



Effects of seasonal drought on net carbon dioxide exchange from a woody-plant-encroached semiarid grassland

Russell L. Scott,¹ G. Darrel Jenerette,² Daniel L. Potts,³ and Travis E. Huxman^{4,5}

Received 21 November 2008; revised 5 June 2009; accepted 28 July 2009; published 4 November 2009.

[1] Annual precipitation in the central and southern warm-desert region of North America is distributed climatologically between summer and winter periods with two prominent dry periods between them. We used energy and carbon dioxide (CO₂) fluxes from eddy covariance along with standard meteorological and soil moisture measurements at a semiarid savanna in southern Arizona, United States, to better understand the consequences of warm or cool season drought on ecosystem CO₂ exchange in these bimodally forced water-limited regions. Over the last 100 years, this historic grassland has converted to a savanna by the encroachment of the native mesquite tree (*Prosopis velutina* Woot.). During each of the 4 years of observation (2004–2007), annual precipitation (P) was below average, but monsoon (July–September) P was both above and below average while cool-season (December–March) P was always less than average by varying degrees. The ecosystem was a net source of CO₂ to the atmosphere, ranging from 14 to 95 g C m⁻² yr⁻¹ with the strength of the source increasing with decreasing precipitation. When the rainfall was closest to the long-term average in its distribution and amount, the ecosystem was essentially carbon neutral. Summer drought resulted in increased carbon losses due mainly to a shortening of the growing season and the length of time later in the season when photosynthetic gain exceeds respiration loss. Severe cool season drought led to decreased spring carbon uptake and seemingly enhanced summer respiration, resulting in conditions that led to the greatest annual net carbon loss.

Citation: Scott, R. L., G. D. Jenerette, D. L. Potts, and T. E. Huxman (2009), Effects of seasonal drought on net carbon dioxide exchange from a woody-plant-encroached semiarid grassland, *J. Geophys. Res.*, 114, G04004, doi:10.1029/2008JG000900.

1. Introduction

[2] In terrestrial ecosystems where biological activity is constrained by water availability, shifts in the amount and seasonal timing of precipitation may strongly influence ecosystem structure and function [Huxman *et al.*, 2004; Noy-Meir, 1973; Potts *et al.*, 2006; Weltzin *et al.*, 2003]. In addition to changes in rainfall, arid and semiarid (or dryland) ecosystems worldwide are under increasing pressure to provide products and services to expanding human populations. One consequence of these increasing societal demands on dryland ecosystems are shifts in plant community composition associated with grazing, fire suppression and the introduction of nonnative species [Archer *et al.*, 1995;

Bradley *et al.*, 2006; Van Auken, 2000]. Devising effective management strategies for dryland regions requires a more complete understanding of the interactive effects of multiple global change factors in these regions [Dukes *et al.*, 2005; Harpole *et al.*, 2007].

[3] Across much of the semiarid southwestern United States and northwestern Mexico, annual precipitation is divided into two, distinct rainfall seasons. During the warm summer months (typically, July–September) rainfall often arrives in brief, intense and highly localized convective storms associated with the North American Monsoon [Adams and Comrie, 1997]. During the cooler winter months (~December–March), precipitation comes in the form of lower intensity, more widespread, frontal storms. At elevations where low temperatures do not preclude the activity of plants and soil microbes, this seasonal pattern of rainfall promotes two distinct periods of biological activity. Recent studies of regional climate change suggest that springtime will be drier and hotter throughout much of the western United States [Barnett *et al.*, 2008; Seager *et al.*, 2007] due to an earlier shift to a warm-season circulation pattern which moves the Pacific frontal storm track northward [McAfee and Russell, 2008]. Predictions on how the monsoon rainfall might change are inconclusive [Lin *et al.*, 2008], but a first-order prediction is greater interannual variability in summer rain [Diffenbaugh *et al.*, 2008]. In either case, the conse-

¹Southwest Watershed Research Center, Agricultural Research Service, USDA, Tucson, Arizona, USA.

²Department of Botany and Plant Sciences, University of California, Riverside, California, USA.

³Biology Department, State University of New York College at Buffalo, Buffalo, New York, USA.

⁴Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona, USA.

⁵B2 Earthscience, University of Arizona, Tucson, Arizona, USA.

quences of such shifts in the seasonality of rainfall for ecosystem function are poorly known.

[4] In dryland ecosystems, rainfall regime likely mediates other facets of global change like shifts in plant community composition [Weltzin *et al.*, 2003]. For example, an increase in the abundance and density of woody plants has been observed worldwide [Archer, 1994; Van Auken, 2000]. Termed “woody encroachment” [Goodale and Davidson, 2002], this shift in plant community composition is hypothesized to influence carbon cycling at the continental scale [Archer *et al.*, 2001; Pacala *et al.*, 2001; Peters *et al.*, 2007] and dramatically alters the structure and, possibly, function of semiarid ecosystems [Bahre and Shelton, 1993; Brown and Archer, 1989; Cabral *et al.*, 2003; Grover and Musick, 1990; Scott *et al.*, 2006; Turner *et al.*, 2003]. Despite broad acknowledgment of the relationship between rainfall and biological activity in dryland ecosystems and the potential for shifts in the seasonal timing of rainfall associated with global climate change, very few studies have documented functional impacts of shifts in rainfall seasonality in woody-encroached ecosystems.

[5] Net ecosystem CO₂ exchange (NEE) is a widely applied metric of ecosystem-level response to climatic variation and is defined as difference between CO₂ assimilation by photosynthesis and CO₂ efflux by plant and soil microbial respiration [Baldocchi, 2008, 2003]. In dryland ecosystems measurements of NEE have highlighted the influence of wet/dry seasonal contrasts and the role of interannual precipitation variability on ecosystem CO₂ balance. Predictably, NEE is tightly linked to patterns of rainfall. During dry periods, dryland ecosystems appear to be low to moderate sources of CO₂ to the atmosphere while during wetter periods, they tend to behave as net sinks of CO₂ [Eamus *et al.*, 2001; Hastings *et al.*, 2005; Kurc and Small, 2007; Leuning *et al.*, 2005; Veenendaal *et al.*, 2004]. The seasonally specific responses of photosynthesis and respiration to rainfall and the implications for annual carbon balance in these ecosystems are less understood.

[6] In this study, we examined a 4-year, near-continuous record of CO₂ exchange in a semiarid mesquite savanna in southeastern Arizona, United States, and asked the question, “What are the consequences of seasonal (cool or warm growing season) drought on ecosystem carbon dioxide (CO₂) exchange in a semiarid savanna”? We predicted the response of photosynthesis and respiration to rainfall is seasonally specific because of differences in the depth of soil water infiltration and because these processes differ in their sensitivity to temperature. For example, cool-season precipitation infiltrates, or may be redistributed by woody plants, to a greater depth and is posited to stimulate the activity of deeply rooted woody plants later in the spring [Archer, 1994; Brown *et al.*, 1997; Cable, 1977; Hastings and Turner, 1965; Scott *et al.*, 2000, 2008; Swetnam and Betancourt, 1998] while relatively low temperatures may limit the respiratory response of shallow soil microbes [Kirschbaum, 1995; Knorr *et al.*, 2005]. In contrast, summer rainfall is thought to primarily influence shallow soil moisture thereby stimulating the activity of shallowly rooted grasses and forbs while a combination of high temperatures and shallow soil moisture stimulate a large respiratory response by soil microbes [Cable, 1975; Culley, 1943; Jenerette *et al.*, 2008; Kemp, 1983; Sponseller,

2007]. As such, we hypothesized that seasonal droughts would lead to decreased ecosystem productivity and a diminished CO₂ sink on an annual basis, but that cool-season droughts would impact the ecosystem CO₂ differently than warm-season ones through differential effects on plant photosynthetic versus soil respiratory processes.

2. Site Description

[7] The Santa Rita mesquite savanna site (31.8214°N, 110.8661°W, elevation: 1116 m) is located on the Santa Rita Experimental Range (SRER), 45 km south of Tucson, AZ USA (Figure 1). Mean annual precipitation (1937–2007) is 377 mm. Winter months of December through March are cool with occasional nighttime frosts and account for about 30% of the annual rainfall. The months of April through June grow increasingly warmer, with daytime maximums often exceeding 35°C in June, and usually have little rainfall. Daytime temperatures decrease and nighttime temperatures increase during the months of July through September due to the increased humidity and rainfall associated with the North American monsoon [Adams and Comrie, 1997]. About 50% of the rainfall comes during the months of July–September. The warm-season rainfall typically begins to decline in September and rainfall becomes more sporadic through October. The first winter freeze typically occurs in the drier month of November.

[8] Over the last 100 years, the rangeland around the Santa Rita mesquite savanna site has changed from a semi-desert grassland into a savanna by the encroachment of the woody leguminous tree, *Prosopis velutina* Woot. (velvet mesquite [Glendening, 1952; McClaran, 2003]). Site vegetation consisted of mesquite growing in a matrix of native (*Digitaria californica* Benth. *Muhlenbergia porteri*, *Bouteloua eriopoda*, *Aristida* spp.) and nonnative (*Eragrostis lehmanniana* Nees) perennial C₄ grasses, subshrubs (most commonly, *Isocoma tenuisecta* Greene) and scattered succulents (*Opuntia* spp.). Total canopy cover of perennial grasses, forbs and subshrubs at this site was ~22% during the study period. Mesquite cover was ~35%, and average overstory mesquite plant area index (LI-2000, LI-COR, Inc., Lincoln, NE) ranged from 0.22 (without leaves) to 0.41 (with leaves fully expanded). Within 30 m of the tower, mesquite ranged in height from 0.25 to 6 m with an average height of 2.5 m (SD = 1.6, n = 95). In the deep sandy loam soils found at our site, mesquite forms deep taproots and extensive lateral root systems that can extend more than 15 m beyond the canopy [Cable, 1977]. Mesquite readily redistribute soil water throughout the year from shallow (~0.1–0.3 m) to deep (>1 m) layers and vice versa [Scott *et al.*, 2008].

