

Carbon dioxide exchange in a semidesert grassland through drought-induced vegetation change

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[1] Global warming may intensify the hydrological cycle and lead to increased drought severity and duration, which could alter plant community structure and subsequent ecosystem water and carbon dioxide cycling. We report on the net ecosystem exchange of carbon dioxide (NEE) of a semidesert grassland through a severe drought which drove succession from native bunchgrasses to forbs and to eventual dominance by an exotic bunchgrass. We monitored NEE and energy fluxes using eddy covariance coupled with meteorological and soil moisture variables for 6 years at a grassland site in southeastern Arizona, USA. Seasonal NEE typically showed a springtime carbon uptake after winter-spring periods of average rainfall followed by much stronger sink activity during the summer rainy season. The two severe drought years (2004 and 2005) resulted in a net release of carbon dioxide (25 g C m^{-2}) and widespread mortality of native perennial bunchgrasses. Above average summer rains in 2006 alleviated drought conditions, resulting in a large flush of broad-leaved forbs and negative total NEE ($-55 \text{ g C m}^{-2} \text{ year}^{-1}$). Starting in 2007 and continuing through 2009, the ecosystem became increasingly dominated by the exotic grass, *Eragrostis lehmanniana*, and was a net carbon sink (-47 to $-98 \text{ g C m}^{-2} \text{ year}^{-1}$) but with distinct annual patterns in NEE. Rainfall mediated by soils was the key driver to water and carbon fluxes. Seasonal respiration and photosynthesis were strongly dependent on precipitation, but photosynthesis was more sensitive to rainfall variation. Respiration normalized by evapotranspiration showed no interannual variation, while normalized gross ecosystem production (i.e., water use efficiency) was low during drought years and then increased as the rains returned and the *E. lehmanniana* invasion progressed. Thus, when dry summer conditions returned in 2009, the potential for ecosystem carbon accumulation was increased and the ecosystem remained a net sink unlike similar dry years when native grasses dominated ecosystem structure.

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1. Introduction

[2] The composition of ecosystems can be perturbed by a variety of disturbances including fire, drought, and excessive herbivory. Protracted drought has been shown to trigger rapid compositional changes through mortality of historical vegetation [Allen and Breshears, 1998; Breshears *et al.*, 2005] and can facilitate the spread of opportunistic invaders when the drought ends [Dukes and Mooney, 2004; King *et al.*, 2008]. Such changes can result in transformations to eco-

system structure and its ecohydrologic functioning that may or may not have lasting effects.

[3] An example of ecosystem composition change of great concern to ranchers and resource managers in the western United States is the spread of exotic grasses into native rangelands [Arriaga *et al.*, 2004; Bradley *et al.*, 2006]. In the semidesert grasslands of the Sonoran and Chihuahuan deserts, the introduction and spread of Lehmann lovegrass (*Eragrostis lehmanniana*) often results in a near replacement of diverse native bunchgrass communities [Anable *et al.*, 1992]. Lovegrass dominance strongly reduces desert grassland plant and animal diversity [Bock *et al.*, 1986], though this may vary regionally [Hupy *et al.*, 2004]. Lehmann lovegrass may better tolerate grazing and fire than most native species, and this may facilitate long-term persistence and conversion of the ecosystem to a new steady state [Anable *et al.*, 1992; McClaran and Anable, 1992]. Invasive success of

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lovegrass has also been linked to increased primary productivity [Anable *et al.*, 1992], suggesting it could alter the fundamental relationships between water and carbon cycling in these semiarid ecosystems (e.g., water use efficiency, ratio of transpiration to evapotranspiration, etc.).

[4] Current research has shown grassland community structure and productivity are highly sensitive to temporal variability in precipitation, especially in water-limited systems [Fay *et al.*, 2003, 2008; Heisler-White *et al.*, 2008, 2009]. However, the response of grassland ecohydrological functioning to dramatically altered community structure following drought is still unclear. Short-term field experiments show lovegrass-dominated ecosystems are less effective at using precipitation pulses than native species due to higher ecosystem respiratory fluxes (R_{eco}) and more rapid declines in net ecosystem CO_2 exchange (NEE) following precipitation pulses [Huxman *et al.*, 2004b; Potts *et al.*, 2006]. However, this may apply only in comparison to certain native species, as a seasonal comparison with another native bunchgrass showed lovegrass-dominated plots accumulate more carbon over the summer growing season [Hamerlynck *et al.*, 2010]. In addition, the transition to lovegrass dominance can increase the bare soil evaporation contributions to total evapotranspiration [Moran *et al.*, 2009]. The coupled carbon and water fluxes of whole ecosystems through these critical transitions in desert grasslands have yet to be observed.

[5] In this paper, we analyzed 6 years of land/atmosphere carbon dioxide exchange in a semidesert grassland undergoing a nearly complete replacement of a diverse perennial bunchgrass community to one nearly completely dominated by Lehmann lovegrass following a severe drought experienced across many southwestern U. S. ecosystems [Bowers, 2005; Breshears *et al.*, 2005; Hereford *et al.*, 2006; McAuliffe and Hamerlynck, 2010; Miriti *et al.*, 2007]. We established the site in the spring of 2004 to measure energy and CO_2 fluxes in a semidesert grassland that lies in the transition zone between the Sonoran and Chihuahuan deserts. We observed 2 years of extreme drought that resulted in mortality of many native bunchgrasses and shrubs. Following this drought, the summer rains of 2006 produced a large flush of herbaceous plants that then gave way to increasing dominance of nonnative Lehmann lovegrass from 2007 through 2009. Summer rainfall in 2009 was low and comparable to the drought year of 2004 enabling us to compare how ecosystem functioning had changed with altered community composition. In tracking ecosystem carbon and water fluxes through this entire period, we now better understand how a water-limited grassland ecosystem responds and recovers from a severe, disturbance-inducing drought. Ecohydrological studies on vegetation change in semiarid ecosystems have shown alterations in the controls and patterns of carbon dioxide exchange when the shift in plant growth form is dramatic (e.g., grass to woody) [Huxman *et al.*, 2005; Kurc and Small, 2007; Prater and DeLucia, 2006; Scott *et al.*, 2006]. In this study, the shift in the dominant vegetation was from a mature, diverse native perennial C_4 bunchgrass community to a less diverse community dominated by one exotic bunchgrass species. Consequently, we hypothesized that, without a dramatic shift in growth form, this replacement would not alter the

controls and pattern of carbon dioxide exchange for this water-limited grassland ecosystem.

2. Site Description

[6] The Kendall grassland (31.74°N, 109.94°W, 1530 m) lies in the upper end of the USDA Agricultural Research Service Walnut Gulch Experimental Watershed [Renard *et al.*, 2008]. This site has been monitored for rainfall and runoff since 1964 and has been the focus of many hydrological experimental campaigns [Jackson *et al.*, 2008; Kustas and Goodrich, 1994]. The 1964–2009 mean annual rainfall is 345 mm with 63% of this coming in the summer months of June–September with the annual recurrence of the North American Monsoon [Adams and Comrie, 1997]. The dominant growing season is in response to the summer rains, but a shorter and less productive springtime (~February–April) growth period does occur given sufficient cool season precipitation [Jenerette *et al.*, 2010]. The 2004–2009 mean annual temperature is 17.4°C with summertime highs of around 37°C and wintertime lows that occasionally dip below freezing.

[7] Historically and at the beginning of this study, the grassland was covered mainly by a diverse mosaic of C_4 bunchgrasses (*Bouteloua eriopoda*, *Bouteloua hirsuta*, *Hilaria belangeri*, and *Aristida hamulosa*) [Wertz *et al.*, 1994] interspersed with C_3 shrubs (*Calliandra eriophylla*, *Dalea formosam*, *Krameria parvifolia*, *Prosopis glandulosa*, *Yucca elata*, and *Isocoma tenuisecta*). Peak leaf area index (LAI) was estimated at ~1 with ~40% canopy cover [Nouvellon *et al.*, 2001]. Following the peak of the drought (2003–2006), most native bunchgrasses were dead with widespread shrub mortality, and the grassland since 2007 has been dominated by Lehmann lovegrass (*Eragrostis lehmanniana*). Soils around Kendall are a complex of Stronghold (coarse loamy, mixed, thermic Ustollic Calciorthids) and Elgin (fine, mixed, thermic, Ustollic Paleargids) [Breckenfeld *et al.*, 1995] and generally are very gravelly, sandy to fine sandy loams with some areas having silty clay to clay loams in the B horizon (~10–60 cm). The grassland was grazed from light to moderate levels throughout this study with minimal visual evidence of heavy foraging.

