

6-20-2007

Soil Moisture Variations and Ecosystem-Scale Fluxes of Water and Carbon in Semiarid Grassland and Shrubland

S. A. Kurc

University of Arizona, shirley.papuga@wayne.edu

Eric E. Small

University of Arizona

Follow this and additional works at: <https://digitalcommons.wayne.edu/geofrp>

 Part of the [Environmental Sciences Commons](#)

Recommended Citation

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](https://doi.org/10.1029/2006WR005011).

This Article is brought to you for free and open access by the Environmental Sciences and Geology at DigitalCommons@WayneState. It has been accepted for inclusion in Environmental Science and Geology Faculty Research Publications by an authorized administrator of DigitalCommons@WayneState.

Soil moisture variations and ecosystem-scale fluxes of water and carbon in semiarid grassland and shrubland

Shirley A. Kurc¹ and Eric E. Small²

Received 2 March 2006; revised 25 March 2007; accepted 9 April 2007; published 20 June 2007.

[1] Soil moisture distribution emerges as a key link between hydrologic and ecologic processes in semiarid grassland and shrubland, as it influences evapotranspiration, respiration, and assimilation. In support, we present three years of data (2002–2004) collected from a semiarid grassland and shrubland within the Sevilleta National Wildlife Refuge of central New Mexico; the two sites are separated by about 5 km. Instrumentation includes an eddy covariance tower and typical micrometeorological devices at both locations. Additionally, the grassland site features six soil moisture profiles and the shrubland site features four soil moisture profiles, with the maximum depth at 52.5 cm. At both sites, most rain falls during the warm season, but large storms do occur at other times of the year, e.g., spring of 2004. Soil moisture pulses at 2.5 cm follow almost all rain events, whereas only four pulses in the 3-year record are observed at 52.5 cm in the grassland and two in the shrubland; these deeper pulses follow large precipitation events or a series of smaller events. The daily time series of evapotranspiration (ET) is similar between the grassland and shrubland, supporting the results of Kurc and Small (2004). ET variations largely reflect changes in the soil moisture at 2.5 cm. In contrast, though the daily time series of net ecosystem exchange (NEE) at both sites covary, the magnitudes of peaks in net negative ecosystem exchange (NEE^-) and net positive ecosystem exchange (NEE^+) are over twice the magnitude at grassland than at the shrubland. Furthermore, pulses associated with NEE^- peaks last much longer than ET pulses, of the order of 1–2 months, without any particular adherence to the climatologically defined rainy season. These NEE^- pulses reflect changes in deeper soil moisture, i.e., 52.5 cm at the grassland and 37.5 cm at the shrubland. Finally, evidence of soil moisture driven respiration is found throughout the NEE time series, with spikes of NEE^+ following most rain events; however, longer periods of NEE^+ also occur during relatively dry periods. Modeled assimilation suggests that the relationship between assimilation and soil moisture is strongest at depths at least 30 cm below the surface.

Citation: 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.

1. Introduction

[2] In arid and semiarid ecosystems, soil moisture is expected to be the primary control on the exchanges of water and carbon between the land surface and atmosphere [Laio *et al.*, 2001; Porporato *et al.*, 2001; Rodriguez-Iturbe *et al.*, 2001]. Away from riparian areas [Scott *et al.*, 2004], the sole source of water for evapotranspiration (ET) is soil moisture distributed via precipitation [Phillips, 1994; Sala *et al.*, 1992]. Concomitantly, the ET flux controls how the soil dries following precipitation events. The interactions between carbon fluxes and soil moisture are a fundamental characteristic of ecohydrological processes. However, the linkages between carbon fluxes and soil moisture are not as direct as between ET and soil moisture. During photosyn-

thesis, soil water is lost via transpiration as plant stomata open to take up carbon. Though activity of plant stomata is optimized to minimize water loss while maximizing carbon gain, this ratio can be variable [Bacon, 2004]. In particular, variability is seen in arid to semiarid ecosystems where heightened temperatures and vapor pressure deficits demand that plants acclimate to avoid wilting, but continue to grow [Bacon, 2004].

[3] In semiarid ecosystems, because rainfall is returned to the atmosphere almost solely as ET , the manner in which ET is partitioned into evaporation (E) or transpiration (T) plays a critical role in the water cycle. Evaporation may account for more than half of ET in many semiarid settings [Huxman *et al.*, 2005]. Only about the top 20 cm of soil contributes to E [Boulet *et al.*, 1997; van Keulen and Hillel, 1974; Yamanaka and Yonetani, 1999]. Given this near-surface source for E , small rainstorms that only wet the top few centimeters of soil are likely the main source of water for E in semiarid areas [Huxman *et al.*, 2005; Sala and Lauenroth, 1982]. Because only a few centimeters of water are stored in

¹School of Natural Resources, University of Arizona, Tucson, Arizona, USA.

²University of Colorado, Boulder, Colorado, USA.

this shallow moisture reservoir, the timescales of drying are expected to be of the order of days [Kurc and Small, 2004].

[4] In contrast, soil water throughout the entire root zone is the source of water for T . Because different plants have different root distributions [Breshears *et al.*, 1997; Cable, 1969; Schenk and Jackson, 2002], the depth-dependence of T on soil moisture should vary between different semiarid ecosystems. Additionally, plant-to-plant differences in water use efficiency, drought tolerance, phenology, leaf area index, and stomatal conductance also influence transpiration rates. Furthermore, because roots access soil moisture within the entire root zone for T , the soil water reservoir is larger for T than for E . This suggests (1) that timescales for T may be longer than those for E and (2) that T may respond more strongly than E to the larger rainfall events that lead to deeper infiltration.

[5] Net ecosystem exchange of carbon dioxide (NEE) between the land surface and the atmosphere also depends on soil moisture. Typically, NEE is considered to be the combination of two components: respiration (F_{RE}) and assimilation (F_{AS}). Respiration by microorganisms and plants releases CO_2 to the atmosphere. Soil moisture controls F_{RE} by driving the activity level of soil microorganisms [Tate, 2000] and by driving growth of belowground biomass which in turn affects the quantity of root respiration and the turnover of the soil organic carbon pool [Connin *et al.*, 1997; Hibbard *et al.*, 2001]. Because most soil microorganisms are concentrated near the surface [Tate, 2000], the soil surface is the primary location from which CO_2 is released to the atmosphere via microbial respiration. Because microbial activity is linked to surface soil moisture, timescales of soil respiration are expected to be rapid [Huxman *et al.*, 2004].

[6] Assimilation is the fixation of carbon that occurs during photosynthesis. Associated with F_{AS} is the concurrent water loss that makes up T . A typical and indirect way of linking F_{AS} to soil moisture is via the ratio of F_{AS} to T , or water use efficiency, i.e., WUE . If F_{AS} is tightly coupled with T , then their soil moisture reservoirs should be similar. At the leaf level (WUE_L), WUE_L tends to increase as the soil dries [Jarvis, 1976]. At the ecosystem scale (WUE_E), however, it is challenging to isolate T and F_{AS} from ET and NEE , respectively, and therefore variations of WUE_E are not well documented. One such study shows that WUE_E actually decreases as the soil dries [Reichstein *et al.*, 2002]. This type of finding supports the need for more observations that supplement the current understanding of variations in WUE_E and thus soil moisture control on F_{AS} at the ecosystem scale.

[7] Because F_{RE} and F_{AS} depend on soil moisture at different depths and because soil dries at different depths on different timescales, we expect the response of NEE to precipitation events and subsequent soil wetting to be complex [Huxman *et al.*, 2004]. For small storms that only wet the surface soil, a precipitation event may only stimulate F_{RE} , yielding positive values of NEE [Huxman *et al.*, 2004]. However, larger storms tend to wet the entire root zone. In these cases, F_{RE} may outpace F_{AS} initially ($NEE > 0$), but after several days, plants will “green up” and net assimilation ($NEE < 0$) may occur [Huxman *et al.*, 2004].

[8] Untangling the complexities of how water and carbon fluxes are controlled by soil moisture and rainfall is funda-

mental to studying how water and carbon cycles are linked in semiarid ecosystems. To gain insight, models have been used to approach the intricacies of the interconnectedness of these cycles. For example, Porporato *et al.* [2001] modeled how wetting and drying of soil controls plant stress, a measure of the extent to which plants take up carbon and lose water. To achieve an analytical solution, this type of ecohydrological model typically assumes that water and carbon fluxes are driven by a single root zone averaged soil moisture [Porporato *et al.*, 2001]. Clearly, this simplification does not allow some important complexities to exist [Guswa *et al.*, 2002], including how fluxes depend on soil moisture in different parts of the soil profile [Breshears and Barnes, 1999; Ogle and Reynolds, 2004; Walter, 1971] or how small rainfall events only wet the surface soil [Sala and Lauenroth, 1982].