[9] The fetch at the site is quite uniform and extends for >1 km in the SW, SE, and NW compass quadrants. In the NE quadrant, the fetch is uniform up to about 0.2 km away from the tower but beyond that the mesquite vegetation is less dense due to soil changes. Flux data from the NE quadrant were rare and excluded from the analysis given in this paper. Based on some seasonal measurements, the leaf area index of this savanna ranges from ~0.2–0.4 during the spring and early summer when only the mesquites are leafed out to a peak of ~1 during the late summer following monsoon rains when the understory is maximally active.

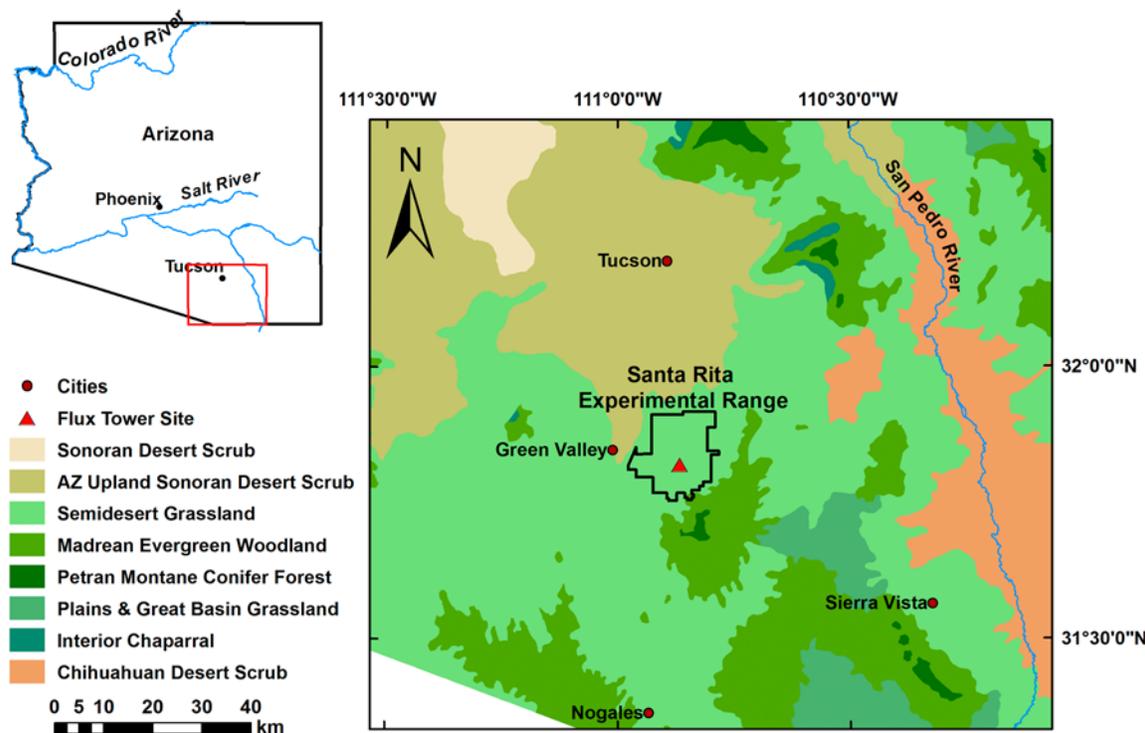


Figure 1. Location of the savanna site within the Santa Rita Experimental Range. Also, shown is the vegetation classification of *Brown et al.* [1979].

[10] Historically limited to washes and riparian areas on the SRER, mesquite encroachment in sandy, upland grasslands occurred between 1902 and 1936 [McClaran, 2003]. Since that time, mesquite cover has been called “dynamically stable,” implying that the cover increases associated with recruitment and canopy expansion have been largely offset by cover contractions associated with tree mortality and reductions in canopy area [Browning et al., 2008]. However, several studies have found that the wetter-than-average period from mid-1970s to mid-1990s, driven by increases in cool season precipitation, led to a substantial increase in mesquite cover and/or density [Browning et al., 2008; Mashiri et al., 2008]. In the pasture where our site is located, year-round cattle grazing was practiced from 1957–2005 with about 0.028 animals $\text{ha}^{-1} \text{yr}^{-1}$, translating to $\sim 50\%$ forage utilization [Martin and Cable, 1974; Martin and Severson, 1988; Ruyle, 2003]. In 2006, the pasture received only minimal grazing of 25 cattle for 9 days and was not grazed by cattle in 2007.

3. Methods

3.1. Environmental Measurements

[11] Temperature/relative humidity probes (HMP35D, Vaisala, Helsinki, Finland) were installed at 2.5 and 6.0 m height, and above-canopy net radiation was measured at a height of 6.5 m using a 4-component radiometer (Model CNR 1, Kipp & Zonen, Delft, The Netherlands) attached to a horizontal boom extending 4 m from the tower. Also, on this boom we installed an up and downward looking photosynthetically active radiation (PAR) sensor (LI-190, LI-COR, Lincoln, NE). Ground heat flux was measured with eight soil heat flux plates (REBS Inc., Seattle, WA) installed 0.05 m

below ground level under both intercanopy and undercanopy positions. 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 soil heat flux at the surface using estimates of the specific heat of the soil layer obtained with a thermal properties sensor (TP01, Hukseflux, Delft, The Netherlands). Average surface ground heat flux (G) was computed as a weighted average based on the fraction of overstory vegetation canopy (35%) at the site. Average soil temperature for 0–5 cm soil depth was determined by averaging the 2 and 4 cm thermocouples located above each of the eight soil heat flux plates. Precipitation was quantified at the tower using a tipping bucket rain gauge, and long-term estimates were obtained from a monthly measured gage (SR#45) located about 0.5 km away from the tower.

[12] We measured volumetric soil water content (θ) using commercial soil moisture probes (CS616, Campbell Scientific, Logan, UT) at 5, 10, 20, 30, 50, 70, 100 and 130 cm depths in a profile in an open area without any tree cover overhead (intercanopy) and another beneath the canopy of a large mesquite tree about 1/2 the radius of the canopy drip line from tree trunk. Measurements were recorded every 30 min and stored on a data logger (CR-10X, Campbell Scientific). Probe output was converted to θ using a laboratory calibration curve produced with soils from the site. In the two profiles, the soils were fairly uniform sandy loams with no visually obvious changes in soil texture between microsites or with depth.

[13] To quantify the seasonality and variation in green biomass at the site, we used the enhanced vegetation index (EVI [Huete et al., 2002]). We used 250 m EVI data from collection 5 (ORNL DAAC, 2008) usually available as a

16-day composite over the period of 2000–2007. As an integrated measure of greenness over a season, we define:

$$EVT^* = \int EVI(t) - \min[EVI(t)]dt \quad (1)$$

where $EVI(t)$ is the interpolated daily EVI value from the 16-day values. Equation (1) is integrated over the winter/spring (January–May) and summer (July–November) growing seasons. The minimum EVI within the season is subtracted from all the daily values before the integration in order to try and account for drifts in the baseline (dry) EVI value.

3.2. Eddy Covariance Measurements

[14] We used the eddy covariance technique to quantify ecosystem evapotranspiration (ET) and carbon dioxide flux (F_C). A three-dimensional, sonic anemometer (Model CSAT-3; Campbell Scientific) and an open-path infrared gas analyzer (LI-7500, LI-COR) were mounted at 8 m height to measure the three components of the wind velocity vector, sonic temperature and concentrations of water vapor and carbon dioxide. Data were sampled at 10 Hz and recorded by a data logger (CR5000, Campbell Scientific). Every one-to-two months, the IRGA were zero- and span-calibrated using a CO_2/H_2O -free gas, a standard $[CO_2]$ gas, and a dew point generator. Fluxes were later calculated off-line after filtering spikes and using a 30-min block average. We also used a two-dimensional coordinate rotation and accounted for density fluctuations [Webb *et al.*, 1980] in the calculation of the fluxes. The sonic temperature was used to calculate sensible heat flux using the method suggested by Paw U *et al.* [2000] which accounts for a missing energy balance term associated with the expansion of air during evaporation under constant pressure. Fluxes measured when the wind was between 35° and 55° N (1.7% of the data) were omitted due to possible interference from the anemometer support and the IRGA mounted behind the anemometer. This site and its data are a part of the Ameriflux network, and its instrumentation, processing software, and techniques have been tested and verified with the network's "gold-standard" (<http://public.ornl.gov/ameriflux/>).

[15] We calculated the net ecosystem exchange of CO_2 (NEE) by adding the 30-min CO_2 storage in the canopy (ΔS) to F_C . Since CO_2 profile data were only available for about half of the 4-year record, the storage terms were estimated using only $[CO_2]$ from the IRGA at the tower top. This approximation did not introduce any appreciable errors as differences between half-hourly NEE with CO_2 storage calculated using just $[CO_2]$ from the IRGA versus those using the profiler's five heights were essentially equivalent [$F_C + \Delta S_{profile} = 0.99(F_C + \Delta S_{top}) - 0.0001$, $n = 7885$, $R^2 = 0.99$, $p < 0.001$].

