m, approximately 16 km northeast of Sierra Vista, Arizona. Previous micrometeorological studies conducted at this site have been reported by Scott *et al.* (2003, 2004) and provide the foundation for our investigation of the ecohydrological impacts of vegetation change. The site is dominated by large velvet mesquite (*P. velutina*) trees, while the understory consists of perennial sacaton bunchgrass (*Sporobolus wrightii*) with greythorn (*Zizyphus obtusifolia*) and various summer-active herbaceous dicots. The Woodland is about 600 m wide east/west and parallels the south-to-north course of the river for at least 1500 m. The average tree canopy cover is approximately 75%. The mean canopy height is 7 m, and the depth to groundwater is ~ 10 m. Analysis of $\delta^{13}\text{C}$ in soil profiles at this site reveal a predominantly C4 grass signature for depth greater than 0.25 m (D. Martens, personal communication), suggesting that the site was more grass dominated in the past.

The grassland and shrubland study sites are located within 1 km of each other on the east side of the San Pedro River at an elevation of ~ 1230 m, about 12 km upstream (south) from the woodland. The grassland lies on a lower alluvial terrace bordering the river. The tower is surrounded by a lush growth of sacaton grass (canopy height ~ 1 m; canopy cover ~ 65%; depth to groundwater ~ 2.5 m) and a variety of summer-active herbaceous dicots that extends roughly 200 m east/west and 800–1000 m north/south. The shrubland lies immediately to the northeast of the grassland in a moder-

ately dense stand of velvet mesquite with the dimensions of ~ 500 m east/west by 500 m north/south. The mesquite cover is ~ 55%, and the tree heights are between 3 and 4 m. Sacaton grasses and various smaller shrubs are abundant in scattered patches in the tree interspaces. The depth to groundwater is ~ 6.5 m. Turner *et al.* (2003) present historical photography taken very near the shrubland and grassland sites, which reveal that they were expansive grasslands in 1891. Soil texture profiles at all three sites are similar and consist mainly of gravelly sandy loam layers interspersed with clay and gravel lenses.

Flux measurements

Evapotranspiration (ET) and the net ecosystem exchange of CO₂ (NEE) were measured using eddy covariance starting in 2001 at the woodland and in 2003 at the grassland and shrubland. At all sites, a three-dimensional sonic anemometer (Model CSAT3, Campbell Scientific Inc., Logan, UT, USA) and an open path infrared gas analyzer (IRGA; Model LI-7500, LI-COR Inc., Lincoln, NE, USA), mounted at 1.5 m (grassland), 3 m (shrubland), and 7 m (woodland) above the height of the canopy, measured the three components of the wind velocity vector, sonic temperature, and the appropriate scalars (water vapor and CO₂ densities). A datalogger (CR5000, Campbell Scientific), sampling at 10 Hz, calculated 30 min covariances on-line using block Reynolds averaging. Every 1–2 months, IRGAs were zero- and span-calibrated using a CO₂/H₂O-free gas, a standard [CO₂] gas, and a dew point generator. Surface fluxes were later calculated off-line, after performing a two-dimensional coordinate rotation and accounting for density fluctuations (Webb *et al.*, 1980). Sensible heat flux was calculated with the sonic temperature (Paw *et al.*, 2000), to account for energy balance error that derives from air expansion during evaporation at a constant pressure. Fluxes measured when the wind originated from a direction within 20° of behind the anemometer were ignored because of possible interference from the anemometer support and the IRGA mounted behind the anemometer.

We also attempted to correct NEE for CO₂ storage in the canopy. As we did not have continuous CO₂ profile data, the storage term was estimated using only [CO₂] from the IRGA at the tower top. To determine what error might have been introduced using this method, we collected profile data over an 11-day period at six heights at the woodland. Differences between half-hourly CO₂ storage terms (ΔS_{top}) calculated using just the top IRGA vs. those using the profiler's six heights ($\Delta S_{\text{profile}}$) were small ($\Delta S_{\text{profile}} = 1.05\Delta S_{\text{top}} + 0.001$, $RMSE = 0.36 \mu\text{mol m}^{-2} \text{s}^{-1}$), and the means were not

significantly different from each other ($\alpha = 0.01$). Similarly, Hollinger *et al.* (1994) showed that this approximation worked well for a tall tower (36 m) over a forested site.

To assess our eddy covariance measurements, we used the ratio of the sum of the average sensible and latent heat fluxes over net radiation minus the ground heat flux as an indication of energy balance closure. The energy balance ratios were similar to the slopes of the least-squares-fitted line fit to all the data. Closure was the lowest for the grassland (0.76), slightly better for the shrubland (0.81), and highest for the woodland (0.92) in comparison with the survey by Wilson *et al.* (2002). Numerous hypotheses explain why closure is rarely obtained for the eddy covariance methods including: (1) source area mismatches for energy balance terms, (2) systematic instrumentation bias, (3) neglected energy sinks, (4) loss of low- and/or high-frequency contributions to flux, and (5) neglected scalar advection (Wilson *et al.*, 2002). Cosine errors in anemometer response over tall vegetation (Gash & Dolman, 2003) and angle-of-attack issues for anemometers (van der Molen *et al.*, 2004) also contribute to lack of energy balance closure.

For our study, the fetches at the grassland and shrubland are less uniform than at the woodland. Density of the dominant cover decreases with distance from the measurement tower at both the grassland and shrubland sites. Thus, net radiation was likely overestimated because of instrument location over rather dense patches of vegetation compared with the average observed in a typical 50–200 m turbulent flux footprint. A more representative net radiation measurement would probably improve closure (perhaps 5–10%) because of the increased albedo of vegetation free surfaces. The lack of energy balance closure found in this study is commonly reported for other semiarid sites (e.g. Scott *et al.*, 2004; Veenendaal *et al.*, 2004; Williams *et al.*, 2004; Hastings *et al.*, 2005). While this introduces some degree of uncertainty in our results, the magnitude is such that it does not significantly alter our conclusions.

Other measurements

Standard meteorological measurements including incoming and reflected photosynthetically active photon flux densities, solar radiation, net radiation, wind speed and direction, temperature, relative humidity, and precipitation were monitored continuously with an array of sensors at all flux sites. Ground heat fluxes at 0.05 m below the soil surface were measured with eight soil heat flux plates at the woodland and with four heat flux plates at the other two sites. Measurements of the rate of change of soil temperature above the heat flux plates (at 0.02 and 0.04 m) allowed calculation of the heat flux at

the soil surface using estimates of the specific heat of the 0.05 m thick layer obtained with a thermal properties sensor (TP01, Hukseflux, Delft, the Netherlands) at the woodland and estimated from soil properties and water content at the other two sites. Volumetric soil moisture at all sites was measured with water content reflectometers (Model CS615 and CS616, Campbell Scientific Inc.) installed in profiles at depths of 0.05, 0.10, 0.20, 0.30, 0.50, 0.70, and 1.0 m. A piezometer was installed at each site to measure water table levels. Piezometers were measured manually until the installation of pressure transducers and periodically afterward to confirm accuracy.