[9] Field studies provide critical information about how soil moisture and rainfall control ecosystem-scale water and carbon fluxes, yet few studies have described these observations within semiarid areas. Williams and Albertson [2004] observed the dynamics of water and carbon fluxes following soil dry-down after a single 85-mm storm within an African savanna. In their paper, they showed that NEE was negatively correlated to ET [Williams and Albertson, 2004]. This linear relationship supports relatively simple models of ecohydrological interactions [e.g., Daly *et al.*, 2004b]. In a similar but longer-term study, Scott *et al.* [2006] showed that different seasons and different storms led to variations in the coupling of water and carbon fluxes. For instance, at the onset of the growing season, ET was dominated by E and NEE was dominated by F_{RE} [Scott *et al.*, 2006]. However, as the growing season progressed, only the periods immediately following storms were dominated by E and F_{RE} while T and F_A dominated afterward [Scott *et al.*, 2006]. Missing from Scott *et al.* [2006] were explicit links between components of the fluxes and specific soil moisture reservoirs within the soil profile. Contrary to a single averaged root zone assumption, Kurc and Small [2004] found a relatively simple relationship between ET and shallow soil moisture, i.e., 0–5 cm, but not between ET and root zone soil moisture. Further field studies are necessary to resolve how soil moisture drives the water and carbon cycling in these environments, and how these cycles are related.

[10] In this paper, we study both water and carbon fluxes between the land surface and the atmosphere over a 3-year period, using measurements made within semiarid grassland and shrubland in central New Mexico located within just a few kilometers of one another. Our study has two main advantages over most previous studies conducted within similar ecosystems. First, we have a long, continuous 3-year record of both carbon and water fluxes. Second, our flux measurements are complemented by continuous soil moisture measurements at several depths. We focus on the relationships between these fluxes and soil moisture, including the effects of vertical heterogeneities of soil moisture within the soil profile. Our measurements do not provide direct information on the partitioning of ET . However, we do examine F_{RE} and F_{AS} as separate fluxes, utilizing nighttime measurements of NEE to model F_{RE} and F_{AS} during the day. The results of this study should provide valuable insights regarding (1) differences between

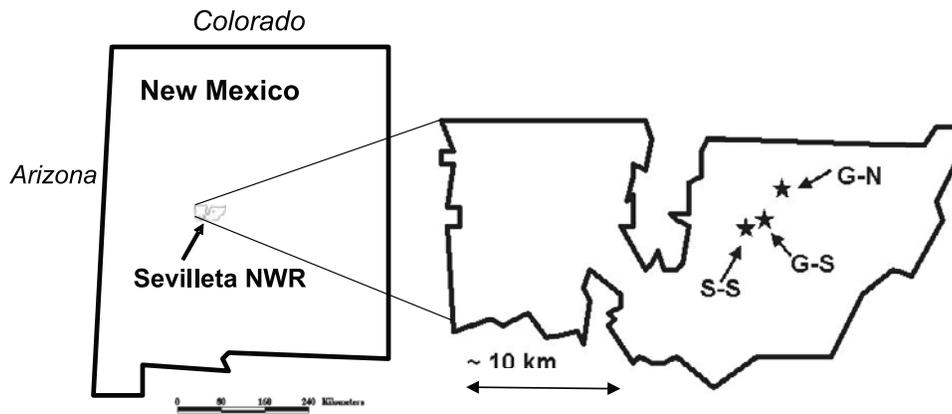


Figure 1. Location of the shrubland (S-S) and grassland (G-N) field sites within the Seville National Wildlife Refuge (NWR), central New Mexico, used within this study. The location of the grassland site studied by *Kurc and Small* [2004] (G-S) is also depicted.

the dynamics of ecosystem-scale water and carbon fluxes at semiarid grassland and shrubland and (2) differentiations in soil moisture reservoirs for consideration when conceptualizing root zone water balance, (3) interannual variability in carbon uptake at these semiarid locations, and (4) the interconnected nature of water and carbon dynamics in water-limited ecosystems.

2. Site Description

[11] Measurements used in this study were made within the McKenzie Flats area of the Seville National Wildlife Refuge (NWR), central New Mexico. Historically, this area has been used for livestock grazing; however, the McKenzie Flats have not been grazed since 1973 and the effects of this previous grazing are considered negligible for the purposes of this study. As the name suggests, McKenzie Flats is an extensive ($\sim 130 \text{ km}^2$), nearly flat, mixed-species desert grassland bounded on the east by Los Piños Mountains and on the west by the Rio Grande. Because the annual precipitation is about 230 mm yr^{-1} , the area is considered to be semiarid, with more than 50% of the precipitation occurring during the summer rainy season (July–September).

[12] We collected measurements from a grassland and a shrubland that are separated by about 5 km. The grassland is nearly monospecific, dominated by C_4 black grama (*Bouteloua eripoda*); percent cover is about 50% and average plant height is about 0.3 m. The shrub location is also nearly monospecific, dominated by C_3 creosotebush (*Larrea tridentata*); percent cover is about 30% and average plant height is about 0.75 m. At both locations the vegetation is essentially uniform for at least 500 m upwind of our instruments. At the grassland the top 40 cm of soil is loamy sand, whereas at the shrubland the top 40 cm of soil is sandy loam. Both sites are classified as sandy loam below 50 cm. The grassland site in this study is farther north than the grassland site studied by *Kurc and Small* [2004] (Figure 1), which accounts for soil textural difference between grassland and shrubland not observed by *Kurc and Small* [2004]. Root density profiles indicate that roots are present to soil depths of 1 m in both the grassland and shrubland, with a

majority of grass roots near the surface and a majority of shrub roots between 20 and 40 cm (Figure 2).

3. Field Methods

[13] The instrumentation in this study includes an eddy covariance tower and typical micrometeorological devices at both the grassland and the shrubland locations [*Moncrieff et al.*, 2000; *Shuttleworth*, 1993]. Here we present data from 1 June 2002 to 1 January 2005, though data from 2001 also exist. These towers make measurements at 10 Hz using Campbell Scientific CR23X data loggers. In the first 2 years of the study the CR23X data loggers recorded a 15-min flux average. In spring of 2003, the programs on the CR23X data loggers were modified to record 30-min flux averages in an effort to adhere to AmeriFlux protocol.

3.1. Ecosystem-Scale Flux Measurements

3.1.1. Radiation

[14] Net radiation was measured using identical Radiation and Energy Balance Systems (REBS) Q*7.1 net radiometers at

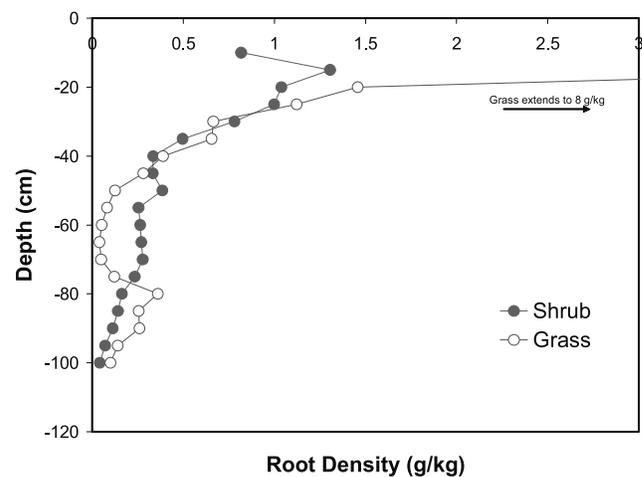


Figure 2. Root density (g root/kg soil) at the shrubland (solid) and grassland (open). Each line represents the average value from six separate profiles.

both grassland and shrubland. These radiometers are placed about 2.5–3 m above the soil surface. Individual components of the radiation budget were not directly measured.

3.1.2. Soil Heat Flux and Soil Moisture

[15] At both sites, the ground heat flux (GHF) was measured using REBS *HFT3* soil heat flux plates. The plates were placed at two locations: under a plant canopy (e.g., grass or shrub) and under a bare patch. Each plate was placed at 5 cm depth. In order to calculate a heat storage term above the soil heat flux plates (storage), soil temperature was measured as an average within in the top 5 cm of soil and soil moisture measurements at 2.5 cm depth were made using REBS STP1 soil temperature probes and Campbell Scientific CS616 water content reflectometers, respectively. These measurements resulted in our total soil heat flux (G) term (i.e., $G = \text{GHF} + \text{storage}$) calculated based on the combined calorimetric heat flux plant approach [Kimball *et al.*, 1976]. Site-specific shrubland and grassland values of G were calculated using a weighted average based on percent cover.

[16] Volumetric water content was measured using Campbell Scientific CS616 water content reflectometers (WCR) with the factory calibration. The factory calibration was considered sufficient as we found at most a 3% difference between the probe value and the gravimetric value under both wet and dry conditions in the lab. At the grassland, a total of 22 WCR probes were placed in the soil in 2002, i.e., 11 canopy probes and 11 bare probes in a total of six profiles. Only a single bare and canopy profile have measurements at all depths: 2.5, 12.5, 22.5, 37.5, and 52.5 cm; the other four profiles have probes at the top three depths: 2.5, 12.5, and 22.5 cm. At the shrubland, a total of 20 WCR probes were buried, 10 canopy probes and 10 bare probes in a total of four profiles. All four profiles had measurements at five depths: 2.5, 12.5, 22.5, 37.5, and 52.5 cm. Shrubland and grassland values of volumetric water at all depths content were calculated as a weighted average based on percent cover. Root zone and 15-cm volumetric water contents were calculated from an appropriately weighted average of the probes in the top 15 cm and top 60 cm, respectively.