[16] The flux data were filtered for spikes, instrument malfunctions, and poor quality (representing 7.8% of the ET and 8.2% of NEE data). The rejection criteria used to screen data were: rain events, out-of-range signals, and spikes with the standard deviation of $[CO_2]$, $[H_2O]$ and/or sonic temperature greater than 2 standard deviations from the mean determined on a yearly basis. Also, we applied a friction velocity or u^* filter to omit fluxes when there was not sufficient turbulence to make representative flux measure-

ments [Malhi *et al.*, 1998]. This occurred 12.8% of the time. We identified the u^* threshold by using a standardized technique [Reichstein *et al.*, 2005] and by comparing annual accumulated NEE with increasing threshold to determine when it plateaued [Saleska *et al.*, 2003]. Neither technique produced a consistent value from season-to-season and year-to-year, so a value of 0.15 m s^{-1} was chosen as an average. We found that yearly NEE totals reported herein were within about 15% of the totals for each year over a range of u^* threshold from 0.10 to 0.30 m s^{-1} . Daily average ET values were calculated by first filling the gaps in the 30 min data. Gaps were filled using 14-day look-up tables of ET and incoming PAR, averaged over $100 \mu\text{moles m}^{-2} \text{ s}^{-1}$ intervals [Falge *et al.*, 2001].

[17] To assess the accuracy of the eddy covariance measurements, we computed the slope of the least squares line fitted through the origin of net radiation minus the ground heat flux (x , abscissa) and the sum of the sensible and latent heat fluxes (y , ordinate). The results are similar in comparison to numerous sites ($y = 0.86x$, $R^2 = 0.95$, on a 30-min basis; $y = 0.92x$, $R^2 = 0.94$, on a daily basis [Wilson *et al.*, 2002]).

[18] We partitioned NEE into ecosystem photosynthesis or gross ecosystem production (GEP) and ecosystem respiration (R). We determined 30-min average R by fitting an exponential function to air temperature and nighttime NEE data over a moving ~ 5 -day window [Reichstein *et al.*, 2005]. The window size was varied to try and ensure that data from prestorm (dry) periods were not grouped together with data following storms. This model was then used to fill missing nighttime NEE data and model daytime respiration. Missing daytime NEE values were filled using a nonrectangular hyperbolic light response function to the NEE and PAR over a 15-day moving window [Gilmanov *et al.*, 2007]. Finally, GEP was determined by:

$$GEP = R - NEE \quad (2)$$

We used the standard sign convention for NEE with $NEE > 0$ indicating a net loss of CO_2 to the atmosphere (source) and $NEE < 0$ indicating CO_2 uptake by the ecosystem (sink). R and GEP are always positive.

4. Results

4.1. Meteorology and Phenology

[19] Mean annual air temperature from 2004 to 2007 was 19.6°C with average monthly values ranging from 8 to 30°C (Figure 2). Air temperatures commonly fluctuated between 15 to 20°C daily, with peak daily maximums of about 40°C in June and minimums of -5°C in winter. Variation in monthly dew point temperatures reflects the influence of the North American Monsoon during July, August, and September. The monsoon also influences the relationship between solar and net radiation by depressing incoming solar radiation due to increased cloudiness and increasing net radiation due to decreased longwave radiation cooling and decreased albedo.

[20] Precipitation was highly variable during the 4-year period (Figure 3). Monsoon (July–September) precipitation was both above and below the long-term mean, but winter rainfall (December–March) was consistently below average

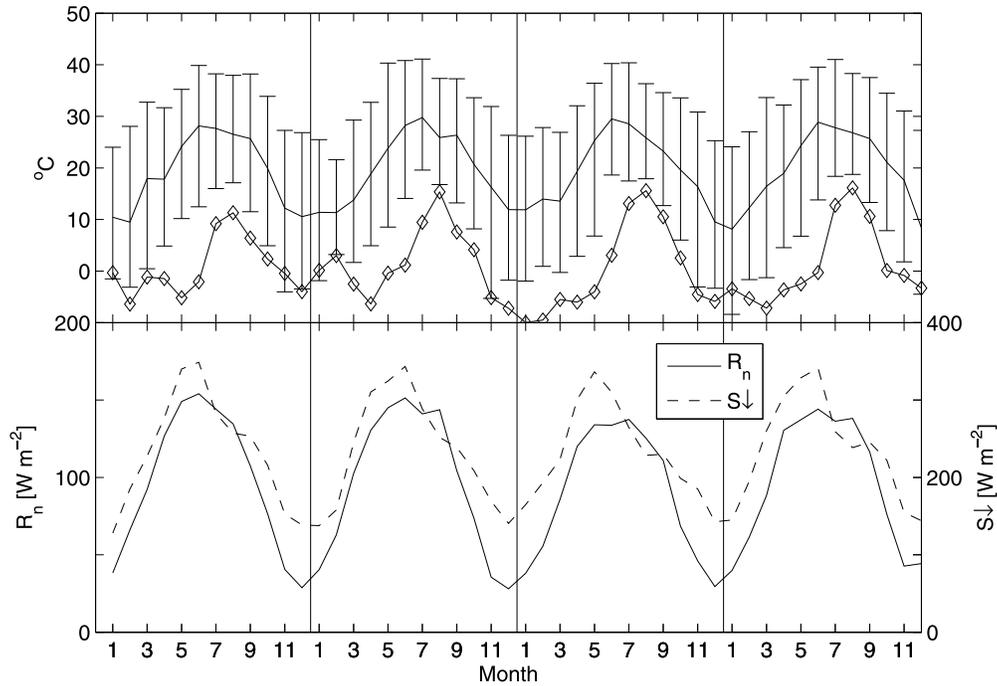


Figure 2. (top) Monthly mean air (solid line) and dew point temperature (diamonds) at 2.5 m height along with monthly maximum and minimum temperatures shown in bars. (bottom) Monthly mean net radiation and incoming solar radiation.

(Table 1). At the extreme, the winter total of 2006 ranked as the third driest for the 1936–2007 period, but the monsoon in 2004 was a milder drought and ranked only as the 23rd driest. Annual precipitation was always below average, which reflected the protracted regional drought conditions occurring during the study period. With the exception of 1998

and 1999, precipitation has been below average since 1995. Total precipitation in 2004 and 2006 were the ninth and tenth lowest on record. The recent dry period followed the unusually wet period from around 1977 to 1994 (Figure 3, inset).

[21] The seasonal rhythm of standing green biomass as quantified by the MODIS enhanced vegetation index (EVI)

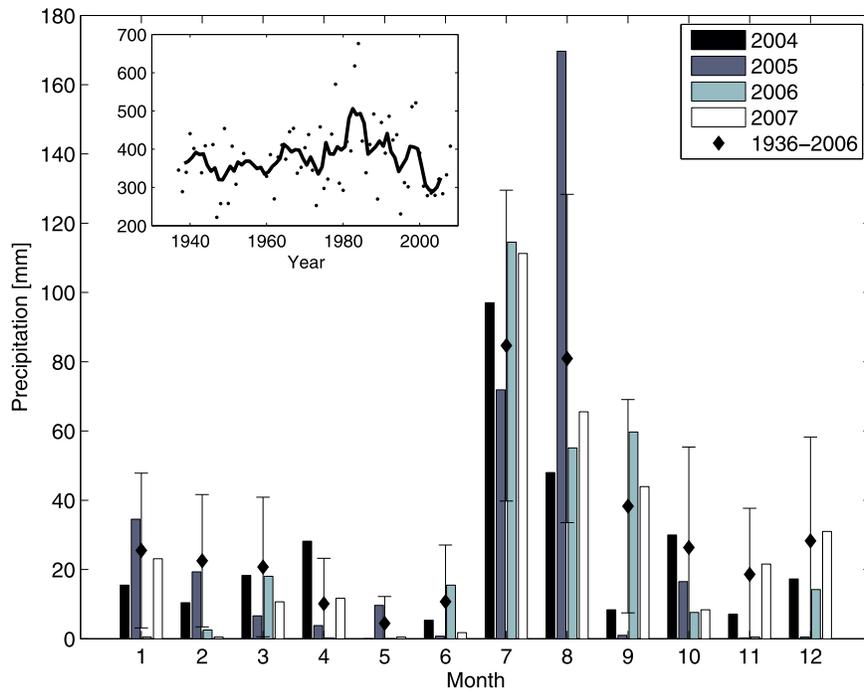


Figure 3. The 2004–2007 monthly precipitation along with the 1936–2006 mean and standard deviation near the site (SR number 45). Inset is annual precipitation with a 5-year running mean.

Table 1. Seasonal and Annual Precipitation and Evapotranspiration^a

	2004	2005	2006	2007	1936–2006
Winter (Dec–Mar)	59	61	35	65	98 (57)
Monsoon (Jul–Sep)	153	243	229	221	203 (70)
Annual precipitation	285	335	289	330	377 (92)
Annual ET	285	332	300	317	

^aUnits are in millimeters. Also shown are the long-term average precipitation and standard deviation (in parentheses).

was on an upward trend over the 2004–2007 period at both the local and regional scale (Figure 4). EVI reflects canopy phenology with a lower-amplitude green-up occurring in springtime and a much larger peak during the summer monsoon. The springtime green-up can consist of two components. First, mesquite produce leaves consistently in April, seemingly independent of antecedent rainfall. Second, winter annual and ephemeral plants, along with the bunchgrass *E. lehmanniana*, put on active photosynthetic tissue in December through March provided sufficient winter rainfall. The second period of yearly green-up is associated with the monsoon, typically beginning around early July. This involves large increases in the canopy cover of warm-season grasses and summer annuals with comparatively smaller increases in the woody perennial overstory [Cable, 1975]. The monsoon growing season is usually more robust and longer-lived, and the spring season is much more ephemeral and variable from year-to-year (Figure 4, bottom). The greater upward trend in peak EVI during the summer at the local scale may in part reflect the limited grazing by cattle

during 2006 and the lack of grazing in 2007 in the pasture where the tower is located, but conditions across much of the range also appeared to be improving.