For each site, we collated all available 2003 data from the NASA Moderate Resolution Imaging Spectroradiometer (MODIS)-derived 16-day composite, 250 m enhanced vegetation index (EVI, Gao *et al.*, 2000), a satellite-derived vegetation greenness index. We also measured average ($n = 40$) plant area index (PAI) on a periodic basis along four 100 m transects at each site. Total PAI at the woodland and shrubland was calculated as the sum of overstory and understory PAI measurements. There was a strong linear relationship between total PAI and EVI ($n = 20$, $R^2 = 0.86$, 0.90, and 0.91 for the woodland, grassland, and shrubland, respectively). The same least-squares, linear fit ($PAI = slope \times EVI + intercept$) described both woody sites well, but a different one (with a larger slope and smaller intercept) was needed for the grassland. The linear relationship was applied to the entire EVI time series to produce a MODIS-derived PAI for each site.

Periodically at each site, plant water status was assessed by measuring predawn water potential (Ψ_{pd}) with a Scholander-type pressure chamber (PMS Instruments Ltd, Corvallis, OR, USA) with N_2 balancing gas. Measurements were carried out for all sites during the same predawn period to avoid the possibility of summer thunderstorms occurring during intervening days. Briefly, mesquite branches were harvested from the west-facing side of trees or shrubs at mid-canopy, while sacaton tillers were removed from the center of a bunchgrass. Material was sealed in a humidified plastic bag and placed in a cooler for typically less than one-half hour until measurements were made using the pressure chamber. Both mesquite and sacaton samples were taken from all sites, except the grassland, where no mesquite was present.

Friction velocity filtering and averaging procedures

Many researchers have pointed out that it is not uncommon for eddy covariance measurements to underestimate fluxes, especially NEE, when turbulent intensity is low (e.g. Lee, 1998; Pilegaard *et al.*, 2001;

Turnipseed *et al.*, 2002). Horizontal advection, low-frequency vertical transport, and accumulation of CO₂ close to the ground at night all contribute to this problem (Malhi *et al.*, 1998). To minimize the effect of poor turbulent mixing in our nighttime CO₂ flux data, we restricted the analysis to data measured when the friction velocity (u^*) was greater than a threshold value. The threshold values were determined as in Saleska *et al.* (2003), whereby we evaluated the average nighttime CO₂ flux over increasing u^* bins for a 70-day dry and a wet period (analysis not shown). The u^* threshold was identified as the point where averaging resulted in no further changes in flux estimation. We attempted to objectively determine this threshold by identifying the point at which the differences in mean values were no longer statistically significant from each other ($P = 0.25$). The u^* thresholds below which the NEE data were rejected were 0.10, 0.15, and 0.2 m s⁻¹ for the grassland, shrubland, and woodland, respectively. As an additional check on these u^* thresholds, cumulative NEE totals presented below decreased for increasing values of u^* up to the threshold values chosen and remained relatively stable for further increases in u^* .

In any long-term field campaign, missing data is unavoidable because of instrumental malfunctions, power failures, and data screening procedures. For the 2003 data presented herein, about 10–15% of the sites' flux data were either missing or screened out because of filtering criteria such as the sonic temperature, water vapor density, CO₂ density values occurring outside reasonable bounds, dew on the IRGA, etc. Additionally, because of the frequently quiescent nocturnal winds, using the u^* filter removed many nighttime data (grassland = 72%, shrubland = 70%, and woodland = 85%), which left only 15–30% of the nighttime flux measurements for analysis. Therefore, we compared weekly average water and CO₂ fluxes to avoid excessive gap filling that would be required for daily averages. We determined weekly ET totals by first computing the average weekly diurnal trace (taking the average of all 30 min data that occurred in hourly bands) and then we summed over the average diurnal ET trace to get a weekly total. We used the same method, but with a larger 2 h bin size, to determine the average net ecosystem exchange of CO₂ (\overline{NEE}). This method is essentially equivalent to gap filling first by using an average diurnal curve centered around the day of the missing data (Falge *et al.*, 2001) and then computing the weekly mean. Next, we calculated weekly average respiration (\overline{R}) as the average nighttime NEE. We computed gross ecosystem production (\overline{GEP}) as $\overline{R} - \overline{NEE}$.

\overline{GEP} was negative for several weeks during the non-growing season. This occurred when the cold nighttime temperatures inhibited respiration at night, and posi-

tive carbon efflux occurred during the daytime, which underestimated respiration. For these weeks, the amount that \overline{GEP} was less than zero was added to \overline{R} and removed from \overline{GEP} . For similar reasons, our estimates of ecosystem respiration during the growing season are probably low. Underestimates in respiration would lead to underestimates in \overline{GEP} as well as $\overline{NEE} = \overline{R} - \overline{GEP}$. Our estimates of \overline{NEE} , however, were not similarly influenced. The underestimation of \overline{R} and \overline{GEP} was likely similar for all sites, and, thus, we only used these derived data to elucidate site-to-site differences.

Results and discussion

Here, we show data from 2003, the first year in which comparable measurements were available across all sites.

Environmental conditions

Precipitation totals were similar at all three sites (Fig. 1). Total annual precipitation was 232 mm at the woodland and 234 mm at grassland and shrubland, much less than the 1971–2000 average of 343 mm at nearby Tombstone, AZ. Above canopy air and dew point temperatures at the grassland and shrubland (data not shown) were very similar to those found at the woodland (Fig. 1). The difference between the daily maximum and minimum

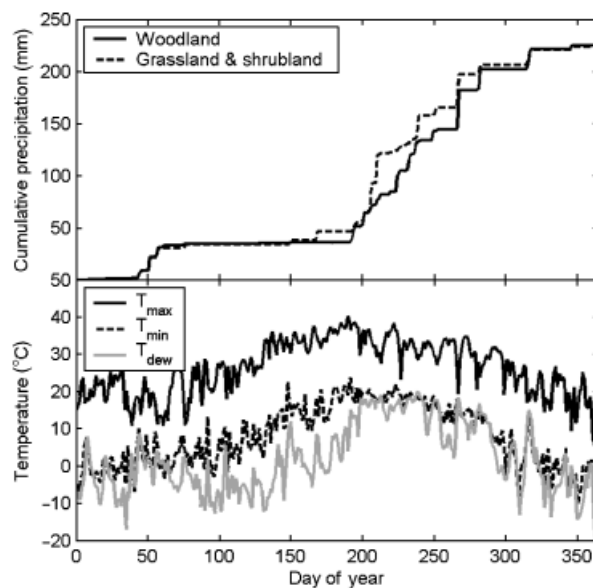


Fig. 1 (Upper) 2003 cumulative precipitation at all sites. As grassland and shrubland are adjacent to each other their precipitation is nearly identical. (Lower) Daily maximum (—), minimum (---) air temperatures, and mean dew point temperature (—) at 14 m at the woodland site. Above canopy air temperatures at the other two sites were very similar.

temperatures often exceeded 20 °C for most of the year and was around 15 °C during the monsoon. Closer to the surface at 2 m height, the dry season daily temperature swing was often greater than 25–30 °C (data not shown). In the San Pedro Valley, the 2003 monsoon began on day of year (DOY) 194 and ended around DOY 255 (using the National Weather Service standard of greater than/less than 12.8 °C dew point temperature for three consecutive days). The actual end of the summer rainy season was not clearly defined, and there were several large rain events between DOY 255 and the end of the growing season. Spring nighttime freezing ended on DOY 131 and sequential nighttime frosts began on DOY 308 in the fall, defining the mesquite-growing season. Minimum temperatures inside the riparian corridor are often as much as 10 °C lower than on the valley floor because of nocturnal cold air drainage (Scott *et al.*, 2004).