3.1.3. Water and Carbon Fluxes

[17] To measure wind speed fluctuations, we used a CSAT three-dimensional (3-D) sonic anemometer. At the grassland the sonic anemometer is arranged at a height of 3 m and at a height of 2.5 m at the shrubland. At both grassland and shrubland, density of carbon dioxide and density of water vapor in the air were measured using a Licor 7500 open path $\text{CO}_2/\text{H}_2\text{O}$ analyzer. The Licor 7500 was placed at a height of 3 m at the grassland and at a height of 2.5 m at the shrubland. At both the grassland and the shrubland the Licor 7500 was tilted approximated 45° to minimize water accumulation on the sensor and was placed about 10 cm from the 3-D sonic anemometer in an effort to maximize collocation and minimize wind distortion. At both sites, a flat uniform upwind fetch of at least 500 m was ensured. On the basis of footprint calculations using the method described by Baldocchi [1997], a fetch of 500 m was considered a conservative estimate for our eddy covariance towers.

3.2. Measurement of Root Density With Depth

[18] Root density was measured at different depths at both the shrubland and grassland locations. At each location, three soil pits of 1-m depth were excavated. The

placements of these soil pits were selected on the basis that each pit could overlap both a canopy patch and a bare soil patch. Within each pit, two profiles of soil were collected, one profile under a canopy patch and one profile under a bare soil patch for a total of six profiles (two profiles in each of three pits). A soil sample 5 cm tall \times 10 cm wide \times 10 cm long was collected at each 5-cm interval in each profile. Each profile was composed of 20 samples: one sample every 5 cm for 100 cm. A total of 240 samples were taken back to the lab to be examined for roots.

[19] In the lab, samples were dried in the oven and then weighed. The soil was then sifted through a variety of sieve sizes, until roots in the soil were indiscernible to the naked eye. Otherwise, as roots became noticeable they were retrieved from the sample. Once all the roots were retrieved from the sample, the collection of roots was weighed. Relative root density was calculated by dividing root weight in grams by the initial soil weight in kilograms (Figure 2).

4. Calculations

[20] Half-hour averages of carbon (NEE) and water (λE) fluxes are corrected for an apparent flux occurring from density fluctuations as described by Webb *et al.* [1980], as is the standard. Additionally, using the method described by Blanken *et al.* [1998], we establish and use a friction velocity (u^*) threshold of 0.25 m s^{-1} . A u^* threshold of 0.25 m s^{-1} results in an exclusion of about 22% of our entire data set of half-hour flux averages and about 45% of our nighttime data. Therefore daily averages are skewed toward daytime values. More specifically, this u^* threshold results may result in (1) a daily underestimation in NEE because daytime values are typically more negative, and (2) a daily overestimate in ET because daytime values are typically higher. We comment on these uncertainties in the discussion.

[21] Within our study, energy balance closure (i.e., $[\lambda E + H]/[R_n - G]$) was 0.73 at the shrubland when using 15-min flux values for year 2002 and half-hourly flux values thereafter. In the shrubland, because of the presence of a neighboring Bowen ratio station, measurements from two extra ground heat flux plates and an additional net radiometer were averaged in to provide a better estimate of available energy (i.e., $R_n - G$) during that time. At the grassland, closure for year 2002 using only 15-min flux averages was 0.64. After June 2002, energy balance closure at the grassland was not calculated because the net radiometer was struck by lightning. For the purposes of this study, we feel it unnecessary to adjust our λE and H values to force closure because we are looking at the relative behavior of the time series, not the exact magnitude of the fluxes; however, the uncertainty associated with the lack of closure should be noted. To evaluate the data, we compare the sum of ET to the sum of precipitation, which should be about equal in these semiarid systems. Because we have many large gaps of missing data throughout the winter months, we only make this comparison during the climatologically defined rainy season (CDS; see section 5.1 for a description) (Table 1). Reasonable agreement is found between the ET and precipitation with discrepancies likely due to measurement error, small data gaps, runoff, and soil moisture changes. Furthermore, previous Bowen ratio measurements made in the shrubland [Kurc and Small, 2004] yield ET time series similar to the ones presented in this study; we describe this

Table 1. Sums of Precipitation and Evapotranspiration at Grassland and Shrubland Over the Duration of the Climatologically Defined Rainy Season for Years 2002, 2003, and 2004

	Grassland		Shrubland	
	Precipitation, mm	ET, mm	Precipitation, mm	ET, mm
2002	96	92	N/A ^a	N/A
2003	N/A	N/A	38	47
2004	144	118	113	106

^aNot applicable.

in section 5 and this is directly shown by *Kurc and Small* [2004]. Last, other studies have compared their estimates of primary productivity and normalized difference vegetation index (NDVI) using remotely sensed data to our eddy covariance measurements of *NEE* and have found the trends of the time series to be similar [Schmidt, 2004; Turner et al., 2005]. Therefore we conclude that our data set is robust.

4.1. Daytime Respiration

[22] When calculating ecosystem-scale respiration, nighttime values of CO_2 are often targeted because carbon uptake is negligible so respiration can be assumed to be the only contribution to *NEE*, i.e., $F_{RE} \gg F_{AS}$ [Franzuebbers et al., 2002]. This is very common, even though measurements of CO_2 exchange are less reliable during the nighttime than during the daytime because of stable air and low wind conditions [Franzuebbers et al., 2002; Pattey et al., 2002]. Using this technique, nighttime soil temperature is related to nighttime CO_2 flux and then this relationship can be extrapolated to model respiration during daylight hours. The relationship is typically defined as an exponential increase of respiration with temperature accounting for around 50% of the variability [Frank et al., 2002; Mielnick and Dugas, 2000]. However, the relationship between respiration and soil temperature is not exponential, but is roughly normal, reaching a peak around 25°C [e.g., Tate, 2000]. Because our nighttime temperatures do exceed 25°C , we see that indeed nighttime CO_2 flux does begin to decline at some soil temperature (i.e., T_{soil}) higher than 25°C . Additionally, because daytime temperatures at both sites often exceed 25°C , an exponential model would highly overestimate respiration at both of these sites. Furthermore, we know at low soil moisture, nighttime CO_2 flux is essentially zero. Therefore we adopt a modified Gaussian model by which to determine half-hourly daytime respiration R_{day} , i.e.,

$$R_{day}(\theta_{15\text{cm}} \geq 0.08) = a \cdot \exp\left(-((T_{soil} - b)/c)^2\right) \quad (1)$$

$$R_{day}(\theta_{15\text{cm}} < 0.08) = 0,$$

where $\theta_{15\text{cm}}$ is average soil moisture in the top 15 cm of the soil and T_{soil} is average soil temperature in the top 5 cm of the soil; we use the notation R_{day} to indicate that although this relationship is valid for all times of day, we are only using this relationship to calculate daytime values. At the grassland using nighttime data, $a = 0.23$, $b = 23.37$, and $c = 6.04$; at the shrubland $a = 0.095$, $b = 23.62$, $c = 4.65$. Our model based on these values allows an estimate of

respiration and assimilation sensitive to both soil temperature and soil moisture. However, it must be noted that in the calculation of R_{day} we introduce some uncertainty. Therefore inferences made from the use of R_{day} must take this uncertainty into consideration.

4.2. Daily Net Ecosystem Exchange, Respiration, and Assimilation

[23] To calculate daily *NEE*, a half-hour average for each day is obtained, i.e., $\text{g CO}_2 \text{ m}^{-2} (\text{half hour})^{-1}$, using all “good” half-hour data. This average is multiplied by 48, i.e., the number of half hours in any given day, to obtain units of $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$. We adopt the following notation throughout the paper: Positive values of *NEE* correspond to net respiration over 24 hours (NEE^+), and negative values of *NEE* correspond to net assimilation over 24 hours (NEE^-).

[24] Because NEE^+ and NEE^- are not equivalent to respiration and assimilation, we make calculations of daily respiration (F_{RE}) and assimilation (F_{AS}). F_{RE} is calculated as the average respiration over the day multiplied by the number of half hours in the day. Here we use the modeled R_{day} for the daytime values, and because we assume no assimilation occurs during the nighttime, *NEE* is used for the nighttime respiration values. To obtain F_{AS} over the day, we let nighttime assimilation equal zero, and we set daytime assimilation to be $NEE - R_{day}$. Again, we average the assimilation over the day and then multiply by the number of half hours in the day. Note that both F_{RE} and F_{AS} are both calculated using R_{day} . Therefore any inferences resulting from values of F_{RE} and F_{AS} must take into consideration the uncertainty associated with the calculation of R_{day} .