4.2. Water

[22] The combined influence of a coarse-textured sandy loam soil and a semiarid climate at the site result in only brief opportunities for plants to access available soil moisture (θ , Figure 5). On a seasonal basis, we found that θ consistently declined to a minimum each June prior to the monsoon. Periods of elevated θ occurred both during the monsoon and the winter, with the exception of 2006 which was very dry. Most soil moisture dynamics occurred above the 50 cm depth, with water occasionally infiltrating below this depth following summer rains. The most substantial deep infiltration occurred in August 2005 (Figure 5), the month with the highest rainfall total for the 4 years (Figure 3). This contrasts with other coarse-textured soils in the region where deeper (>50 cm) soil moisture recharge typically occurs in winter when plants were inactive and evaporative demand is reduced [Cable, 1980; Scott *et al.*, 2000], but all winter/spring periods had below-average precipitation in this study (Table 1).

[23] Annual precipitation (P) and ET were nearly equivalent for most years (Table 1) and reflects the strong link between P and ET in arid regions regardless of the vegetation cover [Williams and Albertson, 2005]. The 4-year sum of annual precipitation and ET were closely matched (1239 mm and 1234 mm, respectively). The implications of this on the site water balance and on the uncertainty of the measurements are discussed below.

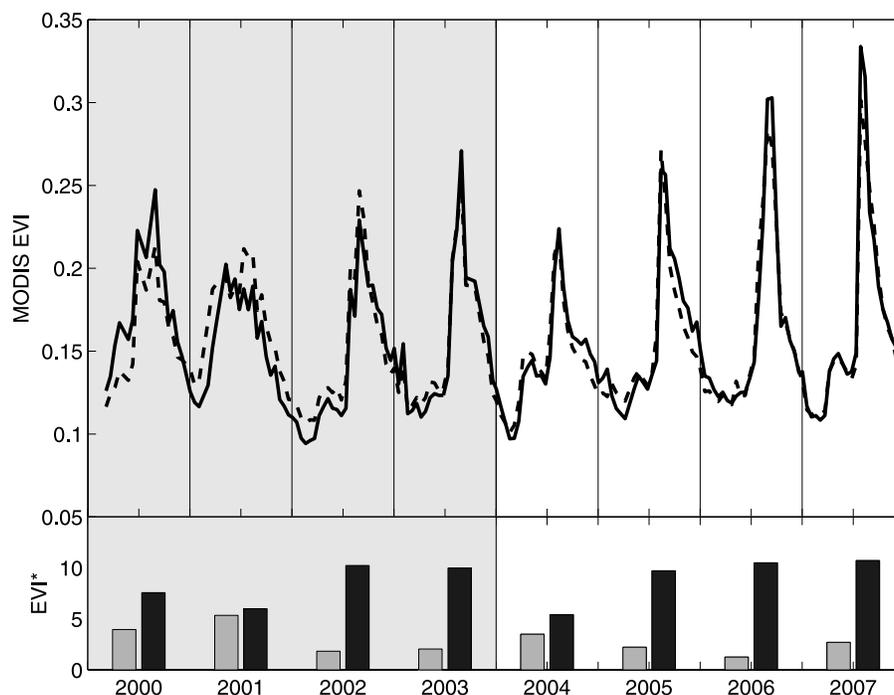


Figure 4. (top) The 2000–2007 MODIS Enhanced Vegetation Index (EVI). (bottom) Cumulative EVI (equation (1)) for the spring and summer growing seasons. The study period was carried out in 2004–2007; 2000–2003 data (shaded) are shown to provide additional context. Data are the average of a 5×5 pixel box (1.25×1.25 km) (solid line) and the average of a 41×41 pixel box (10.25×10.25 km) centered over the tower (dashed line).

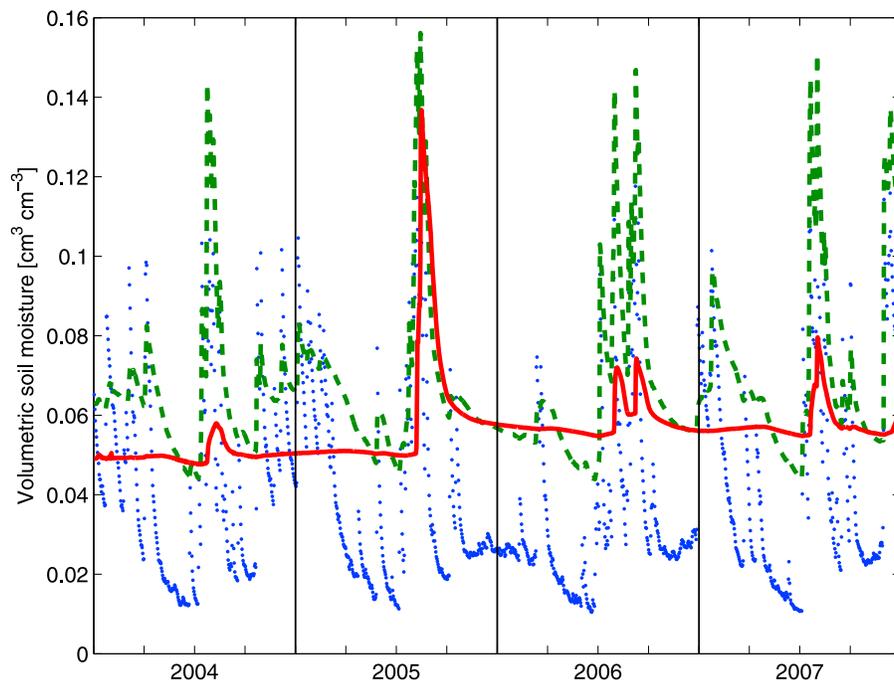


Figure 5. Average volumetric soil moisture for 2.5–10 cm (blue), 15–50 cm (green), and 65–130 cm (red line).

4.3. Carbon Dioxide

[24] Rainfall and temperature seasonality were evident in the monthly comparison of mean diurnal NEE (Figure 6). From January through March, midday NEE gradually increased consistent with increasing respiration associated with warmer daytime temperatures and minimal photosynthetic activity. The exception to this being in 2005 which showed more zero-to-negative daytime NEE, probably associated with the initiation of photosynthetic activity in winter annual plants and the relatively cold-tolerant C_4 grass, *E. lehmanniana*. During April, mesquite leaf flush occurred and is evidenced by a brief period of negative NEE during the midmorning when photosynthesis exceeded respiration. The effect of the severe 2006 cool-season drought can clearly be seen with daytime NEE consistently positive (i.e., $R > GEP$ for January–June).

[25] Although rains associated with the monsoon typically begin around early July, it is not until August that the large increase in photosynthesis becomes readily apparent as large negative values of midday NEE (Figure 6). Positive nighttime values of NEE during August reflect a period of high respiration associated with abundant soil moisture, warm temperatures, and active periods of growth by plants and microbes. From September through December, nighttime NEE decreased and daytime NEE increased (became less negative) as the activity of plants and soil microbes declined, reflecting increasingly dry and cool conditions.

[26] Comparing cumulative rainfall with NEE, R and GEP reveals the tight coupling between water availability and ecosystem CO_2 exchange (Figure 7). For example, the year with the least amount of total and monsoon precipitation (2004, Table 1) had the lowest cumulative annual GEP and respiration (Figure 7), and for 2004–2007, the rank of cumulative annual GEP followed the rank of annual precipitation though GEP was clearly less differentiated than

precipitation in 2005–2007, probably because the monsoon precipitation totals for these years were quite similar (Table 1). Overall, the ecosystem appeared to be a small-to-moderate net source of CO_2 to the atmosphere. The years with the most

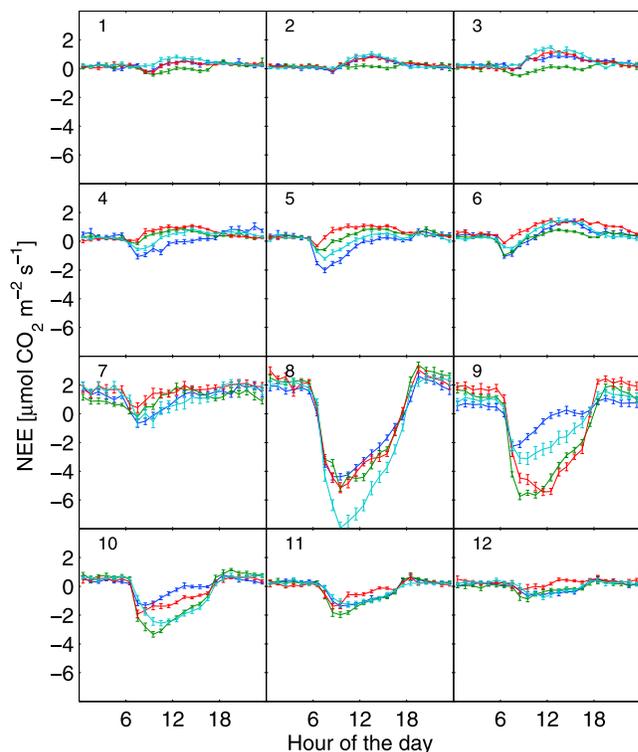


Figure 6. Mean monthly diurnal NEE for 2004 (blue), 2005 (green), 2006 (red), and 2007 (cyan). Numbers represent the month, and error bars are ± 1 standard error.