[8] The fetch at the site is representative of the cover immediately surrounding the micrometeorological tower over several kilometers, but it has considerable topographical variation (see Scott [2010] for a map of the site). The eddy covariance tower stands upon a broad ridge with hillslopes falling fairly steeply away from it at ~10% to the northwest and southeast, at 9% to the southwest and flat to the northeast over a horizontal distance of 200 m. Modeled cross-wind integrated flux footprints had a peak location of 92 ± 23 m (mean and standard deviation) and 90% along-wind extent of 252 ± 62 m [Kljun *et al.*, 2004].

3. Methods

3.1. Environmental Measurements

[9] Temperature/relative humidity probes (HMP35D, Vaisala, Helsinki, Finland) were installed at 3 and 6 m heights, and above-canopy net radiation was measured at a height of 3 m using a four-component radiometer (Model CNR 1, Kipp and Zonen, Delft, Netherlands) attached to a

horizontal boom extending 2 m from a small tripod tower. Also, we have upward and downward facing photosynthetically active radiation (PAR) sensors (LI-190, LI-COR Inc., Lincoln, NE). Ground heat flux was measured with five soil heat flux plates (REBS Inc., Seattle, WA) installed 8 cm below ground level under both intercanopy and undercanopy positions. Measurements of the rate of change of soil temperature above the heat flux plates (at 3 and 6 cm) allowed calculation of the soil heat flux at the surface using estimates of the specific heat of the soil layer estimated from measured bulk density and soil water content. Ground heat flux (G) was computed as an average of these five measurements.

[10] Precipitation (P) was quantified by a Belfort 0.2 m orifice weighing-recording gage [Goodrich *et al.*, 2008]. As a measure of hydrologic drought intensity we used the 12 month standardized precipitation index (SPI, <http://drought.unl.edu/monitor/spi.htm>). The SPI at this time scale reflects long-term precipitation pattern and closely resembles the Palmer Index and provides a strong comparative context to studies in other systems with widely differing seasonal precipitation patterns [McAuliffe and Hamerlynck, 2010].

[11] We measured volumetric soil water content (θ) using a variety of soil moisture probes in different profiles [Keefer *et al.*, 2008]. One profile located midslope on a north facing aspect was instrumented to measure θ at 5, 15, and 30 cm and another profile was located midslope on a south facing aspect to measure θ at 5, 15, 30, 50, 100, and 200 cm. There were three additional profiles of 5 and 15 cm near the flux tower. In this paper, we report on an average of all five profiles at 5 cm, two profiles for 30 cm, and only one profile for the 50 cm depth.

[12] To quantify the seasonality and variation in green biomass at the site, we used the NASA MODIS enhanced vegetation index (EVI [Huete *et al.*, 2002]). We used 250 m EVI data from collection 5 (ORNL DAAC, 2008) available as a 16 day composite over the period of 2000–2009. As an integrated measure of greenness over a season, we define

$$\text{EVI}^* = \int \text{EVI}(t) - \min[\text{EVI}(t)] dt, \quad (1)$$

where $\text{EVI}(t)$ is the interpolated daily EVI value from the 16 day values. The minimum EVI within the season is subtracted from all the daily values within that season and year before the integration in order to try and account for drifts in the (dry) baseline EVI value. Equation (1) is applied over the spring (February–May) and summer (July–November) growing seasons. We examine the average EVI and EVI^* over a 5×5 pixel box (1.25×1.25 km) and over a 41×41 pixel box (10.25×10.25 km) centered over the tower to examine how the vegetation response in the area immediately around the tower and the dominant influence on the fluxes, compared with the surrounding region.

[13] Vegetative canopy and ground cover was measured along paired 33 m line transects about 100 m west of the tower. Line intercepts of canopy cover were recorded and identified to species. Plant basal area was identified as *E. lehmanniana*, forbs, native bunchgrass, shrub, dead native grass, and dead shrub. Vegetation surveys were conducted from August–October during or shortly after vegetation cover peaked.

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 Inc., Logan, UT) and an open-path infrared gas analyzer (IRGA; LI-7500, LI-COR) were mounted at 6.4 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 1–2 months, the IRGA was zero- and span-calibrated using a $\text{CO}_2/\text{H}_2\text{O}$ -free gas, a standard $[\text{CO}_2]$ gas, and a dew point generator. Fluxes were later calculated off-line by 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 to account for a missing energy balance term associated with the water vapor flux [Paw *et al.*, 2000]. Fluxes measured when the wind was between 35° and 55° N (3.7% 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 compared 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 change in CO_2 storage term (ΔS) to F_C . Since CO_2 profile data were only available for about half of the 6 year record, the storage terms were estimated using only $[\text{CO}_2]$ from the IRGA at the tower top. This approximation did not introduce any appreciable errors as differences between half-hourly NEE with storage calculated using just the IRGA versus the profiler were essentially equivalent [$F_C + \Delta S_{\text{profile}} = 1.00(F_C + \Delta S_{\text{top}}) + 0.0006$, $R^2 = 0.99$, $p < 0.001$].

[16] The flux data were filtered for spikes, instrument malfunctions, and poor quality (representing 11.0% of the ET and 11.8% of NEE data). The rejection criteria used to screen data were rain events, out-of-range signals, and spikes with the standard deviation of $[\text{CO}_2]$, $[\text{H}_2\text{O}]$, and/or sonic temperature greater than two 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 measurements [Malhi *et al.*, 1998]. This occurred 13.8% of the daytime and 47.3% of the nighttime periods. 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 or year to year, so a value of 0.15 m s^{-1} was chosen as a conservatively high average. Daily mean ET values were calculated by first filling the gaps in the 30 min data using 14 day look-up tables of ET and incoming PAR averaged over $100 \mu\text{mol m}^{-2} \text{ s}^{-1}$ intervals and separated into before and after noon periods [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

Table 1. Seasonal and Annual Precipitation Totals Along With Long-Term Average Precipitation and Standard Deviation (mm)

	2004	2005	2006	2007	2008	2009	1964–2009
Winter (Dec–Mar)	79	72	12	61	22	39	75 (57)
Monsoon (Jun–Sep)	157	92	240	207	270	168	219 (61)
Annual Precipitation	295	162	274	313	312	246	345 (83)

heat flux (x , abscissa) and the sum of the sensible and latent heat fluxes (y , ordinate). The results are far from ideal ($y = 0.73x + 23.8$, $R^2 = 0.92$), but the ratio of the sum of turbulent fluxes to available energy was near unity on an annual basis, indicating storage terms may have been underestimated [Scott, 2010]. Scott [2010] compared annual sums of latent heat flux (not modified for closure) to the estimates of evaporation from the watershed water balance and found that latent heat flux averaged about ~10% less than the watershed estimate.

[18] We partitioned NEE into ecosystem photosynthesis or gross ecosystem production (GEP) and ecosystem respiration (R_{eco}). We determined 30-minute average R_{eco} 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 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 second-order polynomial fitted to morning or afternoon incoming PAR and NEE data on a 5 day moving window basis. GEP was determined by

$$GEP = R_{eco} - NEE. \quad (2)$$

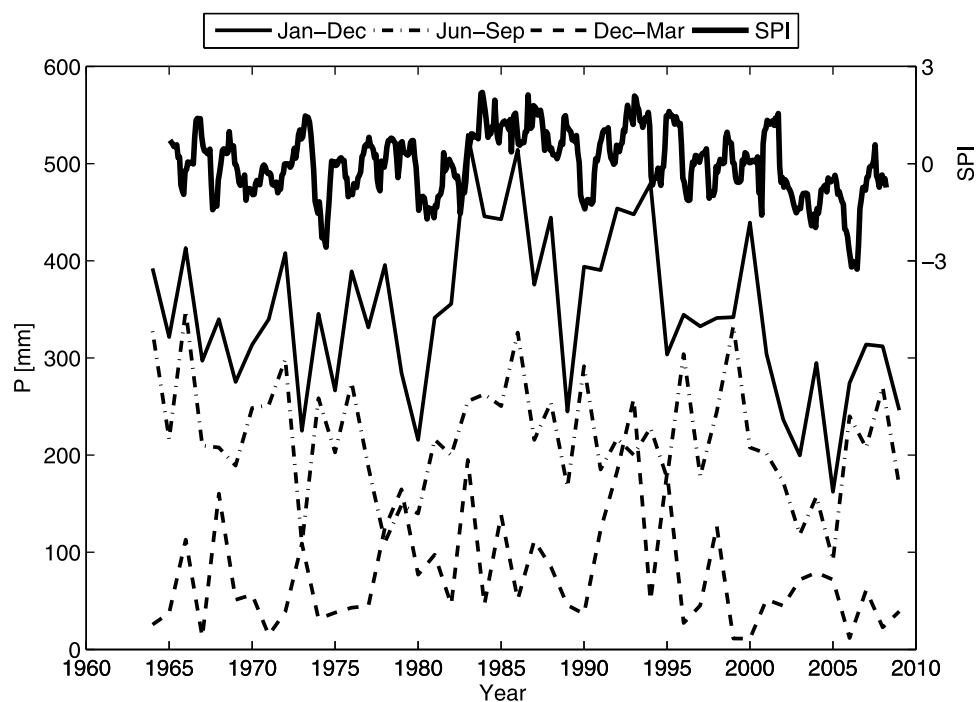
We used the standard sign convention for NEE with $NEE > 0$ indicating a net loss of CO_2 to the atmosphere (source) and $NEE < 0$ indicating CO_2 uptake by the ecosystem (sink). R_{eco} and GEP are always positive.