5. Results

5.1. Rainfall and Soil Moisture

[25] *Small* [2005, p. 5] defined a rainy season as the “shortest continuous period of the year during which 50% of the annual accumulates,” and determined this period from multiyear records. At the Sevilleta, half of the annual precipitation accumulates during a period of 86 days, centered on day of year (DOY) 224. We refer to this period as the climatologically defined rainy season (CDS), i.e., days 178–270. Here the CDS coincides with the period of the year when temperatures are the highest. Year 2002 was typical of the rainfall observed at the Sevilleta NWR over the long-term record (Figure 3), in terms of both the amount and timing of rainfall (see http://sev.lternet.edu/project_details.php?id=SEV001). Year 2003 was an exceptionally dry year with only 137 mm of recorded rainfall at the grassland and about 140 mm of recorded rainfall at the shrubland. Of that, only 32% (45 mm) and 27% (38 mm) fell within the CDS at the grassland and shrubland, respectively. In year 2004, half of the annual precipitation fell during the CDS, but 2004 was an exceptionally wet year with nearly one and a half times the typical annual precipitation, i.e., 301 mm in the grassland and 323 mm in the shrubland (Figure 3).

[26] In years 2002–2004, we recorded eight storms in the grassland over 15 mm; in the shrubland, we observed 11 storms over 15 mm (Figure 3). About half of these large storms occur within the CDS, consistent with the definition of CDS. However, in the dry year of 2003, no 15-mm storms occur within the CDS period (Figure 3), although

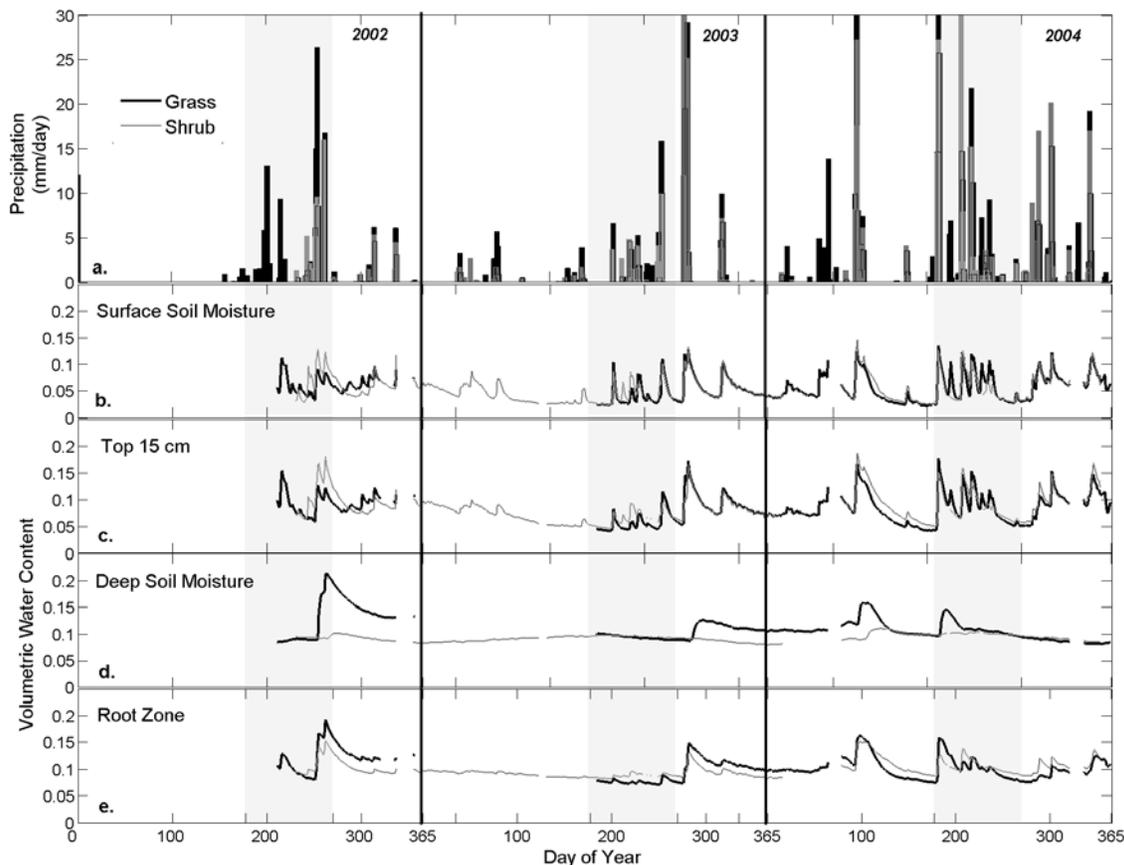


Figure 3. Daily time series of (a) precipitation and (b–e) volumetric water content (VWC) at the grassland (black/thick) and shrubland (gray/thin). Surface soil moisture corresponds to VWC at 2.5 cm (Figure 3a), soil moisture within the top 15 cm is an average of VWC at 2.5 and 12.5 cm (Figure 3b), deep soil moisture corresponds to VWC at 52.5 cm (Figure 3c), and root zone soil moisture is an average of VWC at 2.5, 12.5, 22.5, 37.5 and 52.5 cm (Figure 3e). Shading represents the CDS (day 178–day 270).

one large event occurs just after the CDS. In 2004, the time between these large CDS storms is only about 3 days at both the shrubland and grassland, whereas in the CDS of 2002 these large storms are separated by about 10 days (Figure 3).

[27] To characterize the precipitation in terms of soil moisture response, we look at soil moisture pulses, i.e., extended periods of elevated soil moisture, at the surface (2.5 cm depth), at depth (37.5 cm depth), averaged over the top 15 cm (2.5 cm and 12.5 cm depths), and averaged over the root zone (2.5, 12.5, 22.5, 37.5, and 52.5 cm depths). We average soil moisture over 15 cm because microbial activity in the top 15 cm is correlated with respiration [Tate, 2000]. We average soil moisture over 60 cm, because both grasses and shrubs are expected to be able to utilize water throughout the root zone for transpiration. We find that soil moisture pulses at the surface follow most storms (Figure 3). Deep soil moisture pulses are less frequent. At the grassland, where the soil is slightly more sandy than at the shrubland, only four soil moisture pulses are observed at 52.5 cm in the late CDS of 2002, fall 2003, spring 2004, and the CDS of 2004 (Figure 3). At the shrubland, only two small soil moisture pulses are observed at depths of 52.5 cm: late CDS of 2002 and spring 2004 (Figure 3). We note that these moisture differences are not seen by Kurc and Small [2004] in which the grassland and shrubland sites were

located only 2 km apart (Figure 1) and both had sandy loam soil texture.

5.2. Evapotranspiration and Net Ecosystem Exchange

[28] The time series of ET from the grassland and shrubland are very similar (Figure 4). Maximum ET (4 mm d^{-1}) follows CDS precipitation events (Figure 4). During the warm season, ET decreases rapidly until another precipitation event occurs. These spikes in ET are followed by quick decreases, i.e., 2–3 days, yielding a dynamic time series during the warm summer months (e.g., days 200–250, Figure 4 and Figure 5). Overall, ET observations for the summer months are similar to observations from semiarid grassland and shrubland made using the Bowen ratio technique for the summer months of 2000, 2001, and 2002 [Kurc and Small, 2004]. We should note that these two data sets have some key differences: (1) The grassland locations are different, (2) the time periods are different, and (3) the method of measurement was different. Given these differences in the data sets, the observed similarities in the records, i.e., magnitude of ET maximums and temporal dynamics of ET in relation to precipitation events, suggest the summer ET dynamics presented in this study are reasonable and robust.