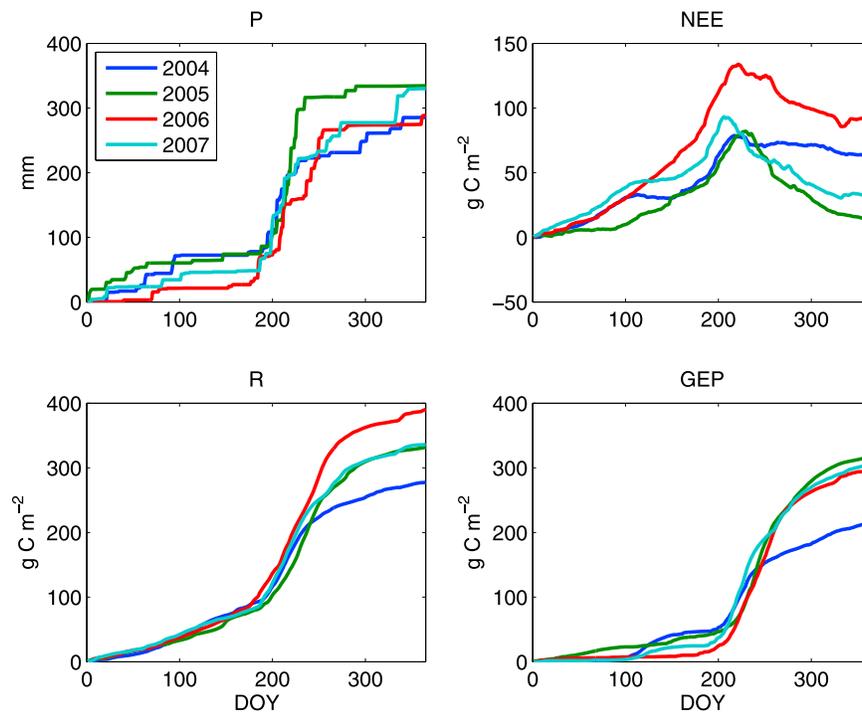


Figure 7. The 2004–2007 cumulative daily fluxes of precipitation (P), net ecosystem exchange of CO₂ (NEE), respiration (R), and gross ecosystem production (GEP). Increasing NEE indicates a net loss of carbon from the ecosystem. Decreasing NEE indicates a net gain.

severe cool season drought (2005) or summer drought (2004) had the largest net efflux, and the net loss diminished for years when rainfall was closest to the long-term mean.

[27] We computed the correlation coefficients between components of the CO₂ flux (NEE, R, GEP) with P and EVI*, all summed over spring, summer and annual periods, to better determine the coupling between the flux, water availability and vegetation status (Table 2). Annual and summer NEE were negatively correlated with annual P. Annual and summer GEP were both correlated with summer P, while spring GEP and NEE were related with spring P. Summer EVI* was highly correlated with summer and annual GEP, but the correlation ($r = 0.88$, $p = 0.13$) with spring EVI* and spring GEP was high but not significant. Curiously, spring EVI* was negatively correlated to both summer and annual R. Likewise, spring GEP was strongly negatively correlated with both summer and annual R ($r = -0.99$, pairing not shown in Table 2).

[28] In contrast to the tight coupling of P and GEP, cumulative R was not correlated with annual or seasonal P (Table 2). Annual R in 2006, the year with the severe cool season drought, clearly surpassed all other years. January

through June R appeared to be insensitive to rainfall in all years, while GEP clearly was not (Figure 7). During the spring growing season (February–May) temperature appears to limit R at the beginning of the season and soil moisture likely limits R during the middle and end of the season (Figure 8). For summer, the ratio of R/GEP at the beginning of the growing season was greatest in 2006 (Figure 9), even though it was nearly equivalent and less than unity with the others years for the rest (August–September) of the growing season.

[29] We used regression analysis to better understand the relationship between spring or summer growing season R or GEP with 0–5 cm soil temperature (T_{soil}) and shallow, middle and deep soil moisture (θ , Table 3). We found some correlation with R and both shallow and midlevel θ in spring, but the correlation coefficients and regression line slopes dramatically increased in value from spring to summer. From spring to summer, the correlations and slopes between θ and GEP decreased somewhat at 0–50 cm, but changed to positive correlations and slopes for deep θ . The nonintuitive negative correlation between spring GEP (derived mainly from the deep-rooted trees) and deep θ can be explained from

Table 2. Statistically Significant Correlation Coefficients^a

	Annual NEE	Summer NEE	Spring NEE	Annual R	Summer R	Annual GEP	Summer GEP	Spring GEP
Annual P	-0.90	-0.97						
Jul–Oct P						0.98	0.96	
Jan–May P			-0.99					0.95
Jan–May EVI*				-0.97	-0.95			
Jul–Oct EVI*					0.92	0.94	0.99	

^aBetween seasonal precipitation (P) and integrated EVI (EVI*) and seasonal sums of NEE, R, and GEP. Values are statistically significant at $\alpha = 0.10$, $n = 4$.

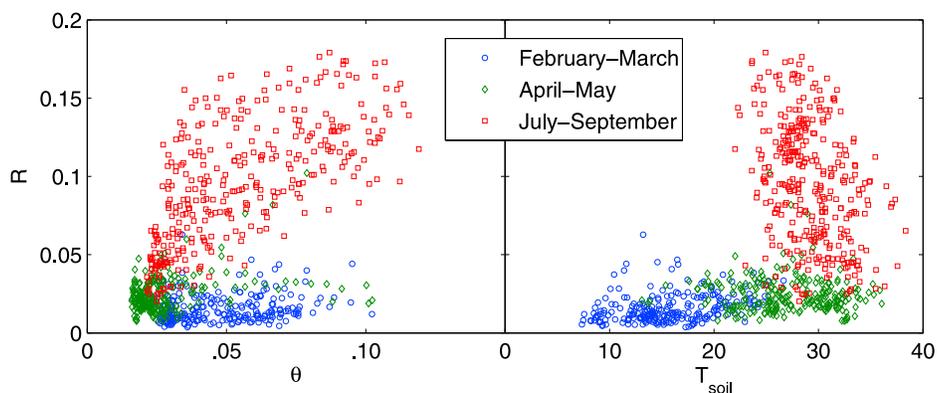


Figure 8. Daily ecosystem respiration (R , g C d^{-1}) versus average volumetric soil moisture at 5 cm (θ) and average soil temperature between 0 and 5 cm (T_{soil} , $^{\circ}\text{C}$).

the findings of *Scott et al.* [2008] who found that the deep soil moisture measurements quantified by two probes at each depth do not detect the significant quantities of soil moisture that can be moved downward in the soil profile by tree hydraulic redistribution. This moisture source redistributed from earlier cool-season rains can be a major moisture source for the mesquites during the dry spring months (usually April and May). Finally, both R and GEP are negatively correlated with T_{soil} . This would be a highly unusual result in less water-limited environments, but here it simply reflects the high degree of negative correlation between T_{soil} and θ (wetter soils are cooler, drier soils are warmer).

4.4. Uncertainty

[30] The lack of energy balance closure (sec. 3.2) likely indicates that turbulent fluxes of latent and sensible heat were underestimated in comparison with available energy. Some studies “force closure” by increasing the turbulent energy fluxes and the CO_2 flux in a manner which conserves the daily Bowen ratio and closes the energy balance

by dividing H , LE , and F_c by the closure ratio [*Twine et al.*, 2000], but the practice is still controversial. In this paper, we report “noncorrected” values and mention that forcing closure would increase ET , R and GEP by about 8% and leave cumulative NEE largely unaltered. The inherent uncertainty in estimating yearly total NEE using eddy covariance has been estimated to be around $\pm 10\text{--}30\%$ [*Goulden et al.*, 1996; *Hagen et al.*, 2006; *Loescher et al.*, 2006; *Moffat et al.*, 2007].

[31] Another way to assess the accuracy of the flux measurements is to look at the water balance. We found that total annual ET and precipitation were nearly balanced in each year of the study (Table 1) and for the 4-year duration of the study ($P = 1239 \text{ mm}$, $\text{ET} = 1234 \text{ mm}$). Looking at the other terms of the site water balance,

$$\text{ET} = P - \Delta\theta - R_o, \tag{3}$$

where $\Delta\theta$ is changes in soil moisture storage and R_o is local runoff or deep percolation, year-to-year variation in $0\text{--}1.3 \text{ m}$

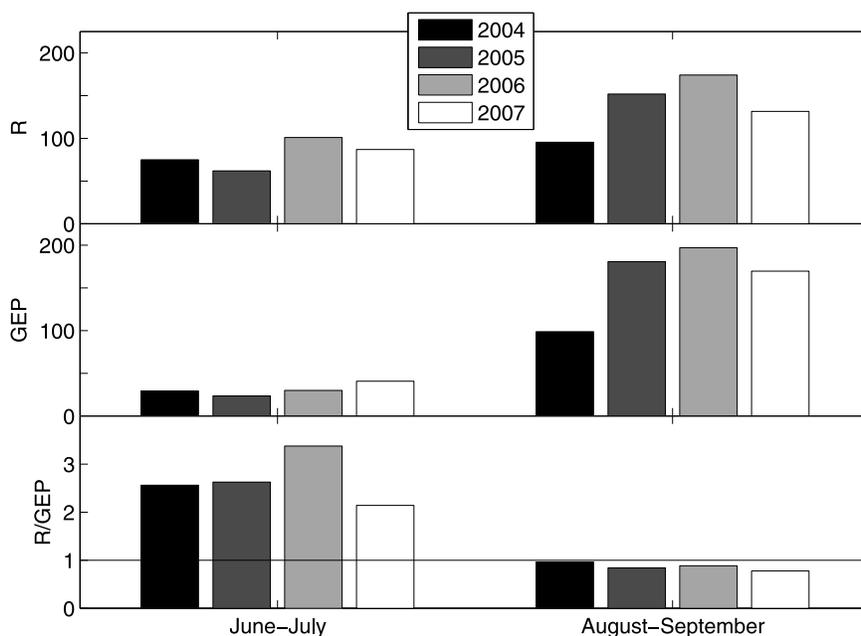


Figure 9. Cumulative respiration (R , g C), gross ecosystem production (GEP , g C), and R/GEP .