[19] Uncertainty in the flux measurements stem from random and systematic errors. Random errors associated with natural variations in atmospheric turbulence and the land surface are generally small (~5%) when data sets reach durations of a year or more [Baldocchi, 2008]. Systematic errors, including data processing methods (e.g., gap-filling methods, u^* filtering, etc.), the type of instrumentation (their frequency response and calibration), and instrumentation placement, are generally harder to quantify and larger than random errors [Lasslop et al., 2010]. A comprehensive analysis of the uncertainty in the measurements at this site was beyond the scope of the paper so we defer to the $\pm 10\%$ – 30% uncertainty range in yearly NEE found by others [Goulden et al., 1996; Hagen et al., 2006; Lasslop et al., 2010; Loescher et al., 2006; Moffat et al., 2007]. Thus, we emphasize the use of the annual sums of NEE and its components as comparative measures allowing us to determine shifts in ecosystem function from year to year, providing a better understanding of what may or may not have changed as the grassland underwent drought and vegetation transitions [Baldocchi, 2008; Lasslop et al., 2010].

4. Results and Discussion

4.1. Precipitation and Soil Moisture

[20] All years of this study had below average annual precipitation (Table 1). Except for year 2004, wintertime precipitation was always below average, especially in years 2006 and 2008. Monsoon precipitation was low in 2004 and 2009 and extremely so in 2005, while 2006 and 2008 had

**Figure 1.** Twelve month standardized precipitation index (SPI), yearly and seasonal precipitation totals for the Kendall grassland site.

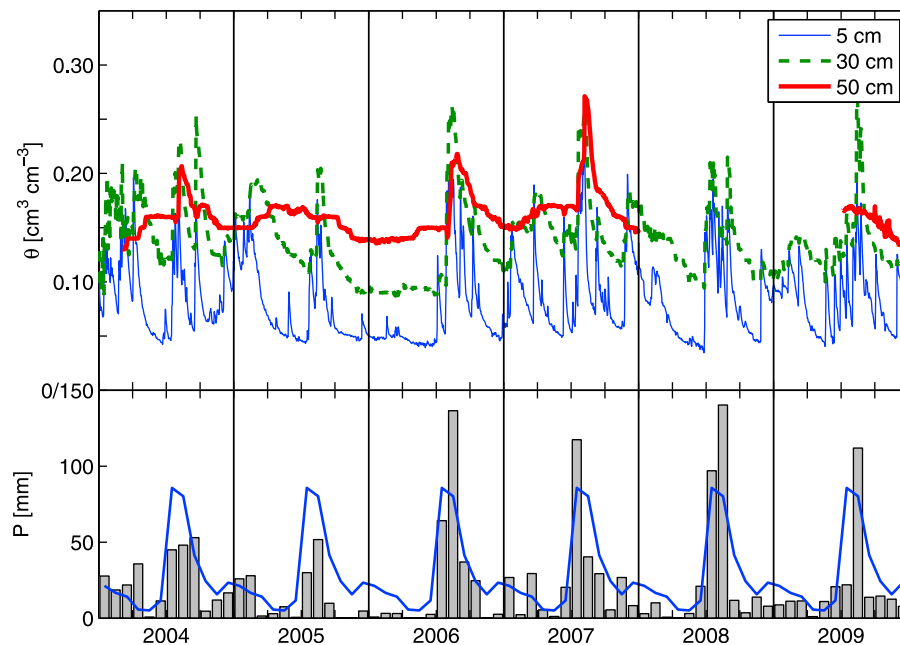


Figure 2. Volumetric soil moisture θ , monthly precipitation P (bars), and 1964–2009 monthly average precipitation. Soil moisture at 50 cm was not available in 2008 to mid-2009.

above average accumulations. Drought conditions as indicated by the 12 month SPI were extreme and without precedent in the spring of 2006 for the 1964–2008 rainfall record (Figure 1), and the low SPI reflects the cumulative effect of consecutively low monsoon totals in 2003, 2004, and 2005 and one of the driest winter and spring periods on record in 2006. While this drought during the turn of the 21st century has at times been severe, it is likely that precipitation conditions were similar during at least one period in the 20th century (1950s) as well as several in the previous millennia [Cook *et al.*, 2010]; however, this drought was combined with the hottest decade on record [Weiss *et al.*, 2009].

[21] Belowground, the mid-2004 to mid-2006 rainfall deficit was manifest in less-frequent positive departures of soil moisture from normally dry states (Figure 2). However, longer-term (multiyear) carryover effects of the drought are not distinguishable in terms of trends in the near-surface soil moisture state because of the frequent and prolonged dry periods that occur in nearly every year that reset the system back to its normal dry state. In the dry years of this study, infiltration was limited to the upper half meter of the soil column. However, in wetter years percolation exceeded this depth but was still limited to the upper meter of soil (data not shown). Shallow infiltration and normally dry soil moisture states are common throughout this region [Kurec and Small, 2007; Scott *et al.*, 2009]. More profound recharge of soil moisture at this site has occurred more typically in wet winter periods when the vegetation was dormant and the evaporative demand was reduced [Scott *et al.*, 2000].

4.2. Vegetation and Watershed Response

[22] The extreme drought conditions prior to the summer of 2006 were followed by large changes to the vegetation cover and composition in the grassland (Figure 3). Even

though summer rains in 2006 were above average (Table 1), native bunchgrass and shrub populations declined dramatically and were subsequently replaced by a flush of annuals (primarily *Allonia incarnata*, *Chamaesyce hyssopifolia*, *Kallstromieia grandiflora*, and *Mimulus* spp.) and perennial forbs (*Bahia absinthifolia* and *Evolvulus arizonicus*) and the nonnative Lehmann lovegrass thereafter. While the turn of the 21st century drought may not have had a higher rainfall deficit as the previous droughts in the last millennia, the combination of severe water limitation likely interacted with record temperatures and evaporative demand to make this event exceptionally lethal to the native bunchgrass community [Adams *et al.*, 2009; Weiss *et al.*, 2009]. In addition to being less sensitive to grazing compared to native bunchgrasses [Angel and McClaran, 2001], Lehmann lovegrass has extremely drought-resistant seeds [Hardegree and Emmerich, 1992] that can endure long dry periods and respond more effectively to postdrought rainfall compared to native grasses [Emmerich and Hardegree, 1996]. Taken together, these attributes likely facilitate Lehmann's rapid spread following prolonged drought [Angel and McClaran, 2001; Geiger and McPherson, 2005; McClaran and Anable, 1992].

[23] Probably not by coincidence, the large runoff events in 2006 from the small 1.9 ha watershed where this site is located resulted in a large transport of sediment from the site [Nearing *et al.*, 2007]. The three largest sediment transport events ever recorded in watershed occurred in 2006 and accounted for 42% of total 19 year sediment loss [Polyakov *et al.*, 2010]. In total, 1.6 t ha⁻¹ of suspended sediment was exported from the watershed in 2006. Sediment loss on the hillslopes within the footprint of the eddy covariance measurements have been shown to be as high as 8 t ha⁻¹ year⁻¹ as there is much less sediment transported out of the watershed than on the hillslopes due to a large flat swale at the base of hillslopes that slows flow and traps sediment

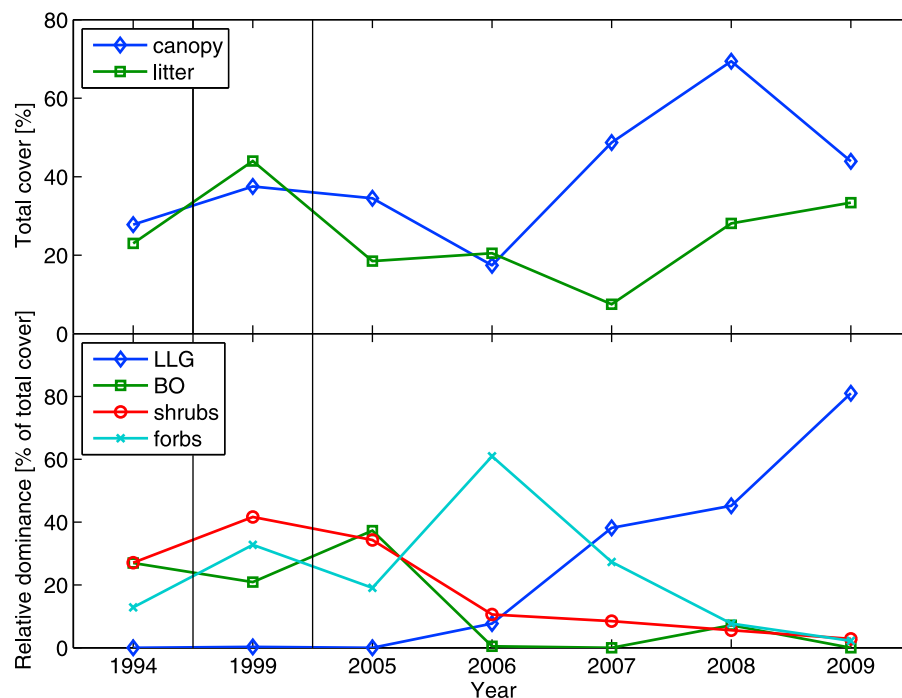


Figure 3. Total plant canopy and ground litter cover and the relative dominance of *E. lehmanniana* (LLG), *Bouteloua* spp. (BO), shrubs, and forbs. Vertical lines indicate discontinuous yearly sampling.