Annual mean depth to groundwater was 2.6, 6.4, and 9.8 m at the grassland, shrubland and woodland, respectively. Annual water level changes were about 0.9 m at the woodland site and 0.4 m at the other sites (Fig. 2). Groundwater levels generally declined from the time of new leaf production until the beginning of the monsoon. During the monsoon, the water levels record the complex effects of passing floods in the river channel with most noticeable effects at grassland and the least detectable at woodland, corresponding to the

increasing distance of each site's piezometer to the nearest stream channel. The presence of regular diurnal fluctuations (with minimum depths in the early morning and maximum depths around sundown) at all sites following leaf flush indicates that, to some extent, all ecosystems used groundwater (inset, Fig. 2). These regular diurnal fluctuations began around DOY 120 at the grassland, about 10 days earlier than the shrubland and 20 days earlier than the woodland. These data were in agreement with visual observations of rank order of green tissue production across sites. Before the diurnal fluctuations began at grassland, water levels had already begun to decline because of the influence of nearby cottonwood trees that greened up around DOY 90. The woodland had a greater density of mesquite trees, which probably contributed to the greater water level decline at this site compared with the shrubland site once the mesquite trees began using groundwater. Water table heights began to recover around DOY 270, but regular fluctuations at both the shrubland and woodland did not cease until DOY 308 when a hard freeze forced mesquite dormancy (diurnal measurements were unavailable at the grassland after DOY 275).

The seasonal phenology of all three sites was similar, although there were some important fine-scale differences (Fig. 3). At the shrubland and woodland, the mesquite leafed out around DOY 130. *In situ* overstorey PAI measurements indicated that the overstorey mes-

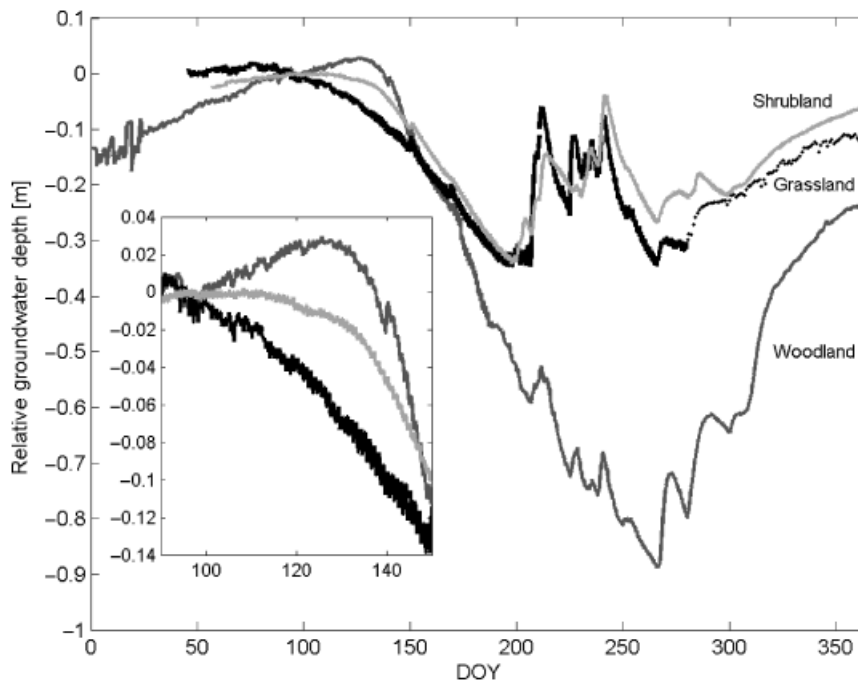


Fig. 2 Year 2003 relative groundwater depths, \hat{z}_{gw} , for all three sites. \hat{z}_{gw} was computed by adding the water table depths from day of year 90 (woodland = 9.51 m, grassland = 2.44 m, shrubland = 6.28 m) to all values. Inset figure shows the water table changes during the spring green up that initiated water table drawdowns and regular diurnal fluctuations because of groundwater extraction by the plants.

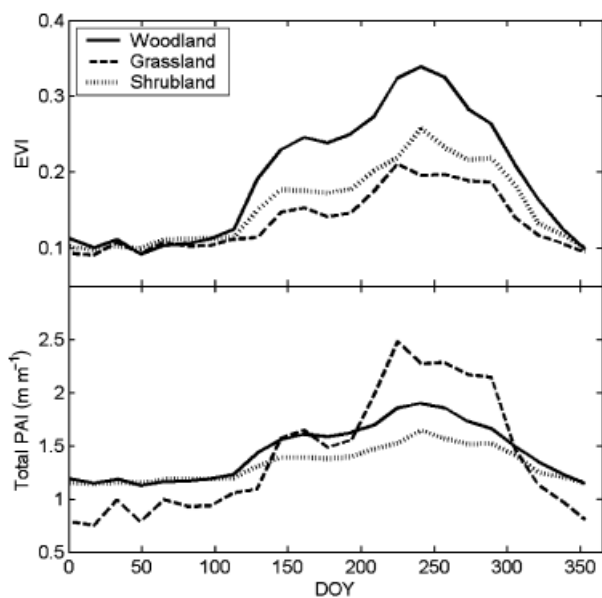


Fig. 3 Year 2003 MODIS enhanced vegetation index (EVI) and total plant area index (PAI) for all three sites. PAI was derived from a linear regression of EVI and periodic *in situ* PAI measurement.

quite leaf area did not vary following initial leaf flush (data not shown) so subsequent increases in total PAI (Fig. 3) at these sites were mainly because of understory grass and herbaceous dicot growth. Plant area showed a much larger change in response to the monsoon rains at the grassland. The seasonal EVI data illustrated differences among the sites (Fig. 3), where growing season EVI was highest at the woodland and lowest at the grassland. EVI better reflects ecosystem green leaf area, while optically measured PAI better represents total plant area.