Table 3. Correlation Coefficients and Slopes by Season^a

	R		GEP	
	Spring	Summer	Spring	Summer
θ , 5 cm	0.26 (0.4)	0.67 (1.0)	0.28 (0.8)	0.24 (0.6)
θ , 15–50 cm	0.42 (0.6)	0.77 (1.1)	0.65 (1.9)	0.52 (1.1)
θ , 60–130 cm		0.50 (1.1)	−0.38 (−1.8)	0.65 (2.2)
T_{soil} , 0–5 cm		−0.36 (−5e-03)		−0.38 (−7e-03)

^aBetween soil moisture (θ) and near-surface soil temperature (T_{soil}), ordinate, and daily respiration (R) or gross ecosystem production of CO_2 (GEP), abscissa. Spring growing season between day 110–140 and summer is between day 190–273. Only statistically significant ($\alpha = 0.05$) values are shown. Slopes are in parentheses.

annual soil moisture storage was small (<1 to 23 mm yr^{-1}), and based on deep soil moisture sensors, we assume deep infiltration was negligible (Figure 5). Annual surface runoff ratios (P/R_0) from three small instrumented watersheds with similar loamy-sands to sandy-loam soils, and less than 1.5 km from the site, ranged from 1 to 7% [Lane and Kidwell, 2003]. While the amount of precipitation left on the site would be reduced due to runoff, this is balanced by an estimated 5–10% precipitation underestimate due to gage under catch [Larson and Peck, 1974]. Thus, by considering the terms in equation (3) and their errors, we estimate that the site water balance was closed within ~ 5 –10%.

5. Discussion

[32] In the present study, we report the ecosystem-atmosphere CO_2 exchange of a semiarid mesquite savanna located in southern Arizona for the period 2004–2007, where annual rainfall was consistently below the long-term average (Table 1). However, there were important differences in the rainfall distribution, such that cool-season rainfall totals were below average (to varying degrees) and monsoon totals were both above and below average (Table 1). This combination of below-average cool season precipitation and near-average summer rainfall may be a preview of changing precipitation regimes under the influence of a warming climate [Barnett et al., 2008; McAfee and Russell, 2008; Seager et al., 2007].

[33] The NEE and EVI data confirmed that there was one dominant growing season which began annually with the onset of the summer rainfall and where the degree and duration of plant activity varied as a function of the intensity and length of the monsoon. During this summer growing season, we observed the widely reported increases in daytime respiration associated with precipitation pulses that initially masked a concurrent increases in photosynthetic activity for drylands (Figure 6, July, and Figure 7) [Huxman et al., 2004; Scott et al., 2006; Veenendaal et al., 2004]. Here we also document the dynamics of the shorter, spring growth period which occurs given sufficient cool season rainfall (Figures 4 and 6). Other seasonally dry ecosystems have shown similar seasonal dynamics in diurnal NEE [Eamus et al., 2001; Hastings et al., 2005; Veenendaal et al., 2004]. In a study conducted at this site in 2004 and 2005, Scott et al. [2008] found that the elevated ET and photosynthesis in April and May was likely aided by downward hydraulic redistribution by mesquite roots in the previous winter months, when surface soil moisture if available was moved down the tap

root of the mesquites and into deeper soil layers. Mesquites were able to access this water stored deep in the soil profile during periods when shallower soil moisture was no longer available. What has been poorly understood to date is the interaction between these two growing seasons and seasonal/annual variation in precipitation.

[34] In this study we found support for our hypothesis that seasonal droughts reduce annual net CO_2 uptake by the ecosystem. The greatest CO_2 loss occurred in 2004 (summer drought) and 2006 (cool-season drought) while the years with closest to average rainfall in amount and its seasonal distribution (2005 and 2007) had the lowest efflux of CO_2 (Figure 7). Summer drought increased CO_2 losses by truncating the main growing season and reducing the growth in the later months of the season when photosynthesis exceeds respiratory losses (Figure 9). Cool-season drought affected the net CO_2 exchange differently than summer drought due to two additional and surprising discoveries found in the seasonal evolution of R and GEP, i.e., (1) the consistent yearly response of cumulative R from January to June despite rainfall differences, and (2) the severe spring drought of 2006 coincided with enhanced monsoon respiration.

[35] The consistent yearly response of January through June R may be explained by a combination of temperature limitation on respiration during the cooler months of January–March and surface moisture limitation during the warmer months of April and May (Figure 8). Thus, cumulative R until monsoon onset was probably the sum of low levels of mainly soil microbial respiration during the cooler months (when plants were usually dormant) and then mostly autotrophic respiration associated with mesquite leaf flush and possibly some understory plant activity in the spring.

[36] The second discovery of the 2006 cool-season drought priming of summer respiration (Figures 7 and 9) may be explained by increased autotrophic and/or heterotrophic respiration at the start of the monsoon. We speculate that the very dry conditions during the spring of 2006 led to a greater down-regulation of the premonsoon mesquite activity so when the monsoon started, mesquite were forced to repair and regrow fine roots, xylem tissues, and leaves to a much larger degree than usual, altering plant carbon balance and leading to a greater proportion of current photosynthesis feeding these growth and maintenance costs. Likewise, heterotrophic respiration may have been enhanced due to a greater amount of labile carbon in the form of senescent biomass associated with drought-induced mortality of mesquite leaves, roots and understory plants during the spring. Because soil microbial activity is linked to soil moisture availability in drylands [Reichstein et al., 2002; Tang and Baldocchi, 2005], persistent dry conditions such as those that occur during a drought, may limit soil microbial activity to the degree that the pool of labile soil carbon increases. When shallow soil water finally becomes available, soil microbes respond with a larger-than-expected burst of respiration as witnessed in 2006 [Jarvis et al., 2007; Yuste et al., 2007].

[37] Formerly grassland, this mesquite savanna was a net annual CO_2 source in all years of the study. In contrast to this finding, several studies have shown that shrub-dominated ecosystems can be significant sinks during years of average to high rainfall [Brummer et al., 2008; Luo et al., 2007; Wohlfahrt et al., 2008]. We observed that below-average

rainfall conditions during the period of study were especially detrimental to mesquite productivity. In particular, reductions in cool-season precipitation significantly truncated or caused a complete absence of mesquite photosynthesis during the spring growing season. Due to the near constancy of winter/spring respiration, increases in cool-season precipitation would arguably lead to gains in photosynthesis that would be directly realized in NEE and lead to net annual carbon sequestration given average or above monsoon rains.

[38] These results highlight the importance of not only the dynamics of vegetation change and intra-annual/interannual variability in climate forcing on biosphere/atmosphere interactions, but also the legacy of multidecadal variation in forcing that may influence source/sink dynamics of terrestrial ecosystems. Significant recruitment of woody plants occurred in the late twentieth century both locally and regionally [Brown *et al.*, 1997; Browning *et al.*, 2008; Mashiri *et al.*, 2008; Tiedemann and Klemmedson, 2004]. This was likely due to the wetter-than-average ~1975–1995 period of precipitation (Figure 3), which coincided with a more consistent period of above-average cool season rainfall [Browning *et al.*, 2008]. Cool season rainfall has been widely hypothesized as a mechanism for driving woody plant increases [Archer, 1994; Brown *et al.*, 1997; Hastings and Turner, 1965]. In this former grassland, woody encroachment has led to increases in belowground carbon stores [Wheeler *et al.*, 2007]. Thus during the 4 years of this study and for probably many of the years since 1995 (Figures 3 and 4), the ecosystem was likely “burning off” much of the CO₂ that may have been sequestered during the period of wetter-than-average rainfall that preceded the present drought.

[39] **Acknowledgments.** This work is supported by mainly by the USDA-ARS and by SAHRA (Sustainability of Semi-Arid Hydrology and Riparian Areas) under the STC Program of the National Science Foundation, agreement EAR-9876800. Other funding includes: NSF-DEB 04189134 and 0414977, the Phileology Foundation, and a Biological Informatics post-doctoral fellowship to G.D.J. awarded in 2004. Rainfall data were provided by the Santa Rita Experimental Range Digital Database. Funding for the digitization of these data was provided by USDA Forest Service Rocky Mountain Research Station and the University of Arizona. Thanks to M. McClaran and M. Heitlinger (University of Arizona) who oversee the research carried out on the experimental range and have been especially helpful in the establishment and operation of this site.