before reaching the outlet [Nearing *et al.*, 2005]. These runoff events, dominated by overland flow, and the low productivity of the grasses during the drought may have caused the minimum in plant litter cover measured in 2007

(Figure 3). Total carbon in the topsoil layer in this watershed is about 2% (1% organic), combined with a suspended sediment enrichment ratio of $2\times$ [Rhoton *et al.*, 2006] and sediment yields of 1.6 (watershed) to 8 (hillslopes) t ha^{-1}

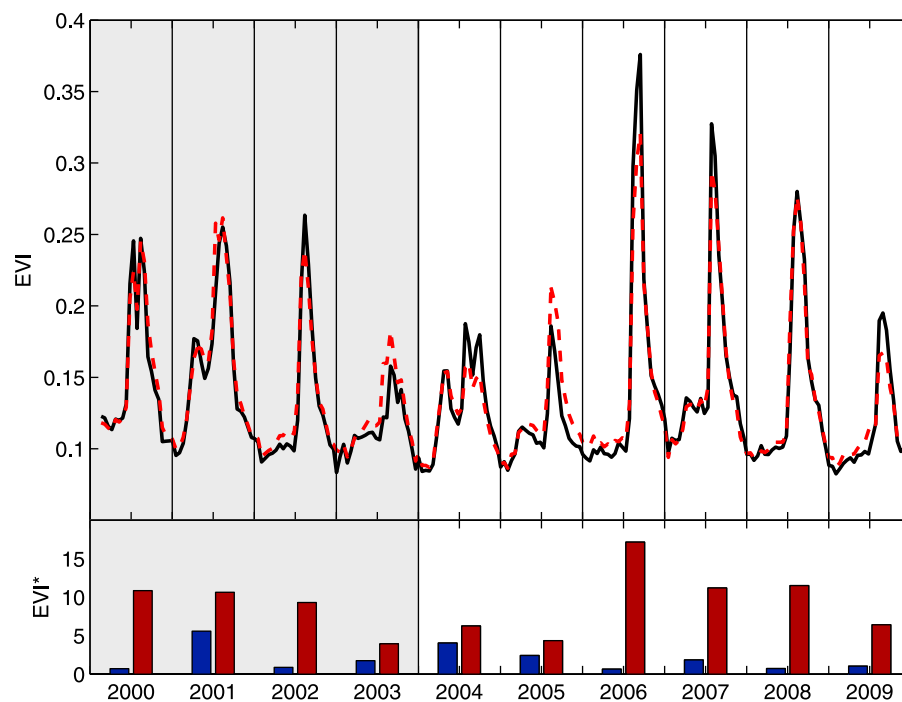


Figure 4. (top) 2000–2009 MODIS enhanced vegetation index (EVI) and (bottom) cumulative EVI (equation (1)) for the spring and summer growing seasons. The study was carried out in 2004–2009, 2000–2003 data (shaded) are shown to provide additional context. Data are the average of a 5×5 pixel box (1.25×1.25 km) (black solid line) and the average of a 41×41 pixel box (10.25×10.25 km) centered over the tower (red dashed line).

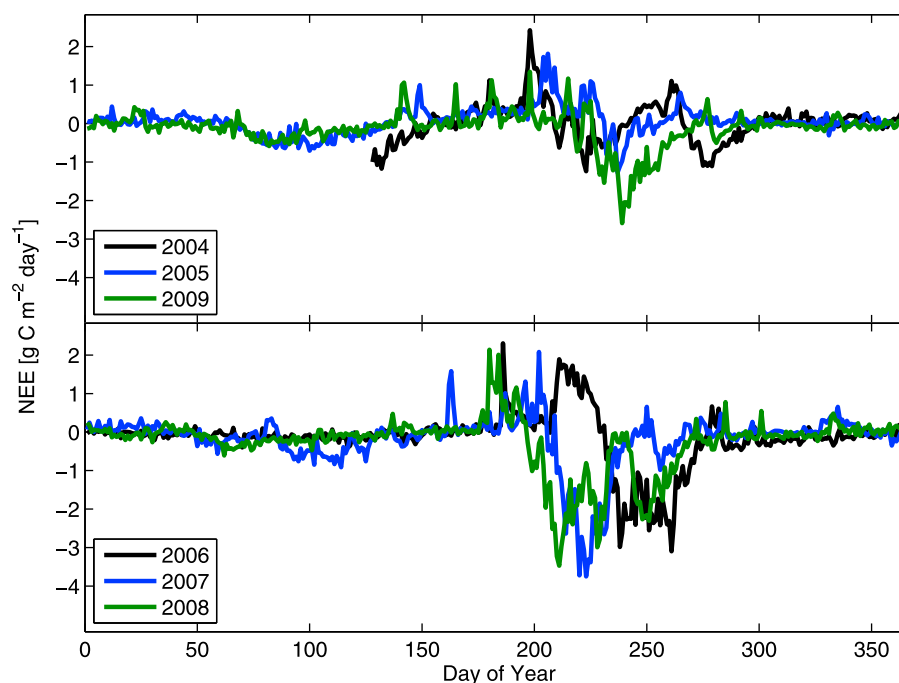


Figure 5. Daily net ecosystem exchange of CO₂ (NEE). The 3 years with the least monsoon rainfall (2004, 2005, 2009) are separated from the rest for comparison purposes.

results in 6–32 g C m⁻² moving away from the hilltops and the eddy covariance footprint. This rough approximation illustrates that such large erosion events likely resulted in significant movement of carbon bound up in the soil organic matter, plant litter, and soil carbonates away from these upland regions [Izaurrealde *et al.*, 2007; Lal, 2003] that was not quantified by the eddy covariance measurements.

[24] Canopy cover peaked in 2008 while litter cover continued to recover and lovegrass dominance increased through 2009 (Figure 3). Moran *et al.* [2009] estimated that the ratio of total bare soil evaporation to total ET for the summer growing season doubled when comparing two similar rainfall years prior and after the peak drought (from 26% in 2002 to 60% in 2007), but their estimates did not extend beyond 2007. They speculated that the increase in soil evaporation was due to the change in ecosystem composition with decreased plant basal area, litter cover, and possibly root water extraction following fewer roots in immature, establishing bunchgrasses.

[25] The vegetation responses following drought were also apparent in the MODIS data (Figure 4). Summertime EVI was much smaller in 2003–2005 and 2009, reflecting the meager monsoon rainfall in those years (Table 1). EVI rebounded in 2006 and decreased slightly in 2007 and 2008, though still higher than EVI in 2000–2002 before the peak drought conditions. Peak or integrated summer EVI* does not correspond well with the total cover of the vegetation transects, which may indicate the lack of spatial representativeness of the transect data or the fact that the different growth forms and ages of the vegetation (grasses to herbs, older grasses to young ones, high litter to low litter) affect EVI differently [Glenn *et al.*, 2008]. This sequence in vegetation response describes the strongly nonlinear biological responses to climate variability where drought causes the mortality of native grasses that are generally resistant to

invasion, followed by a low-resistance intermediate forb-dominated vegetation community, and ending the general displacement of all species by an invasive grass. The occurrence of drought induced community changes will likely increase with continued exotic introductions and projections of future climate changes.