[29] Outside of the summer months, the ET time series behave differently. Though maximum ET values still follow

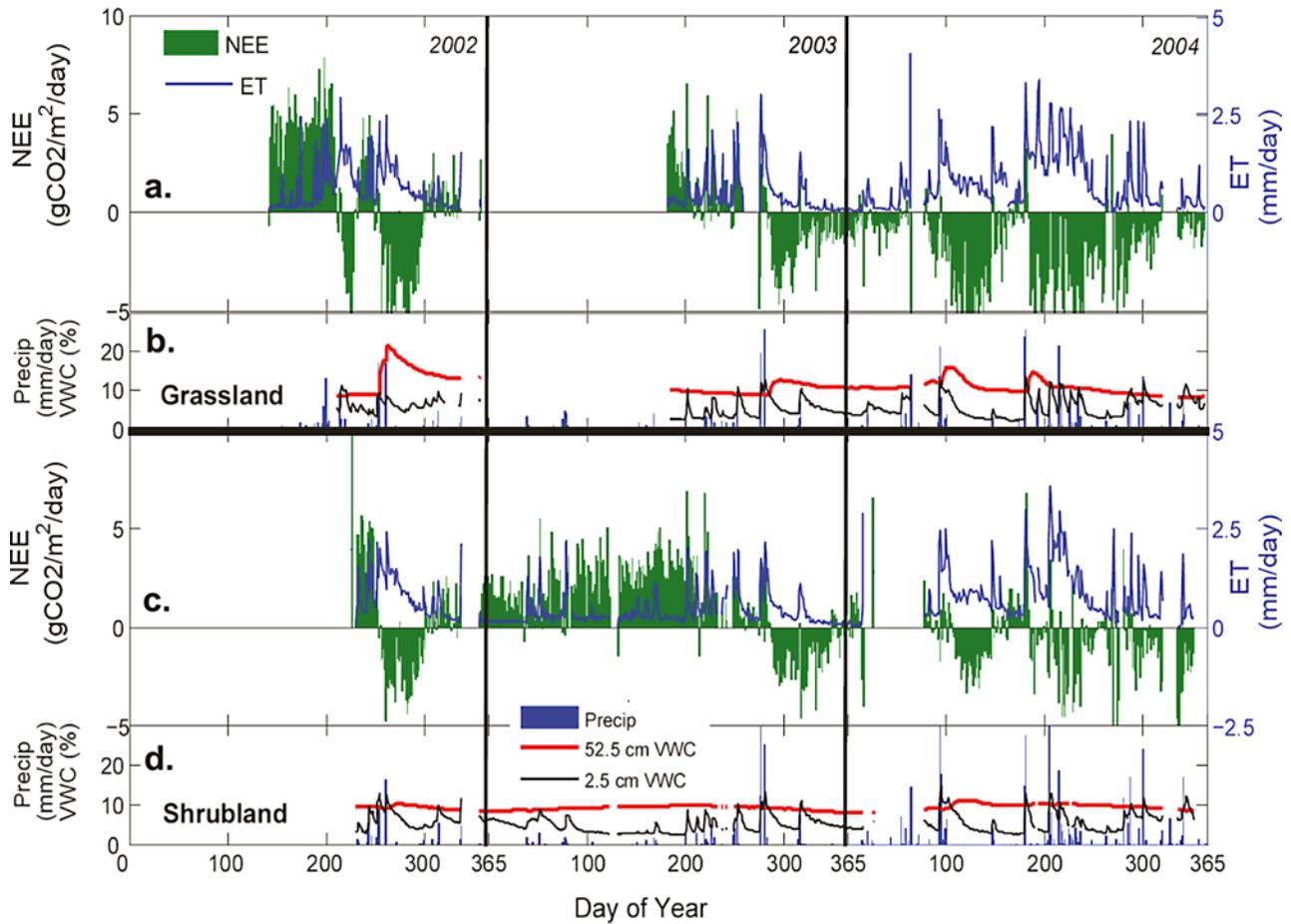


Figure 4. Daily time series of (a and c) *ET* (blue line) and *NEE* (green bars) and (b and d) precipitation (blue bars) and two depths of *VWC* for the (top) grassland and (bottom) shrubland.

precipitation events, the values are not as high, i.e., only 2–3 mm d⁻¹ (Figure 4). As in the summer months, these maximum *ET* values coincide with maximum values of surface soil moisture (Figure 4). However, the decreases in *ET* following *ET* peaks are less rapid than during the

summer months and tend to plateau at a rate around 1 mm d⁻¹ for several days or even weeks (Figure 4).

[30] The *NEE* records indicate that the timing of periods of *NEE*⁻ vary from year to year at the semiarid grassland and shrubland of the Sevilleta NWR (Figure 4). In year

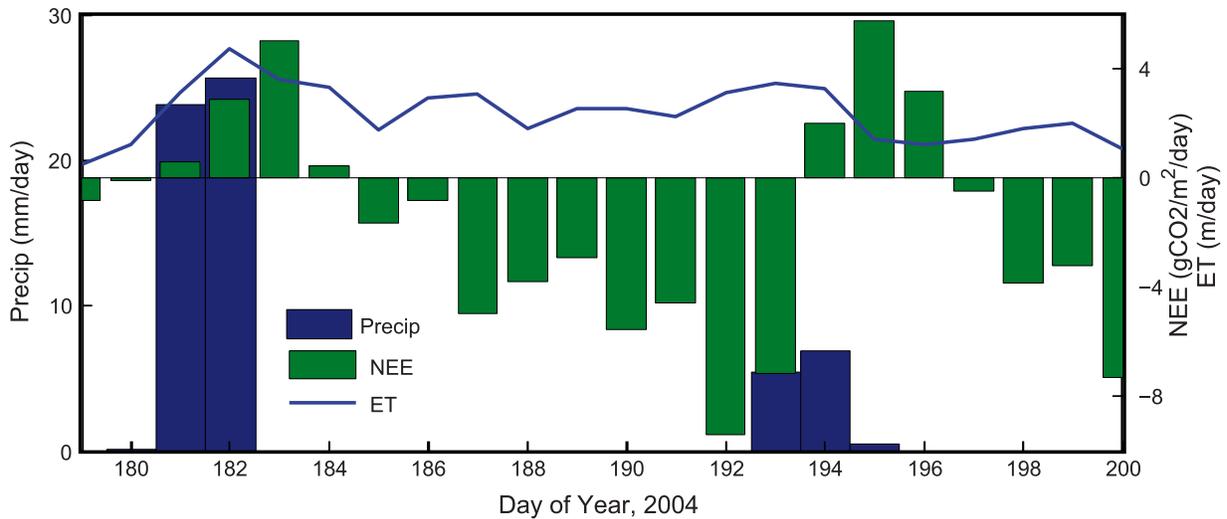


Figure 5. Grassland enlargement of daily time series of precipitation (blue bars), *ET* (black line), and *NEE* (green bars) during summer of 2004.

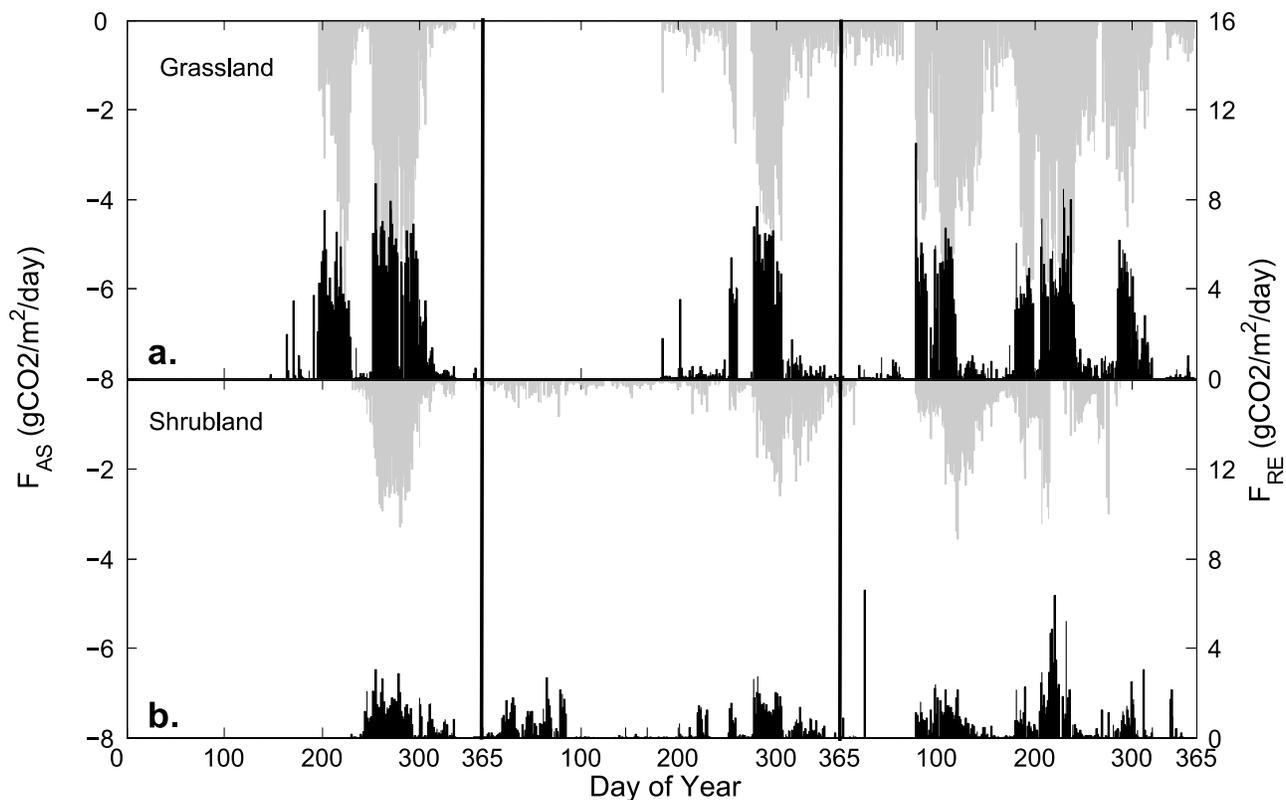


Figure 6. Daily time series of respiration F_{RE} (black bars/positive values) and assimilation F_{AS} (gray bars/negative values) at the (a) grassland and (b) shrubland locations.