References

- Adams, D. K., and A. C. Comrie (1997), The North American monsoon, *Bull. Am. Meteorol. Soc.*, **78**, 2197–2213, doi:10.1175/1520-0477(1997)078<2197:TNAM>2.0.CO;2.
- Archer, S. A. (1994), Woody plant encroachment into southwestern grasslands and savannas: Rates, patterns and proximate causes, in *Ecological Implications of Livestock Herbivory in the West*, edited by M. Vavra *et al.*, pp. 13–68, Soc. for Range Manage, Denver, Colo.
- Archer, S., D. S. Schimel, and E. A. Holland (1995), Mechanisms of shrubland expansion: Land use, climate or CO₂?, *Clim. Change*, **29**, 91–99, doi:10.1007/BF01091640.
- Archer, S., T. W. Boutton, and K. A. Hibbard (2001), Trees in grasslands: Biogeochemical consequences of woody plant expansion, in *Global Biogeochemical Cycles in the Climate System*, edited by D. Schulze *et al.*, pp. 115–138, Academic, Durham, N. C.
- Bahre, C. J., and M. L. Shelton (1993), Historic vegetation change, mesquite increases, and climate in southeastern Arizona, *J. Biogeogr.*, **20**, 489–504, doi:10.2307/2845722.
- Baldocchi, D. D. (2003), Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: Past, present and future, *Global Change Biol.*, **9**, 479–492, doi:10.1046/j.1365-2486.2003.00629.x.
- Baldocchi, D. (2008), Turner Review No. 15. ‘Breathing’ of the terrestrial biosphere: Lessons learned from a global network of carbon dioxide flux measurement systems, *Aust. J. Bot.*, **56**, 1–26, doi:10.1071/BT07151.
- Barnett, T. P., *et al.* (2008), Human-induced changes in the hydrology of the western United States, *Science*, **319**(5866), 1080–1083, doi:10.1126/science.1152538.
- Bradley, B. A., R. A. Houghton, J. F. Mustard, and S. P. Hamburg (2006), Invasive grass reduces aboveground carbon stocks in shrublands of the western US, *Global Change Biol.*, **12**(10), 1815–1822, doi:10.1111/j.1365-2486.2006.01232.x.
- Brown, D. E., C. H. Lowe, and C. P. Puse (1979), A digitized classification system for the biotic communities of North America, with community (series) and association examples for the Southwest, *J. Ariz. Nev. Acad. Sci.*, **14**, 1–16.
- Brown, J. H., T. J. Valone, and C. G. Curtin (1997), Reorganization of an arid ecosystem in response to recent climate change, *Proc. Natl. Acad. Sci. U. S. A.*, **94**, 9729–9733, doi:10.1073/pnas.94.18.9729.
- Brown, J. R., and S. Archer (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, doi:10.1007/BF00789926.
- Browning, D. M., S. R. Archer, and G. P. Asner (2008), Woody plants in grasslands: Post-encroachment stand dynamics, *Ecol. Appl.*, **18**, 928–944, doi:10.1890/07-1559.1.
- Brummer, C., U. Falk, H. Papen, J. Szarzynski, R. Wassmann, and N. Brüggemann (2008), Diurnal, seasonal, and interannual variation in carbon dioxide and energy exchange in shrub savanna in Burkina Faso (West Africa), *J. Geophys. Res.*, **113**, G02030, doi:10.1029/2007JG000583.
- Cable, D. R. (1975), Influence of precipitation on perennial grass production in the semidesert southwest, *Ecology*, **56**, 981–986, doi:10.2307/1936309.
- Cable, D. R. (1977), Seasonal use of soil water by mature velvet mesquite, *J. Range Manage.*, **30**, 4–11, doi:10.2307/3897324.
- Cable, D. R. (1980), Seasonal patterns of soil water recharge and extraction on semidesert ranges, *J. Range Manage.*, **33**, 9–15, doi:10.2307/3898220.
- Cabral, A. C., J. M. De Miguel, A. J. Rescia, M. F. Schmitz, and F. D. Pineda (2003), Shrub encroachment in Argentinean savannas, *J. Veg. Sci.*, **14**, 145–152, doi:10.1111/j.1654-1103.2003.tb02139.x.
- Culley, M. (1943), Grass grows in summer or not at all, *Hereford J.*, **34**, 5–24.
- Diffenbaugh, N. S., F. Giorgi, and J. S. Pal (2008), Climate change hotspots in the United States, *Geophys. Res. Lett.*, **35**, L16709, doi:10.1029/2008GL035075.
- Dukes, J. S., N. R. Chiariello, E. E. Cleland, L. A. Moore, M. R. Shaw, S. Thayer, T. Tobeck, H. A. Mooney, and C. B. Field (2005), Responses of grassland production to single and multiple global environmental changes, *PLoS Biol.*, **3**, e319, doi:10.1371/journal.pbio.0030319.
- Eamus, D., L. B. Hutley, and A. P. O’Grady (2001), Daily and seasonal patterns of carbon and water fluxes above a north Australian savanna, *Tree Physiol.*, **21**, 977–988.
- Falge, E., *et al.* (2001), Gap filling strategies for defensible annual sums of net ecosystem exchange, *Agric. For. Meteorol.*, **107**, 43–69, doi:10.1016/S0168-1923(00)00225-2.
- Gilmanov, T. G., *et al.* (2007), Partitioning European grassland net ecosystem CO₂ exchange into gross primary productivity and ecosystem respiration using light response function analysis, *Agric. Ecosyst. Environ.*, **121**(1–2), 93–120, doi:10.1016/j.agee.2006.12.008.
- Glendening, G. E. (1952), Some quantitative data on the increase of mesquite and cactus on a desert grassland range in southern Arizona, *Ecology*, **33**, 319–328, doi:10.2307/1932827.
- Goodale, C. L., and E. A. Davidson (2002), Uncertain sinks in the shrubs, *Nature*, **418**, 593–594, doi:10.1038/418593a.
- Goulden, M. L., J. W. Munger, S. M. Fan, B. C. Daube, and S. C. Wofsy (1996), Measurements of carbon sequestration by long-term eddy covariance: Methods and a critical evaluation of accuracy, *Global Change Biol.*, **2**, 169–182, doi:10.1111/j.1365-2486.1996.tb00070.x.
- Grover, H. D., and H. B. Musick (1990), Shrubland encroachment in southern New Mexico, U.S.A.: An analysis of desertification processes in the American southwest, *Clim. Change*, **17**, 305–330, doi:10.1007/BF00138373.
- Hagen, S. C., B. H. Braswell, E. Linder, S. Frolking, A. D. Richardson, and D. Y. Hollinger (2006), Statistical uncertainty of eddy flux–based estimates of gross ecosystem carbon exchange at Howland Forest, Maine, *J. Geophys. Res.*, **111**, D08S03, doi:10.1029/2005JD006154.
- Harpole, W. S., D. L. Potts, and K. N. Suding (2007), Ecosystem responses to water and nitrogen amendment in a California grassland, *Global Change Biol.*, **13**(11), 2341–2348, doi:10.1111/j.1365-2486.2007.01447.x.
- Hastings, J. R., and R. M. Turner (1965), *The Changing Mile: An Ecological Study of Vegetation Change With Time in the Lower Mile of an Arid and Semi-Arid Region*, Univ. of Ariz. Press, Tucson.
- Hastings, S. J., W. C. Oechel, and A. Muhlia-Melo (2005), Diurnal, seasonal and annual variation in the net ecosystem CO₂ exchange of