4.3. Net Carbon Dioxide Exchange

[26] Periods of negative NEE (indicating net ecosystem uptake) were smaller in magnitude and spanned a shorter duration in dry summer years (2004, 2005, 2009) compared to 2006–2008 (Figure 5). Sufficient cool season precipitation (2004, 2005, 2007, and even 2009, Table 1) appeared to spark a small springtime growing season with a net uptake of CO₂ that apparently ended with the hot and dry conditions common in May and June. The bulk of the ecosystem production, however, occurred in the summer monsoon. The onset of the monsoon always started with an increase in NEE, indicating a large increase in respiration, which was followed by a decrease in NEE as vegetation uptake eventually caught up to, and then exceeded, respiratory losses. This flush of respiration is characteristic of pulse-driven ecosystems and is composed of both heterotrophic (increased microbial activity due to soil wetting) and autotrophic sources (fine root growth, leaf flush) [Huxman *et al.*, 2004b; Scott *et al.*, 2004, 2009; Veenendaal *et al.*, 2004]. NEE was especially large and positive at the 2006 monsoon onset and may have been due to respiration that was stimulated by the preceding drought [Arnone *et al.*, 2008]. Such a response was also observed at a nearby savanna site [Scott *et al.*, 2009].

[27] Annual NEE totals ranged from -98 to 21 g C m⁻² (Figure 6, Table 2). Total NEE from 8 May to 31 December in 2004 was +4 g C m⁻² but was not quantified annually because monitoring did not begin until late spring. How-

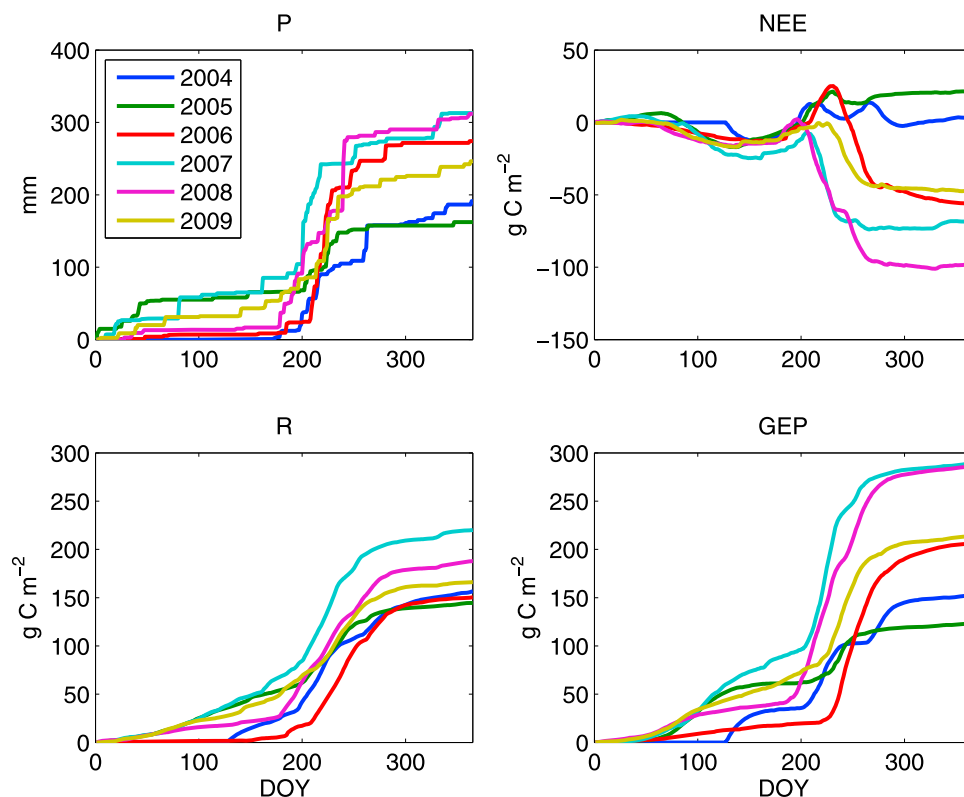


Figure 6. Cumulative precipitation (P), net ecosystem exchange (NEE), respiration (R_{eco}), and gross ecosystem production (GEP). Cumulative totals for 2004 start on DOY 128.

ever, NEE values measured at the May 2004 start date were the most negative for all springtime fluxes, and 2004 had the highest winter precipitation totals (Table 1) so it is likely that total NEE in 2004 also resulted in a small net uptake. The poor monsoons of 2004 and 2005 both resulted in the ecosystem losing more CO_2 than it gained in this period (Figure 6) whereas the average-to-good monsoons (2006–2008) all resulted in net gains. Interestingly, the 2009 summer growing season resulted in a net uptake of carbon even though rainfall was significantly below average and comparable to 2004.

[28] The annual carbon sink/source status for this grassland was much more responsive to summer rainfall alone and did not appear to be as adversely effected by the 6 year series of below-average annual precipitation as a nearby grassland that was invaded by woody plants [Scott *et al.*, 2009]. The carbon sink/source status of grasslands in other parts of the world with very different climates have also been shown to be closely linked to whether precipitation for the growing season was below or above average [Aires *et al.*, 2008; Flanagan *et al.*, 2002; Kjelgaard *et al.*, 2008], though the status of some Mediterranean and annual grass ecosystems has been more closely tied to rainfall timing [Chou *et al.*, 2008; Xu and Baldocchi, 2004].

[29] The results of this study do not confirm the typical large net annual effluxes of CO_2 that were reported for this site from 1997 through 2000 by Emmerich [2003] or at a nearby Chihuahuan desert grassland from 1996 through 2001 by Mielnick *et al.* [2005]. Emmerich [2003] had speculated that this was due to the inorganic cycling of CO_2 as the site has large amounts of carbonates in the soil. His

measurements were made using the Bowen ratio technique, and a side-by-side comparison with our eddy covariance system revealed considerable discrepancy in both ET and NEE (similar to the work of Alfieri *et al.* [2009]) with much more CO_2 release in the dry seasons and uptake in the wet seasons for the Bowen ratio (data not shown). We have found that annual ET estimated using the eddy covariance system comes closer (within 6% for 2005–2007) to that estimated using the precipitation, runoff, and change in soil moisture storage measurements compared to those made with the Bowen ratio (within 25% for same period), but we did not have an independent measure of NEE to do a similar comparison.

4.4. Respiration and Production

[30] We found a very good correspondence of cumulative R_{eco} and GEP fluxes to seasonal rainfall amounts (Figure 6). The years and seasons with the highest rainfall had the highest R_{eco} and GEP ; spring and summer R_{eco} and GEP totals were significantly correlated with winter and summer rainfall, respectively ($r > 0.91$ – 0.94 , $p < 0.05$ in all cases). Summer respiration was correlated with the number of rainy days ($r =$

Table 2. Yearly Precipitation (mm) and CO_2 Fluxes ($g\ C\ m^{-2}$) for Complete Years

	2005	2006	2007	2008	2009
Precipitation	162	274	313	312	246
NEE	21	−55	−69	−98	−47
R_{eco}	145	150	220	188	166
GEP	123	206	289	286	213

Table 3. Significant Correlation Coefficients for February–November Fluxes With Environmental Variables ($p < 0.05$)

	$\theta_{5\text{cm}}$	$\theta_{30\text{cm}}$	$\theta_{50\text{cm}}$	T_a	PAR
R_{eco}	0.68	0.64	0.51	0.45	0.14
GEP	0.53	0.57	0.48	0.28	0.15
ET	0.76	0.65	0.48	NS	-0.11

0.85, $p = 0.03$). Cumulative GEP always exceeded R_{eco} by the end of spring resulting in a small net uptake even following the driest winter/spring in 2006. However in the monsoon, R_{eco} exceeded GEP in the dry summers of 2004 and 2005 but not in 2009 after the vegetation change. Analyzing results from around the world, *Schwalm et al.* [2010] found that sensitivity of assimilation (i.e., decrease) exceeds that of respiration to drought, especially at nonforested sites. We also found the growing season sensitivity (or slope) of total GEP to precipitation ($\text{GEP} = 0.96 \pm 0.16P - 17 \pm 29$, $\alpha = 0.05$) exceeded that of respiration ($R_{\text{eco}} = 0.37 \pm 0.05P + 57 \pm 9$, $\alpha = 0.05$).