Ecosystem water use

Seasonal patterns of ET of the shrubland and grassland were similar to that of the woodland (Fig. 4). The grassland initiated photosynthetic activity and began to transpire earlier in the year than the vegetation at the other sites. However, after mesquite leaf flush, ET rates at shrubland rapidly approached, and then exceeded those of the grassland, because of an enhanced ability of the deeper rooted trees to acquire groundwater. The increase in weekly ET during the monsoon was higher

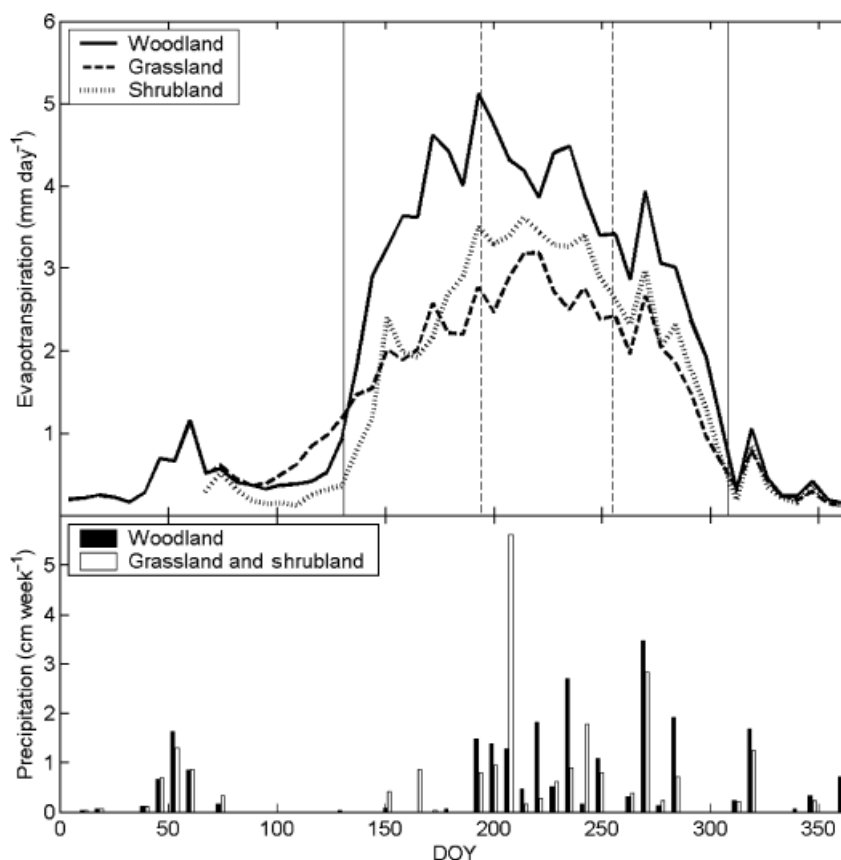


Fig. 4 Year 2003 average weekly evapotranspiration and total weekly precipitation. The days of the last freeze of spring and first freeze of fall (solid line) and monsoon period (between the dashed line) are also indicated by vertical lines.

Table 1 Year 2003 growing season water balance (May 1–December 1)

	Woodland	Grassland	Shrubland
Evapotranspiration (<i>ET</i>)	639	407	450
Precipitation excess ($P-\Delta S$)	166	180	185
Groundwater use per unit area of land (Q_t)	473	227	265
Fractional coverage of dominant vegetation type (f_v)	0.74	0.64	0.55
Groundwater use per unit (phreatophyte) canopy area (Q_{veg})	639	355	482

Units are in millimeters. $Q_t = ET - (P - \Delta S)$ and $Q_{veg} = Q_t / f_v$.

at the shrubland than at the grassland, even though there was a greater increase in PAI at the grassland. In the Shrubland, mesquite may have continued to rely on groundwater, even during the monsoon, whereas the understory plants responded to precipitation. Plants at the grassland likely switched to using a greater fraction of precipitation relative to groundwater throughout the season.

During the growing season, woodland ET always exceeded that at the other two sites (Fig. 4). ET increased proportionally more at shrubland (43%) and grassland (27%) during the monsoon period, whereas it stayed nearly the same at the woodland, suggesting that plants at the grassland and shrubland have limited access to groundwater, and readily utilize summer precipitation (Snyder & Williams, 2000). From the end of the monsoon until the end of the growing season, the grassland and shrubland had similar rates of water loss to the atmosphere. ET rates during the growing season at all sites were highly correlated with EVI ($R^2 \geq 0.78$ for all sites).

Components of the growing season water balance are given in Table 1 where *ET* is the total evapotranspiration, *P* is the precipitation, ΔS is the change of soil moisture in the top 1 m of soil, and $Q_t [= ET - (P - \Delta S)]$ is an estimate of groundwater use. At the sites, runoff was negligible and we assumed that there were only small changes in soil moisture deeper than 1 m as soil moisture probes at all sites showed that wetting fronts did not advance below 0.5 m (data not shown). There probably were some changes in soil water storage in the deep (> 1 m below the surface) vadose zone because of hydraulic redistribution, but we did not have a method for computing this storage change. Hultine *et al.* (2004) showed that mesquite roots (at the woodland site) transfer moisture throughout the vadose zone, even when the canopy is dormant.

The groundwater use by the riparian vegetation is an important component of this basin's water balance, and stakeholders have asked for more vegetation groundwater use data for improved water resources planning (Goodrich *et al.*, 2000). All sites had *ET* in excess of *P* and ΔS , and thus used significant quantities of ground-

water. The groundwater use of the Grassland was less than the adjacent shrubland especially on a per unit canopy area basis ($Q_{veg} = Q_t / f_v$ Table 1). While grasses at the grassland had access to groundwater, they apparently were unable to use this resource as effectively as the trees at the other sites. Shrubland Q_{veg} was less than at the woodland. This is reasonable given there is a greater diversity of tree sizes at the Shrubland, and it is likely that the older and larger trees at the Woodland have established more roots near the water table, while young establishing mesquite may not have yet grown roots to depth.

The water use pattern of the grassland differed considerably from a similar adjacent grassland site that was monitored in 1997–1998 using the Bowen ratio technique (Scott *et al.*, 2000). The grassland monitored in 1997–1998 had a tight coupling between precipitation and ET from which Scott *et al.* (2000) concluded that it used little groundwater. The site monitored in 1997–1998 had a depth to groundwater greater than 3.5 m, whereas at this study's grassland it was often less than 3 m. The dominant grass in this system appears to have limited access to groundwater at sites where groundwater depths exceed ~ 3 m (also see Scott *et al.*, 2000). Stable isotope measurements used to identify plant water sources in this grassland further support this conclusion (J. Stromberg, personal communication).