- a desert shrub community (Sarcocaulis) in Baja California, Mexico, *Global Change Biol.*, 11(6), 927–939, doi:10.1111/j.1365-2486.2005.00951.x.
- Huete, A., K. Didan, T. Miura, E. P. Rodriguez, X. Gao, and L. G. Ferreira (2002), Overview of the radiometric and biophysical performance of the MODIS vegetation indices, *Remote Sens. Environ.*, 83, 195–213, doi:10.1016/S0034-4257(02)00096-2.
- Huxman, T. E., K. A. Snyder, D. Tissue, A. J. Leffler, K. Ogle, W. T. Pockman, D. R. Sandquist, D. L. Potts, and S. Schwinning (2004), Precipitation pulses and carbon fluxes in semiarid and arid ecosystems, *Oecologia*, 141, 254–268.
- Jarvis, P., et al. (2007), Drying and wetting of Mediterranean soils stimulates decomposition and carbon dioxide emission: The “Birch effect,” *Tree Physiol.*, 27, 929–940.
- Jenerette, G. D., R. L. Scott, and T. E. Huxman (2008), Whole ecosystem metabolic pulses following precipitation events, *Funct. Ecol.*, 22, 924–930, doi:10.1111/j.1365-2435.2008.01450.x.
- Kemp, P. R. (1983), Phenological patterns of Chihuahuan desert plants in relation to the timing of water availability, *J. Ecol.*, 71, 427–436, doi:10.2307/2259725.
- Kirschbaum, M. U. F. (1995), The temperature-dependence of soil organic-matter decomposition, and the effect of global warming on soil organic-C storage, *Soil Biol. Biochem.*, 27, 753–760, doi:10.1016/0038-0717(94)00242-S.
- Knorr, W., I. C. Prentice, J. I. House, and E. A. Holland (2005), Long-term sensitivity of soil carbon turnover to warming, *Nature*, 433, 298–301, doi:10.1038/nature03226.
- Kurc, S. A., and E. E. Small (2007), Soil moisture variations and ecosystem-scale fluxes of water and carbon in semiarid grassland and shrubland, *Water Resour. Res.*, 43, W06416, doi:10.1029/2006WR005011.
- Lane, L. J., and M. R. Kidwell (2003), Hydrology and soil erosion, in *Santa Rita Experimental Range: 100 years (1903–2003) of Accomplishments and Contributions*, 197 pp., Rocky Mt. Res. Stn., For. Serv., U.S. Dep. of Agric., Ogden, Utah.
- Larson, L. W., and E. L. Peck (1974), Accuracy of precipitation measurements for hydrologic modeling, *Water Resour. Res.*, 10, 857–863, doi:10.1029/WR010i004p00857.
- Leuning, R., H. A. Cleugh, S. J. Ziegler, and D. Hughes (2005), Carbon and water fluxes over a temperate Eucalyptus forest and a tropical wet/dry savanna in Australia: Measurements and comparison with MODIS remote sensing estimates, *Agric. For. Meteorol.*, 129(3–4), 151–173, doi:10.1016/j.agrformet.2004.12.004.
- Lin, J. L., B. E. Mapes, K. M. Weickmann, G. N. Kiladis, S. D. Schubert, M. J. Suarez, J. T. Bacmeister, and M. I. Lee (2008), North American monsoon and convectively coupled equatorial waves simulated by IPCC AR4 coupled GCMs, *J. Clim.*, 21(12), 2919–2937, doi:10.1175/2007JCLI1815.1.
- Loescher, H. W., B. E. Law, L. Mahrt, D. Y. Hollinger, J. Campbell, and S. C. Wofsy (2006), Uncertainties in, and interpretation of, carbon flux estimates using the eddy covariance technique, *J. Geophys. Res.*, 111, D21S90, doi:10.1029/2005JD006932.
- Luo, H., W. C. Oechel, S. J. Hastings, R. Zulueta, Y. Qian, and H. Kwon (2007), Mature semiarid chaparral ecosystems can be a significant sink for atmospheric carbon dioxide, *Global Change Biol.*, 13(2), 386–396, doi:10.1111/j.1365-2486.2006.01299.x.
- Malhi, Y., A. D. Nobre, J. Grace, B. Kruijt, M. G. P. Pereira, A. Culf, and S. Scott (1998), Carbon dioxide transfer over a Central Amazonian rain forest, *J. Geophys. Res.*, 103, 31,593–31,612, doi:10.1029/98JD02647.
- Martin, S. C., and D. R. Cable (1974), Managing semidesert grass-shrub ranges: Vegetation responses to precipitation, grazing, soil texture, and mesquite control, 45 pp., For. Serv., U.S. Dep. of Agric., Ogden, Utah.
- Martin, S. C., and K. E. Severson (1988), Vegetation response to the Santa Rita grazing system, *J. Range Manage.*, 41, 291–295, doi:10.2307/3899381.
- Mashiri, F. E., M. P. McClaran, and J. S. Fehmi (2008), Long-term vegetation change related to grazing systems, precipitation and mesquite cover, *Rangeland Ecol. Manage.*, 61, 368–379, doi:10.2111/07-109.1.
- McAfee, S. A., and J. L. Russell (2008), Impact of the Northern Annular Mode on cool season climate patterns in the Southwest, *Geophys. Res. Lett.*, 35, L17701, doi:10.1029/2008GL034828.
- McClaran, M. P. (2003), A century of vegetation change on the Santa Rita Experimental Range, in *Santa Rita Experimental Range: One-Hundred Years (1903–2003) of Accomplishments and Contributions*, 197 pp., Rocky Mt. Res. Stn., For. Serv., U.S. Dep. of Agric., Ogden, Utah.
- Moffat, A. M., et al. (2007), Comprehensive comparison of gap-filling techniques for eddy covariance net carbon fluxes, *Agric. For. Meteorol.*, 147(3–4), 209–232, doi:10.1016/j.agrformet.2007.08.011.
- Noy-Meir, I. (1973), Desert ecosystems: Environment and producers, *Annu. Rev. Ecol. Syst.*, 4, 25–51, doi:10.1146/annurev.es.04.110173.000325.
- Pacala, S. W., et al. (2001), Consistent land- and atmosphere-based U.S. carbon sink estimates, *Science*, 292, 2316–2320, doi:10.1126/science.1057320.
- Paw U, K. T., D. D. Baldocchi, T. P. Meyers, and K. B. Wilson (2000), Correction of eddy-covariance measurements incorporating both advective effects and density fluxes, *Boundary Layer Meteorol.*, 97, 487–511, doi:10.1023/A:1002786702909.
- Peters, W., et al. (2007), An atmospheric perspective on North American carbon dioxide exchange: CarbonTracker, *Proc. Natl. Acad. Sci. U. S. A.*, 104(48), 18,925–18,930, doi:10.1073/pnas.0708986104.
- Potts, D. L., T. E. Huxman, J. M. Cable, N. B. English, D. D. Ignace, J. A. Eilts, M. J. Mason, J. F. Weltzin, and D. G. Williams (2006), Antecedent moisture and seasonal precipitation influence the response of canopy-scale carbon and water exchange to rainfall pulses in a semi-arid grassland, *New Phytol.*, 170(4), 849–860, doi:10.1111/j.1469-8137.2006.01732.x.
- Reichstein, M., et al. (2002), Severe drought effects on ecosystem CO₂ and H₂O fluxes at three Mediterranean evergreen sites: Revision of current hypotheses?, *Global Change Biol.*, 8(10), 999–1017, doi:10.1046/j.1365-2486.2002.00530.x.
- Reichstein, M., et al. (2005), On the separation of net ecosystem exchange into assimilation and ecosystem respiration: Review and improved algorithm, *Global Change Biol.*, 11(9), 1424–1439, doi:10.1111/j.1365-2486.2005.01002.x.
- Ruyle, G. B. (2003), Rangeland livestock production: Developing the concept of sustainability on the Santa Rita Experimental Range, in *Santa Rita Experimental Range: One-Hundred Years (1903–2003) of Accomplishments and Contributions*, 197 pp., Rocky Mt. Res. Stn. For. Serv., U.S. Dep. of Agric., Ogden, Utah.
- Saleska, S. R., et al. (2003), Carbon in Amazon forests: Unexpected seasonal fluxes and disturbance-induced losses, *Science*, 302, 1554–1557, doi:10.1126/science.1091165.
- Scott, R. L., W. J. Shuttleworth, T. O. Keefer, and A. W. Warrick (2000), Modeling multiyear observations of soil moisture recharge in the semiarid American Southwest, *Water Resour. Res.*, 36, 2233–2247, doi:10.1029/2000WR900116.
- Scott, R. L., T. E. Huxman, D. G. Williams, and D. C. Goodrich (2006), Ecophysiological impacts of woody-plant encroachment: Seasonal patterns of water and carbon dioxide exchange within a semiarid riparian environment, *Global Change Biol.*, 12(2), 311–324, doi:10.1111/j.1365-2486.2005.01093.x.
- Scott, R. L., W. L. Cable, and K. R. Hultine (2008), The ecophysiological significance of hydraulic redistribution in a semiarid savanna, *Water Resour. Res.*, 44, W02440, doi:10.1029/2007WR006149.
- Seager, R., et al. (2007), Model projections of an imminent transition to a more arid climate in southwestern North America, *Science*, 316(5828), 1181–1184, doi:10.1126/science.1139601.
- Sponseller, R. A. (2007), Precipitation pulses and soil CO₂ flux in a Sonoran Desert ecosystem, *Global Change Biol.*, 13(2), 426–436, doi:10.1111/j.1365-2486.2006.01307.x.
- Swetnam, T. W., and J. L. Betancourt (1998), Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest, *J. Clim.*, 11, 3128–3147, doi:10.1175/1520-0442(1998)011<3128:MDAERT>2.0.CO;2.
- Tang, J., and D. D. Baldocchi (2005), Spatial-temporal variation in soil respiration in an oak-grass savanna ecosystem in California and its partitioning into autotrophic and heterotrophic components, *Biogeochemistry*, 73(1), 183–207, doi:10.1007/s10533-004-5889-6.
- Tiedemann, A. R., and J. O. Klemmedson (2004), Responses of desert grassland vegetation to mesquite removal and regrowth, *J. Range Manage.*, 57, 455–465, doi:10.2307/4003974.
- Turner, R. M., R. H. Webb, and J. E. Bowers (2003), *The Changing Mile Revisited: An Ecological Study of Vegetation Change With Time in the Lower Mile of an Arid and Semiarid Region*, Univ. of Ariz. Press, Tucson.
- Twine, T. E., W. P. Kustas, J. M. Norman, D. R. Cook, P. R. Houser, T. P. Meyers, J. H. Prueger, P. J. Starks, and M. L. Wesely (2000), Correcting eddy-covariance flux underestimates over a grassland, *Agric. For. Meteorol.*, 103, 279–300, doi:10.1016/S0168-1923(00)00123-4.
- Van Auken, O. U. (2000), Shrub invasions of North American semiarid grasslands, *Annu. Rev. Ecol. Syst.*, 31, 197–215, doi:10.1146/annurev.ecolsys.31.1.197.
- Veenendaal, E. M., O. Kolle, and J. Lloyd (2004), Seasonal variation in energy fluxes and carbon dioxide exchange for a broad-leaved semi-arid savanna (Mopane woodland) in Southern Africa, *Global Change Biol.*, 10, 318–328, doi:10.1111/j.1365-2486.2003.00699.x.
- Webb, E. K., G. I. Pearman, and R. Leuning (1980), Correction of flux measurements for density effects due to heat and water vapour transfer, *Q. J. R. Meteorol. Soc.*, 106, 85–100, doi:10.1002/qj.49710644707.

- Weltzin, J. F., et al. (2003), Assessing the response of terrestrial ecosystems to potential changes in precipitation, *BioScience*, 53, 941–952, doi:10.1641/0006-3568(2003)053[0941:ATROTE]2.0.CO;2.
- Wheeler, C. W., S. R. Archer, G. P. Asner, and C. R. McMurtry (2007), Climatic/edaphic controls on soil carbon/nitrogen response to shrub encroachment in desert grassland, *Ecol. Appl.*, 17(7), 1911–1928, doi:10.1890/06-1580.1.
- Williams, C. A., and J. D. Albertson (2005), Contrasting short- and long-timescale effects of vegetation dynamics on water and carbon fluxes in water-limited ecosystems, *Water Resour. Res.*, 41, W06005, doi:10.1029/2004WR003750.
- Wilson, K., et al. (2002), Energy balance closure at FLUXNET sites, *Agric. For. Meteorol.*, 113, 223–243, doi:10.1016/S0168-1923(02)00109-0.
- Wohlfahrt, G., L. F. Fenstermaker, and J. A. Arnone III (2008), Large annual net ecosystem CO₂ uptake of a Mojave Desert ecosystem, *Global Change Biol.*, 14(7), 1475–1487, doi:10.1111/j.1365-2486.2008.01593.x.
- Yuste, J. C., D. D. Baldocchi, A. Gershenson, A. Goldstein, L. Misson, and S. Wong (2007), Microbial soil respiration and its dependency on carbon inputs, soil temperature and moisture, *Global Change Biol.*, 13, 2018–2035, doi:10.1111/j.1365-2486.2007.01415.x.
-
- T. E. Huxman, Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA.
- G. D. Jenerette, Department of Botany and Plant Sciences, University of California, Riverside, CA 92521, USA.
- D. L. Potts, Biology Department, State University of New York College at Buffalo, Buffalo, NY 14222, USA.
- R. L. Scott, Southwest Watershed Research Center, Agricultural Research Service, USDA, 2000 East Allen Road, Tucson, AZ 85719, USA. (russ.scott@ars.usda.gov)