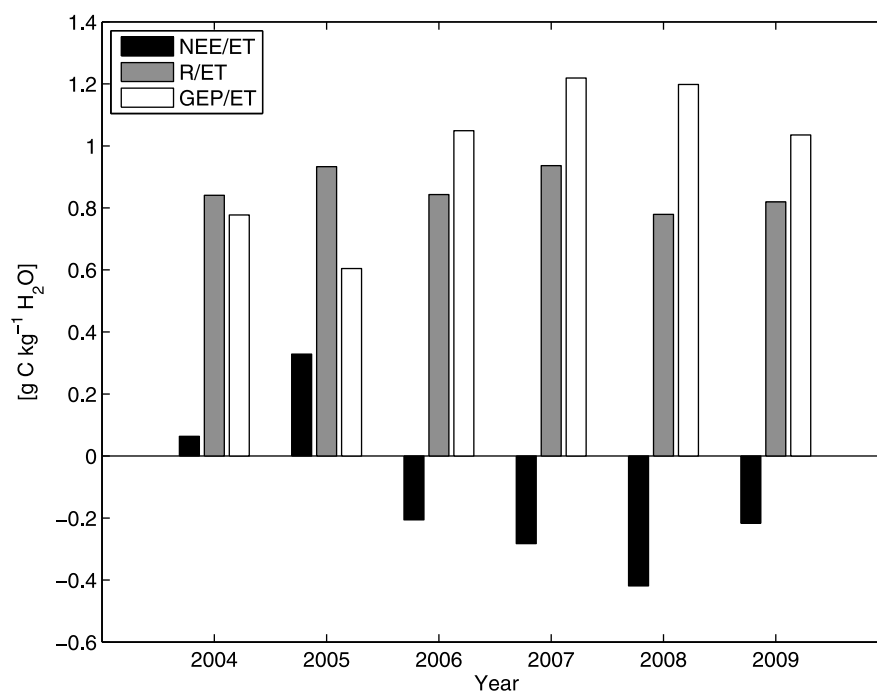
[31] To examine the influence of environmental forcing variables, we calculated correlations coefficients between daily values of nonwinter (February–November) carbon dioxide and water fluxes with θ at 5, 30, and 50 cm, air temperature (T_a), and PAR. We found significant correlations for R_{eco} decreased with soil moisture depth while those for GEP peaked at 30 cm (Table 3). They both shared a weaker relationship with T_a and even weaker for PAR. On the other hand, ET was most correlated with moisture at the shallowest depth and also very slightly anticorrelated with PAR (lower ET and higher PAR in the dry season). The higher correlation of GEP and $\theta_{30\text{cm}}$ revealed that the plant activity was more strongly linked to deeper root zone water content. The correlation of R_{eco} with θ at all depths and T_a

likely reveals the importance of both heterotrophic and autotrophic respiration and the strong influence of temperature on these rates. The higher correlation of ET with $\theta_{5\text{cm}}$ along with GEP correlation peaking at $\theta_{30\text{cm}}$ provides evidence that bare soil evaporation is an important part of total ET [*Moran et al.*, 2009]. The strong relationships between shallow soil moisture and mass and energy exchange at this site mirrors those found at other sites in the region [*Kurc and Small*, 2007; *Scott et al.*, 2009].

4.5. Effects of Vegetation Change on NEE

[32] Given the strong coupling across the years between seasonal precipitation and the components of NEE, the effects of the vegetation change on the carbon exchange dynamics were not immediately obvious. Because water is the dominant driver of the system, we normalized the components of NEE by the total ET and found that the ratio R_{eco}/ET was relatively constant in all six years. However, GEP/ET , a measure of ecosystem water use efficiency (WUE^*), plummeted in 2005 and then increased in 2006 and 2007 and decreased somewhat in 2009, but not to pre-2006 levels (Figure 7). On a net exchange basis, NEE/ET continued to decrease to 2008 after peaking in 2005. These values of WUE^* are on the low end of the $1\text{--}6 \text{ g C kg}^{-1} \text{ H}_2\text{O}$ range surveyed by *Beer et al.* [2009], probably due to the low LAI and large amount of ET that is lost via soil evaporation ($\sim 25\text{--}60\%$ [*Moran et al.*, 2009]) in this ecosystem.

[33] To further evaluate if the change in community composition altered carbon cycling in this ecosystem, we compared the grassland response in 2004 and 2009, years with comparably low summer rainfall. The timing of the summer rainfall was different in these years (Figure 2) so it is important to compare across similar environmental and

**Figure 7.** Ratios of total June–November net ecosystem exchange (NEE), respiration (R_{eco}), and gross ecosystem production (GEP) divided by evapotranspiration (ET).

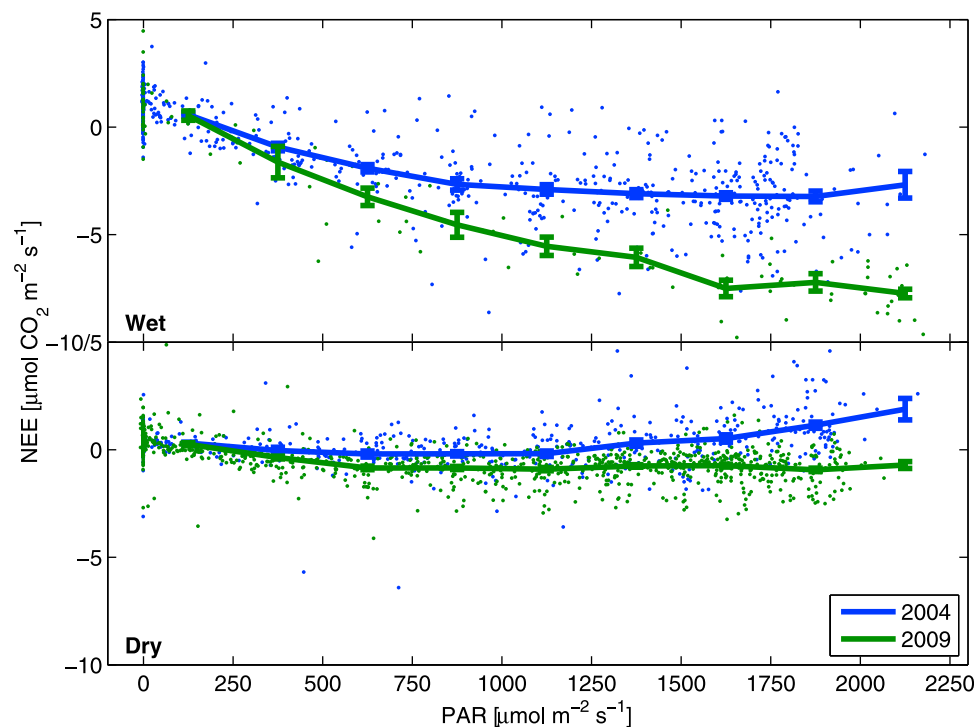


Figure 8. Ecosystem light response curves for wet ($\theta_{30\text{cm}} > 0.18$) and dry monsoon ($\theta_{30\text{cm}} < 0.14$) summer periods following peak in GEP.

phenological conditions. Quantifying the response of NEE to PAR levels for both wet and dry periods following the peak in GEP (ensuring maximum phenological response) revealed that the NEE was more negative across almost all light levels for both wet and dry conditions in 2009 (Figure 8). At high light levels the response was clearly different, and it is interesting to note the increase in NEE in the dry periods of 2004 while 2009 stayed flat. This behavior is consistent with the increase in canopy cover that followed the invasion (Figure 3) and lovegrass' reputation as being more drought tolerant [Hamerlynck *et al.*, 2010].

5. Conclusions

[34] The goal of this study was to determine how NEE was affected by drought and vegetation change in a semidesert grassland. We investigated the seasonal variation in NEE and its controls by environmental variation in water and energy input. Conclusions drawn from 6 years of monitoring revealed:

[35] 1. The cumulative effects or “memory” of meteorological drought are difficult to detect in the near-surface soil moisture state in this type of dry system because soil moisture is consistently driven to very low levels due to the high evaporative demand in the premonsoon season. Nevertheless, years of paltry rainfall and record high evaporative demand within this drought resulted in widespread mortality of most native bunchgrass and shrub species at this site.

[36] 2. NEE was markedly suppressed in drought years and cumulative NEE showed perhaps a small uptake in 2004 and net release in 2005. After the large die-off of native grasses, the remaining years (2006–2009) all had a net uptake of CO_2 even though summer rainfall was below

average in 2007 and 2009. The transition to forb and then lovegrass dominance was accompanied by large runoff and erosion events that likely transported significant amounts of carbon out of the tower footprint.

[37] 3. Rainfall mediated by soils is the key driver to water and CO_2 fluxes in this semiarid ecosystem. Strong correlations of GEP, R_{eco} , and ET with daily values and near-surface soil moisture were found. Even with only a 6 year data set, we also found significant correlations between growing season assimilation and total respiration both in the spring and summer. The sensitivity of seasonal GEP to P was higher than R_{eco} to P , resulting in net carbon uptake increasing with greater water input.

[38] 4. Carbon fluxes normalized by ET for the summer growing season revealed that R_{eco}/ET was not altered by drought or vegetation composition, while GEP/ET (WUE^*) increased after replacement of the native bunchgrasses. Increased water use efficiency was partly a function of higher summer rainfall, but comparison between the dry 2004 and 2009 summers showed greater net carbon gains in the lovegrass-dominated system, especially under higher levels of light and water limitation.

[39] These findings contradict our hypothesis that a shift in community composition from a diverse C_4 bunchgrass assemblage to dominance by an exotic C_4 bunchgrass would not affect behavior of ecosystem carbon dioxide exchange. While it is not clear if leaf-level ecophysiology of *E. lehmanniana* differs from native Southwest grasses [Hamerlynck *et al.*, 2010; Huxman *et al.*, 2004a; Potts *et al.*, 2006], the effects of lovegrass invasion to ecosystem functioning were readily apparent in this study.