2002, a short 15-day period of NEE^- begins to occur in August, around day 215, with another longer 50-day period of NEE^- beginning in September, around day 250. In year 2003, however, there is no measurable NEE^- until October around day 280. In year 2004, a long 90-day period of NEE^- begins in the middle of March, around day 70. Another long period of NEE^- begins in late June to early July (day 180). We note that throughout the study, periods of NEE^- occur both within and outside of the CDS. In addition, more than one period of NEE^- occurs in at least two of the three years.

[31] All periods of NEE^- follow a large precipitation event or several smaller storms that occurred within a few days (Figure 4). These periods of NEE^- are typically of the order of a month or two. The duration of these periods tends to be longer in the grassland than in the shrubland, as clearly seen in year 2004. Although the time series are similar, we note that periods of elevated NEE^- tend to be greater in magnitude at the grassland than in the shrubland (Figure 4). For instance, the magnitude of the grassland spring pulse in year 2004 is about 3 times that of shrubland pulse. Additionally, during monthlong periods of NEE^- , NEE^+ tends to spike up following a precipitation event and remain high for 1 or 2 days; this is illustrated in detail for the summer of 2004 in Figure 5. Longer periods of elevated NEE^+ also occur, but only during dry periods with little precipitation, as in the spring of 2003 (Figure 4).

[32] Figure 6 shows the daily time series of calculated assimilation (F_{AS}) and respiration (F_{RE}) values. In general, the daily time series of F_{AS} adheres to the same trends as NEE^- . The pulses of F_{AS} are long and follow a big

precipitation event or series of several smaller events. NEE^+ appears to mirror F_{AS} with peaks occurring during wetter periods or following large precipitation events. We also observe that both the pulses of F_{AS} and of F_{RE} are more than twice the magnitude at the grassland than at the shrubland. Because these calculated values of F_{AS} and F_{RE} represent the actual values as opposed to the relative net fluxes that NEE^+ and NEE^- represent, we make use of calculated F_{AS} and F_{RE} throughout the paper, reminding the reader of uncertainty in the calculation of F_{AS} and F_{RE} .

5.3. Regression of NEE Versus ET

[33] We plot all of our observations of daily NEE against daily ET for all 3 years (Figure 7). The points fall in a cloud, showing that a single relationship between NEE and ET does not exist (r^2 values < 0.01 in both the grassland and shrubland). This result is not surprising: A balanced carbon budget requires both positive and negative NEE values that could occur during times of high or low ET . However, this result does not indicate that carbon and water fluxes are completely independent. Because we know that evaporation and respiration should be more influenced by soil moisture near the surface than by deep soil moisture, we break up the soil profile into two regions: soil moisture at 2.5 cm (surface) and soil moisture at 37.5 cm (deep). Using the soil moisture time series, we locate the point at which there is no more dry-down to define dry as $< 6\%$ volumetric water content at 2.5 cm; at 37.5 cm we define dry as $< 12\%$ volumetric water content. We perform a regression of NEE versus ET for four cases: (1) dry surface, wet deep; (2) wet surface, dry deep, (3) wet surface, wet deep, and (4) dry

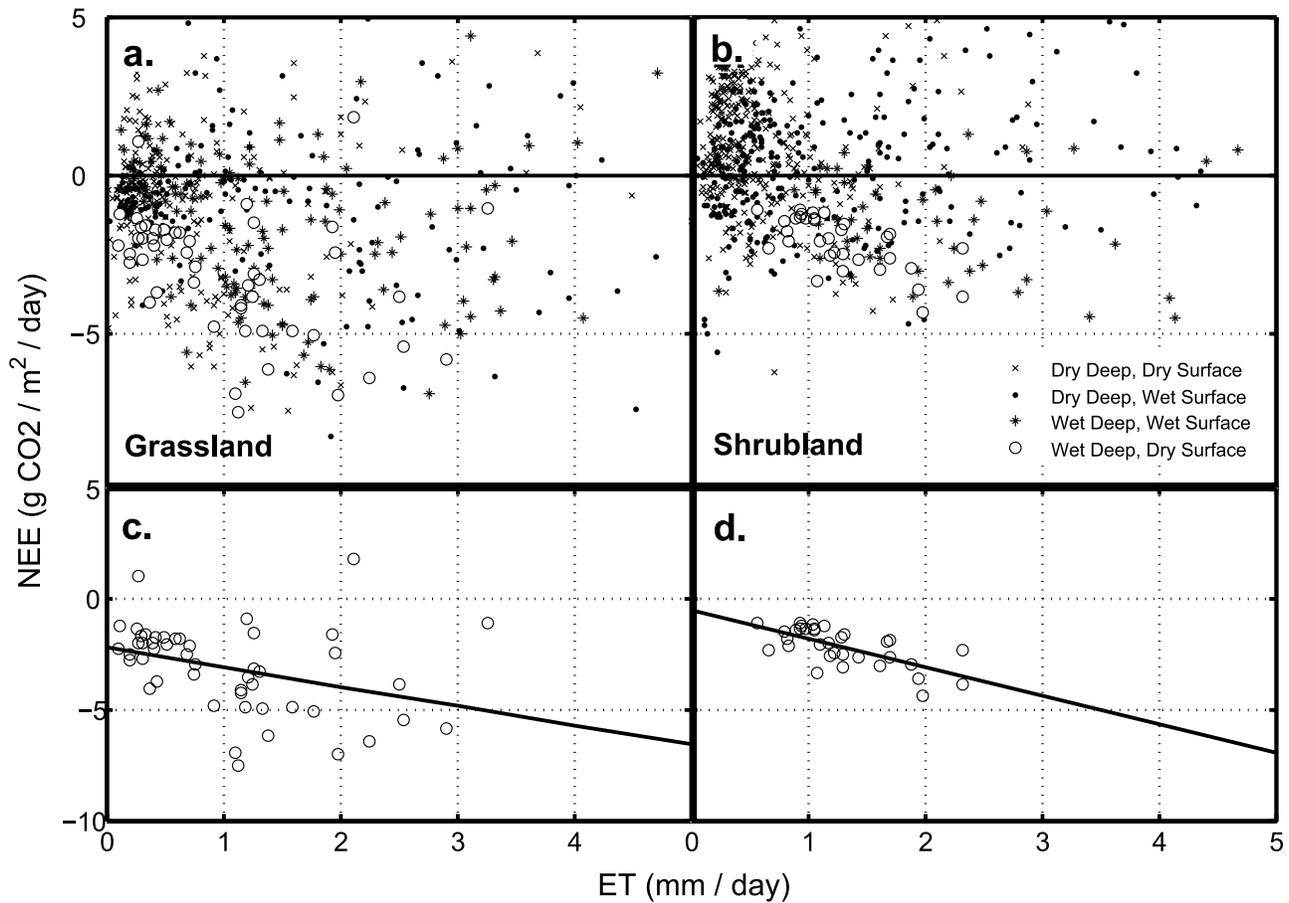


Figure 7. Daily NEE ($\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) versus daily ET (mm d^{-1}) at (a) grassland and (b) shrubland. The shapes represent different soil moisture conditions as indicated in the legend. The condition where the surface is dry but deeper in the profile the soil is wet is shown for grassland with (c) $r^2 = 0.12$ and (d) shrubland with $r^2 = 0.46$. All other soil moisture conditions yield r^2 values < 0.1 .

surface, wet deep. In the first three cases, the r^2 values for the regressions are all less than 0.1 (Table 2). However, in the fourth case where the surface is dry and the deep soil is wet, the r^2 values are 0.12 and 0.46 at the grassland and shrubland, respectively (Table 2). A few key things should be noted regarding the grassland value being lower than the shrubland value. First, the grassland reaches higher soil moisture values at the 37.5 cm depth (Figure 4) and at 52.5 cm (Figure 3). Second, the grassland roots are denser higher in the soil profile than the shrubland (Figure 2). Third, though the value 0.12 for case 4 is lower at the grassland than at the shrubland, it is still significantly higher than the r^2 values for grassland cases 1, 2, and 3 (Table 2).

5.4. Relationships With Soil Moisture

[34] *Kurc and Small* [2004] found a strong relationship between surface soil moisture (0–5 cm) and ET , but not between root zone soil moisture and ET . In the current study, we also see that daily ET tends to increase with surface soil moisture (Figure 4). However, performing a linear regression of ET versus surface soil moisture over all days, we find a much lower correlation than is found for *Kurc and Small* [2004] (Table 3). *Kurc and Small* [2004] use only observations made from 1 June to 15 September for 3 years when calculating their regressions. Therefore we

perform a similar regression using only observations made within the CDS. Making this modification, the linear relationship is more similar to that found by *Kurc and Small* [2004], with r^2 values of 0.59 and 0.69 in the grassland and shrubland, respectively (Table 3). Likewise, we also confirm that daily ET is less correlated with root zone soil moisture than it is with surface soil moisture, at least for days within the CDS (Table 3). We note that the r^2 values at the grassland are lower than those at the shrubland and lower than those seen by *Kurc and Small* [2004].