The water use of the shrubland also differed from an adjacent mesquite shrubland site monitored in 1997–1998 (Scott *et al.*, 2000). Both sites had similar stand characteristics, but the depth to groundwater was about 3 m less at the site monitored in the present study. While the 1997 site did have an annual ET in excess of precipitation (157 mm for the same period), the source of precipitation excess was uncertain. The ET excess may have been derived from deeper vadose moisture (Scott *et al.*, 2000). Using high-resolution aerial photography we estimated the amount of mesquite canopy cover to be 32% for the shrubland site monitored in 1997. This yields a Q_{veg} of 491 mm, a quantity, considering year-to-year variability, very much in agreement with the current study.

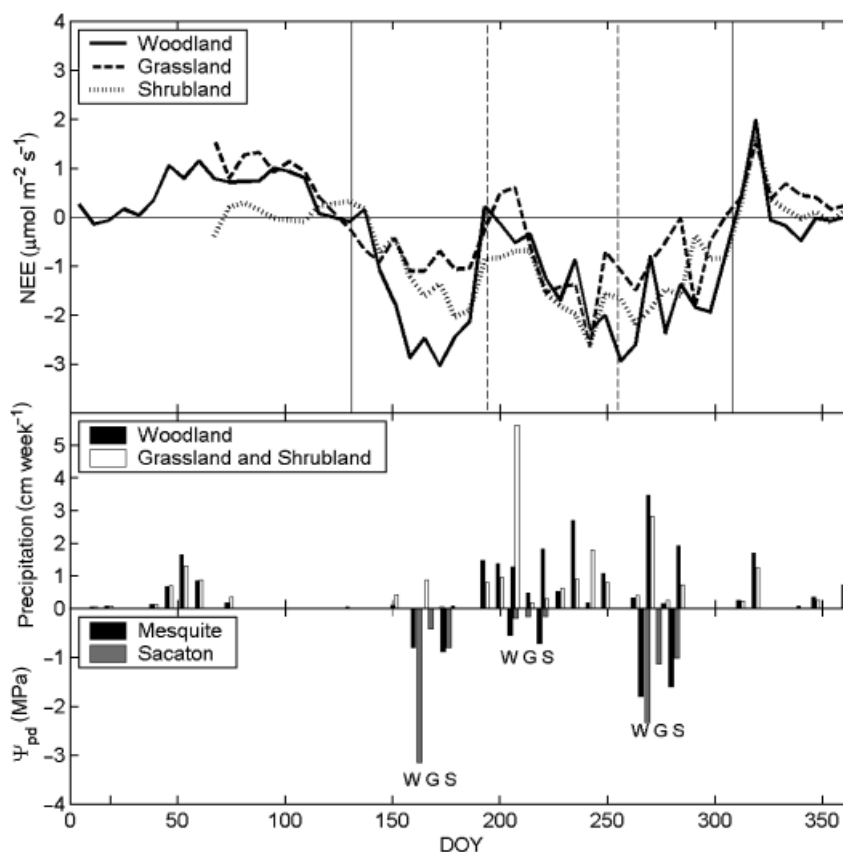


Fig. 5 (Top panel) Year 2003 weekly average net ecosystem exchange of carbon dioxide (NEE). The days of the last freeze of spring and first freeze of fall (solid line) and monsoon period (between the dashed lines) are also indicated. (Middle panel) Weekly total precipitation. (Lower panel) Predawn water potentials, Ψ_{pd} , of the mesquite trees and sacaton grass at the woodland (W), grassland (G), and shrubland (S) sites for the premonsoon, monsoon, and postmonsoon periods. There was no mesquite at the grassland.

Ecosystem CO_2 exchange

Factors influencing NEE, plant carbon acquisition, and autotrophic and heterotrophic respiration, were differentially expressed over the growing season at our three sites (Fig. 5). Plants at all sites were dormant during the winter, and substantial respiratory losses were evident at the grassland and woodland. During the premonsoon summer period, high rates of photosynthesis and low ecosystem respiration resulted in substantial rates of CO_2 uptake. Uptake was greatest at the woodland and shrubland sites, where the deep-rooted woody vegetation could access groundwater, and likely related to low rates of respiration from soil microbial communities during this dry premonsoon period.

Monsoon rains brought increases in near-surface soil moisture and a strong respiration response that temporarily reduced NEE despite an improved water status for the dominant plants (Fig. 5). Others have observed high soil respiration rates upon rewetting after prolonged dry periods (e.g. Fisher & Whitford, 1995; Hux-

man *et al.*, 2004). Despite the transition to a net loss at the beginning of the monsoon, the grassland eventually became a sink for CO_2 and had the largest increase in uptake compared with the other sites, presumably because of the relatively greater effect the available soil surface water had on plant water status (lower panel, Fig. 5). The greatest monsoon decrease in NEE was at the Woodland (50% decrease in net uptake). This was arguably because of the degree in which the ecosystem's carbon gain had become decoupled (or at least, less dependent) from precipitation (Scott *et al.*, 2004). The Woodland trees had ready access to groundwater (tree water status at this site premonsoon was equivalent to that of the shrubland mesquite peak monsoon, Fig. 5). Thus, the woodland was able to acquire CO_2 at high rates during the dry season when the soil microbial communities were water limited. Through the years, the high dry-season productivity of the woodland has led to a large accumulation of surface litter which fuels even greater heterotrophic respiratory fluxes when the surface soils and litter are wet. This