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References

- Adams, D. K., and A. C. Comrie (1997), The North American Monsoon, *Bull. Am. Meteorol. Soc.*, **78**, 2197–2213.
- Adams, H. D., M. Guardiola-Claramonte, G. A. Barron-Gafford, J. C. Villegas, D. D. Breshears, C. B. Zou, P. A. Troch, and T. E. Huxman (2009), Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought, *Proc. Natl. Acad. Sci.*, **106**, 7063–7066, doi:10.1073/pnas.0901438106.
- Aires, L. M. I., C. A. Pio, and J. S. Pereira (2008), Carbon dioxide exchange above a Mediterranean C3/C4 grassland during two climatologically contrasting years, *Global Change Biol.*, **14**, 539–555, doi:10.1111/j.1365-2486.2007.01507.x.
- Alfieri, J. G., P. D. Blanken, D. Smith, and J. Morgan (2009), Concerning the measurement and magnitude of heat, water vapor, and carbon dioxide exchange from a semiarid grassland, *J. Clim.*, **48**, 982–996, doi:10.1175/2008JAMC1873.1.
- Allen, C. D., and D. D. Breshears (1998), Drought-induced shift of a forest-woodland ecotone: Rapid landscape response to climate variation, *Proc. Natl. Acad. Sci. USA*, **95**, 14,839–14,842.
- Anable, M. E., M. P. McClaran, and G. B. Ruyle (1992), Spread of introduced Lehmann lovegrass *Eragrostis lehmanniana* Nees. in Southern Arizona, USA, *Biol. Conserv.*, **61**, 181–188.
- Angel, D. L., and M. P. McClaran (2001), Long-term influences of livestock management and a non-native grass on grass dynamics in the Desert Grassland, *J. Arid Environ.*, **49**, 507–520.
- Arnone, J. A., III, et al. (2008), Prolonged suppression of ecosystem carbon dioxide uptake after an anomalously warm year, *Nature*, **455**, 383–386, doi:10.1038/nature07296.
- Arriaga, L., A. E. Castellanos V, E. Moreno, and J. Alarcon (2004), Potential ecological distribution of alien invasive species and risk assessment: A case study of buffel grass in arid regions of Mexico, *Conserv. Biol.*, **18**, 1504–1514, doi:10.1111/j.1523-1739.2004.00166.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.
- Beer, C., et al. (2009), Temporal and among-site variability of inherent water use efficiency at the ecosystem level, *Global Biogeochem. Cycles*, **23**, GB2018, doi:10.1029/2008GB003233.
- Bock, C., J. Bock, K. Jepson, and J. Ortega (1986), Ecological effects of planting African lovegrasses in Arizona, *Natl. Geogr. Res.*, **2**, 456–463.
- Bowers, J. E. (2005), Effects of drought on shrub survival and longevity in the northern Sonoran Desert, *J. Torrey Bot. Soc.*, **132**, 421–431.
- 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**, 1815–1822, doi:10.1111/j.1365-2486.2006.01232.x.
- Breckenfeld, D. J., W. A. Svetlik, and C. E. McGuire (1995), Soil Survey of Walnut Gulch Experimental Watershed, USDA-Soil Conservation Service and Agricultural Research Service Special Report, 131 pp, Soil Conservation Service, U.S. Department of Agriculture Tucson, AZ.
- Breshears, D. D., et al. (2005), Regional vegetation die-off in response to global-change-type drought, *Proc. Natl. Acad. Sci. USA*, **102**, 15,144–15,148, doi:10.1073/pnas.0505734102.
- Chou, W. W., W. L. Silver, R. D. Jackson, A. W. Thompson, and B. Allen-Diaz (2008), The sensitivity of annual grassland carbon cycling to the quantity and timing of rainfall, *Global Change Biol.*, **14**, 1382–1394, doi:10.1111/j.1365-2486.2008.01572.x.
- Cook, E. R., R. Seager, R. R. Heim Jr, R. S. Vose, C. Herweijer, and C. Woodhouse (2010), Megadroughts in North America: Placing IPCC projections of hydroclimatic change in a long-term palaeoclimate context, *J. Quat. Sci.*, **25**, 48–61, doi:10.1002/jqs.1303.
- Dukes, J., and H. Mooney (2004), Disruption of ecosystem processes in western North America by invasive species, *Rev. Chilena Hist. Nat.*, **77**, 411–437.
- Emmerich, W. E. (2003), Carbon dioxide fluxes in a semiarid environment with high carbonate soils, *Agric. For. Meteorol.*, **116**(1–2), 91–102.
- Emmerich, W. E., and S. P. Hardegree (1996), Partial and full dehydration impact on germination of four warm season grasses, *J. Range Manage.*, **49**, 355–360.
- 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.
- Fay, P., J. Carlisle, A. Knapp, J. Blair, and S. Collins (2003), Productivity responses to altered rainfall patterns in a C4-dominated grassland, *Oecologia*, **137**(2), 245–251, doi:10.1007/s00442-003-1331-3.
- Fay, P., D. Kaufman, J. Nippert, J. Carlisle, and C. Harper (2008), Changes in grassland ecosystem function due to extreme rainfall events: implications for responses to climate change, *Global Change Biol.*, **14**, 1600–1608, doi:10.1111/j.1365-2486.2008.01605.x.
- Flanagan, L. B., L. A. Wever, and P. J. Carlson (2002), Seasonal and inter-annual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland, *Global Change Biol.*, **8**, 599–615, doi:10.1046/j.1365-2486.2002.00491.x.
- Geiger, E. L., and G. R. McPherson (2005), Response of semi-desert grasslands invaded by non-native grasses to altered disturbance regimes, *J. Biogeogr.*, **32**, 895–902, doi:10.1111/j.1365-2699.2004.01235.x.
- Glenn, E. P., A. R. Huete, P. L. Nagler, and S. G. Nelson (2008), Relationship between remotely-sensed vegetation indices, canopy attributes and plant physiological processes: What vegetation indices can and cannot tell us about the landscape, *Sensors*, **8**, 2136–2160, doi:10.3390/s8042136.
- Goodrich, D. C., T. O. Keefer, C. L. Unkrich, M. H. Nichols, H. B. Osborn, J. J. Stone, and J. R. Smith (2008), Long-term precipitation data base, Walnut Gulch Experimental Watershed, Arizona, United States, *Water Resour. Res.*, **44**, W05S04, doi:10.1029/2006WR005782.
- 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.
- 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**(8), D08S03, doi:10.1029/2005JD006154.
- Hamerlynck, E. P., R. L. Scott, M. S. Moran, T. O. Keefer, and T. E. Huxman (2010), Growing season ecosystem and leaf-level gas exchange of an exotic and native semiarid bunchgrass, *Oecologia*, **163**, 561–570, doi:10.1007/s00442-009-1560-1.
- Hardegree, S. P., and W. E. Emmerich (1992), Effect of matric-priming duration and priming water potential on germination of four grasses, *J. Exp. Bot.*, **43**, 233–238.
- Heisler-White, J., A. Knapp, and E. Kelly (2008), Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland, *Oecologia*, **158**, 129–140, doi:10.1007/s00442-008-1116-9.
- Heisler-White, J., J. Blair, E. Kelly, K. Harmaney, and A. Knapp (2009), Contingent productivity responses to more extreme rainfall regimes across a grassland biome, *Global Change Biol.*, **15**, 2894–2904, doi:10.1111/j.1365-2486.2009.01961.x.
- Hereford, R., R. H. Webb, and C. I. Longpré (2006), Precipitation history and ecosystem response to multidecadal precipitation variability in the Mojave desert region, 1893–2001, *J. Arid Environ.*, **67**, 13–34, doi:10.1016/j.jaridenv.2006.09.019.
- 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(1–2), doi:10.1016/S0034-4257(02)00096-2.
- Hupy, C. M., W. G. Whitford, and E. C. Jackson (2004), The effect of dominance by an alien grass species, Lehmann lovegrass, *Eragrostis lehmanniana*, on faunal-pedoturbation patterns in North American Desert grasslands, *J. Arid Environ.*, **58**, 321–334, doi:10.1016/j.jaridenv.2003.08.004.
- Huxman, T. E., J. M. Cable, D. D. Ignace, J. A. Eilts, N. B. English, J. Weltzin, and D. G. Williams (2004a), Response of net ecosystem gas exchange to a simulated precipitation pulse in a semi-arid grassland: The role of native versus non-native grasses and soil texture, *Oecologia*, **141**, 295–305, doi:10.1007/s00442-003-1389-y.
- 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 (2004b), Precipitation pulses and carbon fluxes in semiarid and arid ecosystems, *Oecologia*, **141**, 254–268, doi:10.1007/s00442-004-1682-4.
- Huxman, T. E., B. P. Wilcox, D. D. Breshears, R. L. Scott, K. A. Snyder, E. E. Small, K. Hultine, W. T. Pockman, and R. B. Jackson (2005), Ecohydrological implications of woody plant encroachment, *Ecology*, **86**, 308–319.
- Izaurrealde, R. C., J. R. Williams, W. M. Post, A. M. Thomson, W. B. McGill, L. B. Owens, and R. Lal (2007), Long-term modeling of soil C erosion and sequestration at the small watershed scale, *Clim. Change*, **80**, 73–90, doi:10.1007/s10584-006-9167-6.