[35] Linear regressions between F_{AS} and soil moisture show very different results than for ET and soil moisture. We see that the magnitude of F_{AS} tends to increase with increases in soil moisture at all depths. However, this relationship is strongest when considering root zone soil moisture with r^2 values of 0.52 and 0.70 at the grassland and

Table 2. R^2 Values for Linear Regressions of Daily NEE Versus Daily ET at Grassland and Shrubland for Four Cases

	Grass	Shrub
Dry surface soil and dry deep soil	0.001	0.035
Wet surface soil and dry deep soil	0.033	0.083
Wet surface soil and wet deep soil	0.025	0.035
Dry surface soil and wet deep soil	0.124	0.458

Table 3. R^2 Values for Linear Regressions of Daily Evapotranspiration (ET), Assimilation (F_{AS}), and Respiration (F_{RE}) Versus Soil Moisture Averaged Over Three Depths, for Days When There Is No Rainfall^a

	ET		F_{AS}		F_{RE}	
	All Year	CDS	All Year	CDS	All Year	CDS
<i>Grass</i>						
Surface (5 cm)	0.23	0.59	0.06	0.31	0.21	0.58
Top 15 cm	0.17	0.56	0.14	0.51	0.28	0.68
Root zone	0.09	0.29	0.31	0.52	0.39	0.59
<i>Shrub</i>						
Surface (5 cm)	0.26	0.69	0.09	0.32	0.16	0.32
Top 15 cm	0.26	0.65	0.23	0.55	0.19	0.35
Root zone	0.33	0.57	0.40	0.70	0.20	0.29

^aAdditionally, these regressions are performed both for all days and for only days which occur within the CDS.

shrubland, respectively, when considering only days within the CDS (Table 3). This is compared with looking at the linear relationship between F_{AS} and surface soil moisture where we see r^2 values of 0.31 and 0.32 for grassland and shrubland, respectively. We also present r^2 values for the linear relationship between F_{RE} and soil moisture at different depths. We show that using only days within the CDS, the best relationship is found between F_{RE} and moisture in the top 15 cm of the soil, though this relationship is strongest in the grassland (Table 3). We remind the reader that some uncertainty associated with the daily values of F_{AS} and F_{RE} is disclosed in section 4.4 of this paper.

6. Discussion and Conclusions

6.1. Influence of Vegetation on Water and Carbon Fluxes

[36] Consistent with previous studies, the ET time series are similar at our grassland and shrubland sites [Dugas *et al.*, 1996; Kurc and Small, 2004]. More specifically, during the CDS ET varies from 0 to 4 mm d⁻¹ and ET declines rapidly from relatively high values following rainstorms to relatively low values within several days (Figure 4). Similarly, outside of the CDS maximum ET values coincide with maximum values of surface soil moisture (Figure 4) at both grassland and shrubland. However, during these times of the year, the declines in ET are less rapid than during the CDS.

[37] Soil moisture observations at depth allow for important insights regarding the differences in the components of ET between the two locations. For instance, time series of soil moisture at 2.5 cm and averaged over 15 cm are very similar at the grassland and shrubland (Figures 3b and 3c). This is true even though grasses distribute the majority of their roots in the top soil layers, whereas the shrubs allocate far fewer roots to those locations (Figure 2). These observations could suggest E is dominant over T in the shallow soil layers at both grassland and shrubland and differences in plant type and soil texture play a small role at these depths. Another explanation is that in the grassland, moisture is able to travel deeper into the soil before being quickly evaporated because of the sandier soil and higher percent cover than at the shrubland; this explanation is

supported by a land surface model study where loamy sand and sandy loam soils contribute significantly less latent heat flux than other soil textures [Gutmann and Small, 2005].

[38] In fact, deeper in the soil profile where soil texture is sandy loam at both sites, the time series of soil moisture is noticeably different between grassland and shrubland (Figure 3d). Specifically, the grassland accumulates more water at depth than the shrubland (Figure 3d). To reiterate, it is possible that sandier soil near the surface at the grassland accounts for water movement deeper into the profile more quickly, or perhaps more bare soil at the shrubland may account for more runoff during these periods immediately following large storms or series of storms. In any case, at depths between about 45 and 75 cm, E is expected to have no effect on ET and the shrubland is characterized by a larger root density than the grassland (Figure 2). With more roots at depth, it is possible that the shrubs transpire using more deep moisture than the grasses or that the rate of T from this deep reservoir is higher in the shrubland than in the grassland. This is supported by the higher r^2 value in the shrubland for the relationship between F_{AS} and root zone soil moisture in the shrubland than in the grassland (Table 3). We note that volumetric water content almost never drops below about 0.1 in the deep soil layer (Figure 3d). At this depth in the soil at both grassland and shrubland, a calcite layer is breached and it is possible that the plants are not capable of pulling more water out of that layer. Alternatively, a soil moisture value of 0.1 at this depth might represent a threshold below which the plants are water-stressed and therefore cease to transpire.

[39] With respect to carbon fluxes, we find that although the timing of the pulses of NEE^+ and NEE^- are similar between our grassland and shrubland sites, the magnitudes of these pulses are different (Figure 4). In fact, using our modeled values, we are able to suggest that F_{AS} and F_{RE} (Figure 6) at this particular grassland are more than twice the magnitude of those at this particular shrubland. If T/ET is the same for the grassland and the shrubland, this result is surprising, but we suspect this is not the case due to the differences in percent vegetative cover and photosynthetic pathway between the sites. Our result is consistent with the work of Emmerich [2003], who described annual fluxes of carbon at a semiarid mixed-species grassland and a mixed-species shrubland within the Walnut Gulch Watershed of southeastern Arizona. In this study, Emmerich [2003] notes higher carbon uptake at the grassland than at the shrubland. The higher carbon uptake is attributed to higher total biomass accumulations during the growing season at the grassland [Emmerich, 2003]. In our study, we did not measure biomass accumulations, but we know that the grassland has a higher percent cover than the shrubland. Additionally, we know that C_4 plants may be prone to greater biomass production, at least under ambient CO_2 conditions, than C_3 plants [Coleman and Bazzaz, 1992; Nguyen *et al.*, 2005; Saunders *et al.*, 2006], further supporting higher carbon uptake at the C_4 grassland.

[40] Higher F_{AS} pulses at the grassland (Figure 6) combined with the minimized water loss during transpiration that characterizes C_4 grasses [Ehleringer and Monson, 1993; McClaran, 1995] suggest a higher WUE_E at the grassland than at the shrubland. Additionally, C_4 plants are generally expected to reach assimilation rates similar to C_3 plants at a

lower stomatal conductance, thereby increasing their WUE_L [Bacon, 2004; Ehleringer and Monson, 1993]. Thus our speculation that the C_4 grassland presented in this study reaches a higher WUE_E than the C_3 shrubland is consistent with the current literature.

6.2. Implications for Models of Root Zone Water Balance

[41] The research presented in this study reveals important differentiations in moisture reservoirs that contribute to ecosystem-scale water and carbon fluxes in semiarid grassland and shrubland, at least during the CDS. These differentiations challenge the use of a single averaged root zone soil moisture as the driver of the water and carbon fluxes used within many ecohydrological models [Daly et al., 2004a; Fernandez-Illescas et al., 2001; Guswa et al., 2002; Laio et al., 2001; Montaldo et al., 2005] as follows. First, we have supported previous research in demonstrating that in these two ecosystems ET is largely correlated with surface soil moisture, not root zone soil moisture (Table 3) [Kurc and Small, 2004]. Second, despite the grasses having a higher density of roots in the top 15 cm than the shrubs, the two ecosystems have identical soil moisture time series in the top 15 cm, possibly suggesting that E is dominant over T within the top 15 cm of soil as discussed in section 6.1. Third, because E should have a minor influence on soil moisture below about 15–20 cm [Boulet et al., 1997; van Keulen and Hillel, 1974; Yamanaka and Yonetani, 1999], T will dominate moisture loss in these deeper soil layers. Fourth, we demonstrate that F_{RE} is governed by soil moisture in the top 15 cm (Table 3) [Tate, 2000]. Finally, we show that NEE^- is well correlated with deep soil moisture (Figure 7) and that our modeled F_A is well correlated with averaged root zone soil moisture (Table 3).

[42] By differentiating between key contributing moisture reservoirs to the components of the water and carbon fluxes, we can argue a simple modification to the conceptual model for the root zone water balance for semiarid ecosystems. This simple modification would be a compromise between bucket models and the sophisticated vertically resolved models that require more detailed information about the ecosystem, making them far less efficient [Guswa et al., 2002]. In this modification the root zone would be split into two layers: a shallow layer (e.g., 0–15 cm) and a deep layer (e.g., >15 cm). Moisture within the shallow layer would govern E and F_{RE} , whereas moisture within the deep layer would govern T and F_{AS} . Our data suggest that the proposed modification for similar ecosystems would be more robust than a bucket model driven by a single root zone soil reservoir [Laio et al., 2001; Guswa et al., 2002; Daly et al., 2004b] yet simple enough to be more efficient than the vertically discretized one-dimensional Richards model [Guswa et al., 2002].