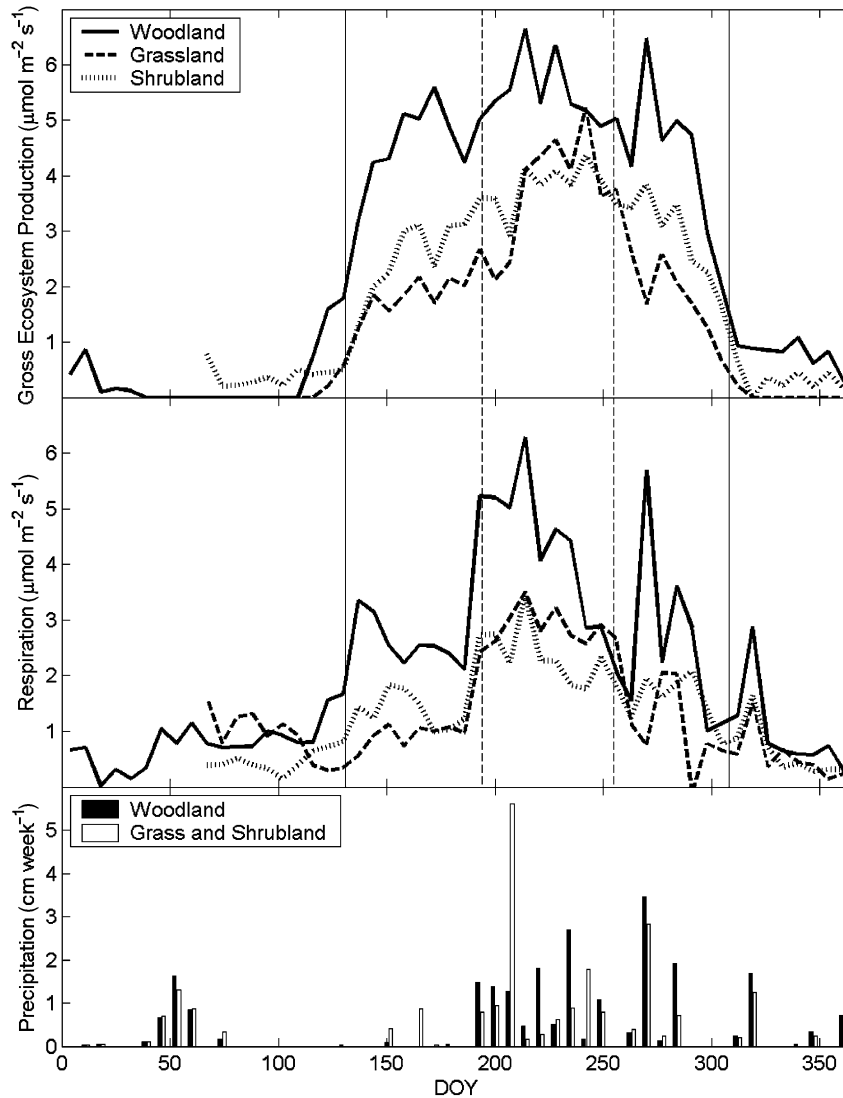


Fig. 6 Year 2003 weekly average gross ecosystem production, respiration, and precipitation. The days of the last freeze of spring and first freeze of fall (solid line) and monsoon period (between the dashed line) are also indicated.

effect has been observed most commonly in forests that are seasonally dry (Savage & Davidson, 2001; Saleska *et al.*, 2003; Scott *et al.*, 2004).

Following the monsoon, the grassland NEE and plant water potential declined faster than the other two sites. All species at all sites had declines in plant water status. Near the end of the growing season, NEE remained negative at all sites in the same rank order as seen in the premonsoon, until the hard frost of DOY 308 when photosynthetic tissues were lost from dominant species.

The course of weekly average GEP in 2003 at all sites showed the same general seasonal cycle as NEE, but highlights important differences between the sites (Fig. 6). While the groundwater levels and ET seemed to indicate that the grassland greened up first, GEP revealed that the woodland began to acquire carbon ear-

lier in the spring than the other two sites. This early photosynthetic activity at the woodland could not be attributed to the phreatophytic mesquite trees, which had not leafed out by this date, but to the understory plants. The understory plants are the first component of the ecosystem to respond to the warmer spring temperatures and the small amount of plant-available soil moisture that is recharged during the winter rains. During the premonsoon, there was limited soil moisture available for plants; thus the vegetation that was better able to access the groundwater was more productive. Even though the shrubland phreatophyte cover was less (55%), it was still more productive than the denser 65% cover of grass at the grassland. The grassland had the greatest increase in GEP (205%) after the monsoon began. While the shrubland and woodland received

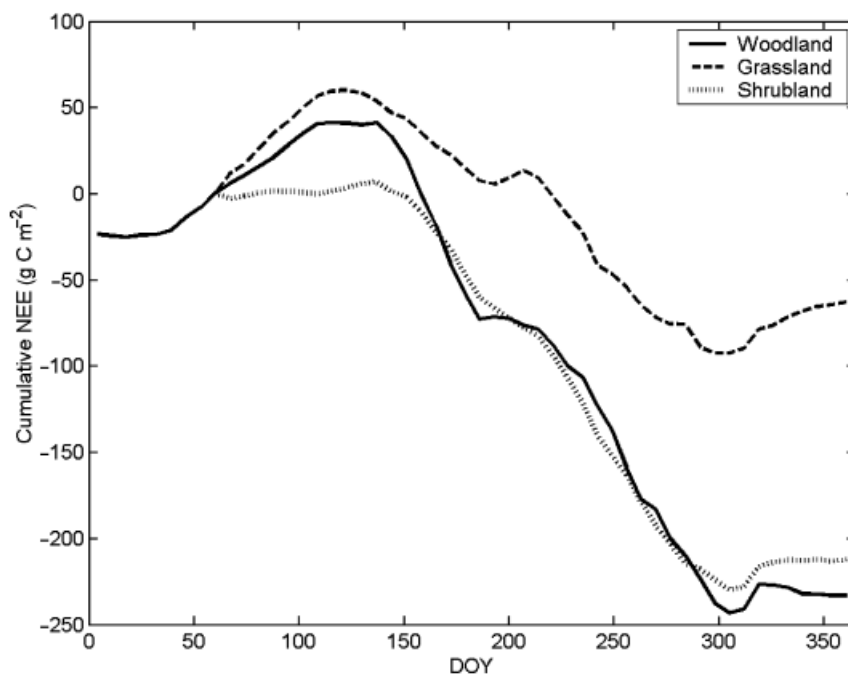


Fig. 7 Year 2003 cumulative weekly net ecosystem exchange of carbon (NEE). Woodland NEE has been shifted down 25 g C m^{-2} so that the cumulative value would be equal to zero when the other sites began. Negative values of NEE indicate a net gain of carbon by the ecosystem.

about the same amount of monsoon rainfall, their GEP did not increase as much as the grassland's even though we might expect that they would be even more productive given their better access to an additional moisture source. With comparable leaf area displays, the C4-dominated grassland should maintain higher GEP than our C3 shrubland and woodlands, for favorable water status conditions. There were moderate increases in shrubland GEP (132%) during the monsoon, whereas at the woodland there were little (112%). Postmonsoon GEP decreased most rapidly at the grassland as the rainfall became less frequent.

Strong respiration responses to precipitation inputs were seen during all seasons for all sites (Fig. 6). Prior to green-up, the respiration increases following precipitation were most evident at the grassland and woodland as compared with the shrubland. We hypothesize that this was likely a result of the greater availability of labile carbon in the surface soils at these sites as evident by the copious amounts of plant litter and debris found at them (Martens & McLain, 2003). The premonsoon respiration at all sites increased during and after green-up. With the negligible soil moisture, this was most likely autotrophic activity fueled by greater activity following access to groundwater. Respiration increased dramatically at the onset of monsoon rains; the woodland had the largest increase in magnitude and the other two sites had similar but smaller increases. The

amount of plant litter is much greater at the woodland because of the many years of nonwater-limited carbon acquisition, and the higher nitrogen content of the mesquite litter in combination with the greater amount of litter production has led to greater accumulation of organic carbon in the soil (Martens & McLain, 2003). We hypothesize that this is why the woodland respiration following precipitation events was always greater than at the other two sites, but we cannot rule out the potential role that plant respiration, augmented by the new source of moisture at the surface, may have had on the monsoon respiration response. Despite the continuation of rainfall, respiration decreased through the monsoon perhaps because the frequent drying–rewetting cycles can impose stress on the microbial community that results in reduced heterotrophic respiration (Fierer & Schimel, 2002).