- Jackson, T. J., M. S. Moran, and P. E. O'Neill (2008), Introduction to Soil Moisture Experiments 2004 (SMEX04) Special Issue, *Remote Sens. Environ.*, **112**, 301–303, doi:10.1016/j.rse.2007.01.021.
- Jenerette, G. D., R. L. Scott, and A. R. Huete (2010), Functional differences between summer and winter season rain assessed with MODIS-derived phenology in a semi-arid region, *J. Veg. Sci.*, **21**, 16–30, doi:10.1111/j.1654-1103.2009.01118.x.
- Keefer, T. O., M. S. Moran, and G. B. Paige (2008), Long-term meteorological and soil hydrology data base, Walnut Gulch Experimental Watershed, Arizona, United States, *Water Resour. Res.*, **44**, W05S07, doi:10.1029/2006WR005702.
- King, D. M., S. M. Skirvin, C. D. Holifield Collins, M. S. Moran, S. H. Biedendener, M. R. Kidwell, M. A. Weltz, and A. Diaz-Gutierrez (2008), Assessing vegetation change temporally and spatially in south-eastern Arizona, *Water Resour. Res.*, **44**, W05S15, doi:10.1029/2006WR005850.
- Kjelgaard, J. F., J. L. Heilman, K. J. McInnes, M. K. Owens, and R. H. Kamps (2008), Carbon dioxide exchange in a subtropical, mixed C3/C4 grassland on the Edward Plateau, Texas, *Agric. For. Meteorol.*, **148**, 953–963, doi:10.1016/j.agrformet.2008.01.006.
- Kljun, N., P. Calanca, M. W. Rotach, and H. P. Schmid (2004), A simple parameterisation for flux footprint predictions, *Boundary Layer Meteorol.*, **112**, 503–523.
- 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.
- Kustas, W. P., and D. C. Goodrich (1994), Monsoon '90 multidisciplinary experiment, *Water Resour. Res.*, **30**, 1211–1225.
- Lal, R. (2003), Soil erosion and the global carbon budget, *Environ. Int.*, **29**(4), 437–450.
- Lasslop, G., M. Reichstein, D. Papale, A. Richardson, A. Arneeth, A. Barr, P. Stoy, and G. Wohlfahrt (2010), Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: Critical issues and global evaluation, *Global Change Biol.*, **16**, 187–208, doi:10.1111/j.1365-2486.2009.02041.x.
- 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.
- 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**(D24), 31,593–31,612, doi:10.1029/98JD02647.
- McAuliffe, J. R., and E. P. Hamerlynck (2010), Perennial plant mortality in the Sonoran and Mojave Deserts in response to severe, multi-year drought, *J. Arid Environ.*, **74**, 885–896, doi:10.1016/j.jaridenv.2010.01.001.
- McClaran, M. P., and M. E. Anable (1992), Spread of introduced Lehmann lovegrass along a grazing intensity gradient, *J. Appl. Ecol.*, **29**, 92–98.
- Mielnick, P., W. A. Dugas, K. Mitchell, and K. Havstad (2005), Long-term measurements of CO₂ flux and evapotranspiration in a Chihuahuan desert grassland, *J. Arid Environ.*, **60**, 423–436, doi:10.1016/j.jaridenv.2004.06.001.
- Miriti, M. N., S. Rodriguez-Buritica, S. J. Wright, and H. F. Howe (2007), Episodic death across species of desert shrubs, *Ecology*, 32–36.
- Moffat, A. M., et al. (2007), Comprehensive comparison of gap-filling techniques for eddy covariance net carbon fluxes, *Agric. For. Meteorol.*, **147**, 209–232, doi:10.1016/j.agrformet.2007.08.011.
- Moran, M. S., R. L. Scott, E. P. Hamerlynck, K. N. Green, W. E. Emmerich, and C. D. Holifield Collins (2009), Soil evaporation response to Lehmann lovegrass (*Eragrostis lehmanniana*) invasion in a semiarid watershed, *Agric. For. Meteorol.*, **149**, 2133–2142, doi:10.1016/j.agrformet.2009.03.018.
- Nearing, M. A., A. Kimoto, M. H. Nichols, and J. C. Ritchie (2005), Spatial patterns of soil erosion and deposition in two small, semiarid watersheds, *J. Geophys. Res.*, **110**, F04020, doi:10.1029/2005JF000290.
- Nearing, M. A., M. H. Nichols, J. J. Stone, K. G. Renard, and J. R. Simanton (2007), Sediment yields from unit-source semiarid watersheds at Walnut Gulch, *Water Resour. Res.*, **43**, W06426, doi:10.1029/2006WR005692.
- Nouvellon, Y., et al. (2001), Coupling a grassland ecosystem model with Landsat imagery for a 10-year simulation of carbon and water budgets, *Remote Sens. Environ.*, **78**, 131–149, doi:10.1016/S0034-4257(01)00255-3.
- 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.
- Polyakov, V. O., M. A. Nearing, J. J. Stone, E. P. Hamerlynck, M. H. Nichols, C. D. Holifield-Collins, and R. L. Scott (2010), Runoff and erosional responses to a drought-induced shift in a desert grassland community composition, *J. Geophys. Res.*, doi:10.1029/2010JG001386, in press.
- 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**, 849–860, doi:10.1111/j.1469-8137.2006.01732.x.
- Prater, M. R., and E. H. DeLucia (2006), Non-native grasses alter evapotranspiration and energy balance in Great Basin sagebrush communities, *Agric. For. Meteorol.*, **139**, 154–163, doi:10.1016/j.agrformet.2006.08.014.
- 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**, 1424–1439, doi:10.1111/j.1365-2486.2005.001002.x.
- Renard, K. G., M. H. Nichols, D. A. Woolhiser, and H. B. Osborn (2008), A brief background on the U. S. Department of Agriculture Agricultural Research Service Walnut Gulch Experimental Watershed, *Water Resour. Res.*, **44**, W05S02, doi:10.1029/2006WR005691.
- Rhoton, F. E., W. E. Emmerich, D. C. Goodrich, S. N. Miller, and D. S. McChesney (2006), Soil geomorphological characteristics of a semiarid watershed: Influence on carbon distribution and transport, *Soil Sci. Soc. Am. J.*, **70**, 1532–1540, doi:10.2136/sssaj2005.0239.
- Saleska, S. R., et al. (2003), Carbon in Amazon forests: Unexpected seasonal fluxes and disturbance-induced losses, *Science*, **302**(5650), 1554–1557, doi:10.1126/science.1091165.
- Schwalm, C. R., et al. (2010), Assimilation exceeds respiration sensitivity to drought: A FLUXNET synthesis, *Global Change Biol.*, **16**, 657–670, doi:10.1111/j.1365-2486.2009.01991.x.
- Scott, R. L. (2010), Using watershed water balance to evaluate the accuracy of eddy covariance evaporation measurements for three semiarid ecosystems, *Agric. For. Meteorol.*, **150**, 219–225, doi:10.1016/j.agrformet.2009.11.002.
- 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**(8), 2233–2247, doi:10.1029/2000WR900116.
- Scott, R. L., E. A. Edwards, W. J. Shuttleworth, T. E. Huxman, C. Watts, and D. C. Goodrich (2004), Interannual and seasonal variation in fluxes of water and carbon dioxide from a riparian woodland ecosystem, *Agric. For. Meteorol.*, **122**, 65–84, doi:10.1016/j.agrformet.2003.09.001.
- 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**, 311–324, doi:10.1111/j.1365-2486.2005.01093.x.
- 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.
- 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.
- Weiss, J. L., C. L. Castro, and J. T. Overpeck (2009), Distinguishing Pronounced Droughts in the Southwestern United States: Seasonality and Effects of Warmer Temperatures, *J. Clim.*, **22**, 5918–5932, doi:10.1111/j.1365-2486.2003.00699.x.
- Weltz, M. A., J. C. Ritchie, and H. D. Fox (1994), Comparison of laser and field measurements of vegetation height and canopy cover, *Water Resour. Res.*, **30**(5), 1311–1319, doi:10.1029/93WR03067.
- Xu, L., and D. D. Baldocchi (2004), Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California, *Agric. For. Meteorol.*, **123**, 79–96, doi:10.1016/j.agrformet.2003.10.004.

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