A running total of weekly NEE reveals that the sites with greater access to additional moisture sources (i.e. deep-rooted trees accessing groundwater) were much larger carbon sinks (Fig. 7). The carbon uptake from March to December 2003 was 63, 212, and 233 g C m^{-2} at the grassland, shrubland and woodland, respectively. The grassland, with its weaker coupling to groundwater, was a small carbon sink, and its net annual exchange for 2003 was close to zero if we extrapolate to a complete annual cycle. The woodland carbon uptake was only slightly greater than the shrubland

despite the greater amount of woody plants. At the woodland, the greater amount of woody plants with ready access to groundwater leads to a greater decoupling of primary productivity from precipitation, which has the countering effects of a greater acquisition of atmospheric CO₂ during the dry part of the growing season and a greater loss of CO₂ when it rains.

We stress that it is important to keep in mind that these results should not be over-generalized as climate variability in this region is high and the rainfall totals for 2003 were below average. The dynamics of NEE at all of the sites were highly influenced by precipitation; thus, changes in the timing and distribution of seasonal rainfall from year to year are expected to yield different results. Many years of additional data will be necessary to begin to understand the role that interannual climate variability has on the patterns elucidated herein. Additionally, like most studies that use eddy covariance, there is considerable uncertainty in the magnitude of these totals. The lack of energy balance closure and the poor sampling of nighttime fluxes are of particular concern; thus, these early results elucidate more qualitative, rather than quantitative, site-to-site differences.

Summary

With alterations in vegetation being the most predictable feature of global change, how ecosystem processes in turn are altered becomes an important question. In this paper, we looked at how woody-plant encroachment might affect ecohydrological dynamics comparing patterns of ET and NEE along a gradient of woody-plant encroachment within a riparian area. Data support the following:

1. Seasonal ET totals increased with woody-plant abundance.
2. Regular diurnal groundwater fluctuations occurred at all sites and ET exceeded precipitation; thus, dominant plants at all ecosystems used groundwater to supplement their water use. Groundwater use increased with the amount of woody plant cover despite increasing depths to groundwater at these sites, which indicated that larger trees at the shrubland and woodland were better able to acquire groundwater.
3. All sites had high respiration losses of carbon following precipitation events during the summer monsoonal period. The response was strongest and longer lasting at the woodland, where abundant litter deposition supplied ample carbon for the soil microbial community.
4. While the grassland had a small increase in carbon gain during the rainy growing season, the woody sites had a net decrease relative to the dry part of the

growing season. This decreased gain in carbon was magnified by woody-plant abundance.

Taken together, these data suggest that carbon and water cycling in semiarid riparian ecosystems of the southwestern US are fundamentally altered by vegetation change. Woody-plant encroachment is a global phenomenon that also includes encroachment in upland regions without the possibility of groundwater access, but our results highlight the change that is possible when the shift in vegetation is associated with a shift in the availability of a primary limiting resource. This shift in resource availability substantially alters the relationship between gross photosynthetic and respiratory activities. In addition, vegetation change appears to alter how precipitation drives each of these important ecosystem processes, suggesting that the interrelationships between ecosystem structure, function, and climate are fundamentally altered.

Acknowledgements

This work is supported in part by SAHRA (Sustainability of semi-Arid Hydrology and Riparian Areas) under the STC Program of the National Science Foundation, Agreement No. EAR-9876800 and NSF award DEB-0415977 to Huxman and Williams. Additional financial support was provided by the University of Arizona and to the USDA-ARS from the Upper San Pedro Partnership. We would also like to thank B. Cable for his expert field assistance, A. Huete for providing MODIS EVI data, and S. Saleska, S. Skirvin and two anonymous reviewers for helping to improve an earlier version of this manuscript. D. Potts, J. Cable, D. Ignace, A. Eilts, and E. Yezpe helped with tower construction.

References

- Adams DK, Comrie AC (1997) The North American monsoon. *Bulletin of American Meteorology Society*, **78**, 2197–2213.
- Archer SA (1994) Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. In: *Ecological Implications of Livestock Herbivory in the West* (eds Vavra M, Laycock W, Pieper R), pp. 13–68. Society for Range Management, Denver, CO.
- Archer S, Boutton TW, Hibbard KA (2001) Trees in grasslands: biogeochemical consequences of woody plant expansion. In: *Global Biogeochemical Cycles in the Climate System*, pp. 115–138. Academic Press, Durham, NC.
- Archer S, Schimel DS, Holland EA (1995) Mechanisms of shrubland expansion: land use, climate or CO₂? *Climatic Change*, **29**, 91–99.
- Bahre CJ, Shelton ML (1993) Historic vegetation change, mesquite increases, and climate in southeastern Arizona. *Journal of Biogeography*, **20**, 489–504.
- Brown JR, Archer S (1989) Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecologia*, **80**, 19–26.

- Cabral AC, Rescia AJ, Schmitz MF *et al.* (2003) Shrub encroachment in Argentinean savannas. *Journal of Vegetation Science*, **14**, 145–152.
- Campbell CJ, Green W (1968) Perpetual succession of stream-channel vegetation in a semiarid region. *Journal of the Arizona Academy of Science*, **5**, 86–98.
- Falge E, Baldocchi D, Olson R *et al.* (2001) Gap filling strategies for long term energy flux data sets. *Agricultural Forest Meteorology*, **107**, 71–77.
- Fierer N, Schimel JP (2002) Effects of drying–rewetting frequency on soil carbon and nitrogen transformations. *Soil Biology and Biochemistry*, **34**, 777–787.
- Fisher FM, Whitford WG (1995) Field simulation of wet and dry years in the Chihuahuan desert: soil-moisture, N mineralization and ion exchange resin bags. *Biology and Fertility of Soils*, **20**, 137–146.
- Gao X, Huete AR, Ni W *et al.* (2000) Optical–biophysical relationships of vegetation spectra without background contamination. *Remote Sensing of Environment*, **74**, 609–620.
- Gash JHC, Dolman AJ (2003) Sonic anemometer (co)sine response and flux measurement: I. The potential for (co)sine error to affect sonic anemometer-based flux measurements. *Agricultural Forest Meteorology*, **119**, 195–207.
- Goodale CL, Davidson EA (2002) Uncertain sinks in the shrubs. *Nature*, **418**, 593–594.
- Goodrich DC, Scott R, Qi J *et al.* (2000) Seasonal estimates of riparian evapotranspiration using remote and in situ measurements. *Agricultural Forest Meteorology*, **105**, 281–309.
- Grover HD, Musick HB (1990) Shrubland encroachment in southern New Mexico, U.S.A.: an analysis of desertification processes in the American Southwest. *Climatic Change*, **17**, 305–330.
- Hastings SJ, Oechel WC, Muhlia-Melo A (2005) Diurnal, seasonal and annual variation in the net ecosystem CO₂ exchange of a desert shrub community (Sarcocaulis) in Baja California, Mexico. *Global Change Biology*, **11**, 927–939 doi: 10.1111/j.1365-2486.2005.00951.x
- Hibbard KA, Archer S, Schimel DS *et al.* (2001) Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology*, **82**, 1999–2011.
- Hollinger DY, Kelliher FM, Byers JN *et al.* (1994) Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. *Ecology*, **75**, 134–150.
- Hultine KR, Scott RL, Cable WL *et al.* (2004) Hydraulic redistribution by a dominant, warm desert phreatophyte: seasonal patterns and response to precipitation pulses. *Functional Ecology*, **18**, 530–538.
- Huxman TE, Snyder KA, Tissue D *et al.* (2004) Precipitation pulses and carbon balance in semi-arid and arid ecosystems. *Oecologia*, **141**, 258–264.
- Huxman TE, Wilcox BP, Breshears DD *et al.* (2005) Ecohydrological implication of woody plant encroachment. *Ecology*, **86**, 308–319.
- Jackson RB, Banner JL, Jobbagy EG *et al.* (2002) Ecosystem carbon loss with woody plant invasion of grasslands. *Nature*, **418**, 623–626.
- Kepner WG, Watts CJ, Edmonds CM *et al.* (2000) A landscape approach for detecting and evaluating change in a semi-arid environment. *Environment Monitoring and Assessment*, **64**, 179–195.
- Lee X (1998) On micrometeorological observations of surface-air exchange over tall vegetation. *Agricultural Forest Meteorology*, **91**, 39–49.
- Malhi Y, Nobre AD, Grace J *et al.* (1998) Carbon dioxide transfer over a Central Amazonian rain forest. *Journal of Geophysical Research*, **103**, 31–31,612.
- Martens DA, McLain JET (2003) Vegetation community impacts on soil carbon, nitrogen and trace gas fluxes. In: *First Interagency Conference on Research in the Watersheds, October 27–30, 2003* (eds Renard KG, McElroy SA, Gburek WJ, Canfield HE, Scott RL), U.S. Department of Agriculture, Agricultural Research Service, pp. 542–547, Washington D.C., USA.
- Mayeux HS, Johnson HB, Polley HW (1991) Global change and vegetation dynamics. In: *Noxious Range Weeds* (eds James LF, Evans JO, Ralphs MH, Child RD), 62–74. Westview Press, Boulder.
- McClain ME, Boyer EW, Dent CL *et al.* (2003) Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. *Ecosystems*, **6**, 301–312.
- McCulley RL, Archer SR, Boutton TW *et al.* (2004) Soil respiration and nutrient cycling in wooded communities developing in grassland. *Ecology*, **85**, 2804–2817.
- McPherson GR (1997) *Ecology and Management of North American Savannas*. University of Arizona Press, Tucson.
- Noy-Meir E (1973) Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*, **4**, 23–51.
- Pacala SW, Hurtt GC, Baker D *et al.* (2001) Consistent land- and atmosphere-based US carbon sink estimates. *Science*, **292**, 2316–2320.
- Paw UKT, Baldocchi DD, Meyers TP *et al.* (2000) Corrections of eddy covariance measurements incorporating both advective effects and density fluxes. *Boundary-Layer Meteorology*, **97**, 487–511.
- Pilegaard K, Hummelshøj P, Jensen NO *et al.* (2001) Two years of continuous CO₂ eddy flux measurements over a Danish beech forest. *Agricultural Forest Meteorology*, **107**, 29–41.
- Saleska SR, Miller SD, Matross DM *et al.* (2003) Carbon in Amazon Forests: unexpected seasonal fluxes and disturbance-induced losses. *Science*, **302**, 1554–1557.
- Savage KE, Davidson EA (2001) Interannual variation of soil respiration in two New England forests. *Global Biogeochemical Cycles*, **15**, 337–350.
- Scott RL, Edwards EA, Shuttleworth WJ *et al.* (2004) Interannual and seasonal variation in fluxes of water and carbon dioxide from a riparian woodland ecosystem. *Agricultural Forest Meteorology*, **122**, 65–84.
- Scott RL, Shuttleworth WJ, Goodrich DC *et al.* (2000) The water use of two dominant vegetation communities in a semiarid riparian ecosystem. *Agricultural Forest Meteorology*, **105**, 241–256.
- Scott RL, Watts C, Garatuza J *et al.* (2003) The understory and overstory partitioning of energy and water fluxes in an open canopy, semiarid woodland. *Agricultural Forest Meteorology*, **114**, 127–139.
- Smith DL, Johnson L (2004) Vegetation-mediated changes in microclimate reduce soil respiration as woodlands expand into grasslands. *Ecology*, **85**, 3348–3361.

- Snyder K, Williams DG (2000) Water sources used by riparian trees varies among stream types on the San Pedro river, Arizona. *Agricultural Forest Meteorology*, **105**, 227–240.
- Stromberg JC, Wilkins SD, Tress JA (1993) Vegetation-hydrology models: implications for management of *Prosopis velutina* (velvet mesquite) riparian ecosystems. *Ecological Applications*, **3**, 307–314.
- Turner RM, Webb RH, Bowers JE *et al.* (2003) *The Changing Mile Revisited: An Ecological Study of Vegetation Change with Time in the Lower Mile of an Arid and Semiarid Region*. The University of Arizona Press, Tucson.
- Turnipseed AA, Blanken PD, Anderson DE *et al.* (2002) Energy budget above a high-elevation subalpine forest in complex topography. *Agricultural Forest Meteorology*, **110**, 177–210.
- van der Molen MK, Gash JHC, Elbers JA (2004) Sonic anemometer (co)sine response and flux measurement: II. The effect of introducing an angle of attack dependent calibration. *Agricultural Forest Meteorology*, **122**, 95–109.
- Veenendaal EM, Kolle O, Lloyd J (2004) Seasonal variation in energy fluxes and carbon dioxide exchange for a broad-leaved semi-arid savanna (Mopane woodland) in Southern Africa. *Global Change Biology*, **10**, 318–328.
- Webb EK, Pearman GI, Leuning R (1980) Correction of flux measurements for density effects due to heat and water vapor transfer. *Quaternary Journal of Royal Meteorological Society*, **106**, 85–100.
- Wilcox BP (2002) Shrub control and streamflow on rangelands: a process-based viewpoint. *Journal of Range Management*, **55**, 318–326.
- Williams DG, Cable W, Hultine K *et al.* (2004) Components of evapotranspiration determined by stable isotope, sap flow and eddy covariance techniques. *Agricultural Forest Meteorology*, **125**, 241–258.
- Wilson K, Goldstein A, Falge E *et al.* (2002) Energy balance closure at FLUXNET sites. *Agricultural Forest Meteorology*, **113**, 223–243.