6.3. Interannual and Seasonal Variability in Water and Carbon Fluxes

[43] Our observations of soil moisture, ET , and NEE suggest the grassland and shrubland fix carbon during a specific period or periods favorable for photosynthesis (Figure 6). These appear to be particularly wet periods of persistent soil moisture following a large storm or series of storms that may or may not occur during the CDS, and vary in timing from year to year. This concept is consistent with a

recent modeling study that concluded that periods of biological activity coincide with a single large storm or collection of storms that produce reliable soil moisture at depth [Reynolds et al., 2004]. In a different type of study, Turner et al. [2005] compare modeled predictions of gross primary production (GPP) conditioned on Moderate Resolution Imaging Spectroradiometer (MODIS) satellite data to ground-based predictions using eddy covariance towers. They found that the Sevilleta NWR grassland, during a year with two wet periods (2002), had a unique bimodal GPP time series whereas five other ecosystems had a more standard unimodal time series of GPP [Turner et al., 2005]. Combined results from this study and the Turner et al. [2005] study suggest that net carbon uptake at the Sevilleta NWR grassland is strongly coupled with periods favorable for growth and is quite different from ecosystems that see net carbon uptake throughout an entire growing season. Accordingly, future field efforts should take this seemingly unpredictable nature of growth periods into account when estimating primary productivity and/or making predictions regarding the carbon balance.

[44] Other studies in water-limited ecosystems have seen similar interannual variability in water and carbon cycling. Paruelo et al. [2000] found that within a precipitation gradient in the Patagonian steppe, interannual variability of annual T and E increased as amount of rainfall decreased from 500 to 100 mm. In another study, Hastings et al. [2005] showed that at their desert shrubland site, with 174 mm of rainfall annually, the magnitude of the peak seasonal carbon uptake varied year to year. They suggest that this type of interannual variability may be a cause for the ecosystem to shift from a carbon source to a carbon sink in particularly dry years [Hastings et al., 2005].

6.4. Interconnected Water and Carbon Dynamics in Water-Limited Ecosystems

[45] In a recent study, Huxman et al. [2004] describe a conceptual model (hereinafter the Huxman model) where dynamics of ecosystem F_{RE} and F_{AS} in arid environments are determined by pulses of water availability delivered by precipitation events. In their model, rapid microbial response is expected following even small rainfall events, but larger events are required for water to penetrate deep enough into the soil profile so that this deeper soil moisture can be used for F_{AS} without being quickly lost to E [Huxman et al., 2004]. Additionally, peak carbon accumulation is expected to lag behind arrival of soil moisture at depth as physiological processes may require time to adjust to the available moisture [Huxman et al., 2004; Ogle and Reynolds, 2004]. The observations from our study are consistent with the Huxman model. We observe carbon efflux spike immediately following rainstorms (Figure 4 and Figure 5). Furthermore, carbon uptake only follows a large event or series of events that provides enough water to infiltrate deep into the soil profile (Figure 4). During these pulses of F_{AS} , peak carbon uptake occurs several days or weeks after the storm or series of storms (Figure 4).

[46] Similar to our study, Scott et al. [2006] found evidence supporting the Huxman model using Bowen ratio observations made in a desert shrubland. In their study, they show that F_{RE} spikes immediately in response to moisture pulses. Additionally, they provide evidence of soil moisture pulse response for T using sap flow techniques [Scott et al.,

2006]. These observations demonstrate that E and F_{RE} peak the day after a precipitation event followed by a lagged T response that peaks a few days after the event [Scott *et al.*, 2006]. Given that T is well correlated with F_{AS} in their study, this is indirect evidence of lagged F_{AS} response. Other studies in semiarid ecosystems have shown similar results where the ratio of transpiration to evapotranspiration (T/ET) or the ratio of assimilation to net ecosystem exchange ($|F_A|/|NEE|$) is initially low following a storm, increases for a few days, and then decreases again [Hastings *et al.*, 2005; Yepez *et al.*, 2005].

[47] Clearly, precipitation events yield soil moisture pulses with a wide range of soil moisture conditions throughout the root zone, leading to various combinations of F_{RE} and F_{AS} and also E and T . Therefore different precipitation events should lead to a wide range of WUE_E values. However, using data from a semiarid African savanna, Williams and Albertson [2004] showed evidence that ET/NEE is constant (over 20 days), using daytime hour values, i.e., 0900–1600, and therefore report a constant WUE_E . However, if WUE_E should represent T/F_{AS} at the ecosystem level, their results are misleading because while F_{RE} is probably minimized at these times, E may still be a large component of ET especially given their fraction of bare soil was at least 20%. Similarly misleading, in an arid forest of the Negev desert, Grunzweig *et al.* [2003] found that ET/NEE was constant from month to month when using only daytime values and report a constant WUE_E , without reporting a percent of bare soil. In our study, looking at ET/NEE over the entire day, we report a possible constant WUE_E but under very rare occurrences (Figure 7). These occurrences coincide with times when the surface soil is dry but soil deeper in the profile was still wet, i.e., times when ecosystem fluxes of E and F_{RE} should be negligible and when fluxes of T and F_{AS} should be relatively high (Figure 7), allowing for ET to consist mainly of T and for NEE to consist mainly of F_{AS} . Again, these soil moisture conditions are rare occurrences, possibly only 5% of the entire year. We suspect that a constant WUE_E can occur at other times but that these times would be difficult to generalize.

[48] **Acknowledgments.** This study is based on research supported in part by the National Science Foundation under grant EAR-0241604 and by SAHRA (Sustainability of Semi-Arid Hydrology and Riparian Areas) under the STC program of the National Science Foundation (agreement 9876800). Additional support was provided by the Sevilleta LTER Program (NSF grant DEB-0080529). We thank Jim Elliott and John Boulanger for their assistance in the collection of this data. Finally, we would like to thank Russ Scott, Peter Blanken, Ethan Gutmann, Dave Bedford, Jason Neff, and four anonymous reviewers for their helpful insights and suggestions.

References

- Bacon, M. (2004), *Water Use Efficiency in Plant Biology*, Blackwell, Malden, Mass.
- Baldocchi, D. (1997), Flux footprints within and over forest canopies, *Boundary Layer Meteorol.*, *85*, 273–292.
- Blanken, P. D., et al. (1998), Turbulent flux measurements above and below the overstory of a boreal aspen forest, *Boundary Layer Meteorol.*, *89*, 109–140.
- Boulet, G., et al. (1997), Study of the mechanisms of evaporation under arid conditions using a detailed model of the soil-atmosphere continuum: Applications to the EFEDA I experiment, *J. Hydrol.*, *193*, 114–141.
- Breshears, D., et al. (1997), Differential use of spatially heterogeneous soil moisture by two semiarid woody species: *Pinus edulis* and *Juniperus monosperma*, *J. Ecol.*, *85*, 289–299.
- Breshears, D. D., and F. J. Barnes (1999), Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland continuum: A unified conceptual model, *Landscape Ecol.*, *14*, 465–478.
- Cable, D. (1969), Competition in the semidesert grass-shrub type as influenced by root systems, growth habits, and soil moisture extraction, *Ecology*, *50*(1), 27–38.
- Coleman, J. S., and F. A. Bazzaz (1992), Effects of CO₂ and temperature and growth and resource use of cooccurring C3 and C4 annuals, *Ecology*, *73*(4), 1244–1259.
- Connin, S. L., et al. (1997), Carbon isotopes reveal soil organic matter dynamics following arid land shrub expansion, *Oecologia*, *110*, 374–386.
- Daly, E., et al. (2004a), Coupled dynamics of photosynthesis, transpiration, and soil water balance: Part I. Upscaling from hourly to daily level, *J. Hydrometeorol.*, *5*, 546–558.
- Daly, E., et al. (2004b), Coupled dynamics of photosynthesis, transpiration, and soil water balance: Part II. Stochastic analysis and ecohydrological significance, *J. Hydrometeorol.*, *5*, 559–566.
- Dugas, W. A., et al. (1996), Structure and function of C3 and C4 Chihuahuan desert plant communities: Energy balance components, *J. Arid Environ.*, *34*, 63–79.
- Ehleringer, J., and R. Monson (1993), Evolutionary and ecological aspects of photosynthetic pathway variation, *Annu. Rev. Ecol. Syst.*, *24*, 411–439.
- Emmerich, W. E. (2003), Carbon dioxide fluxes in a semiarid environment with high carbonate soils, *Agric. For. Meteorol.*, *116*, 91–102.
- Fernandez-Illescas, C. P., A. Porporato, F. Laio, and I. Rodriguez-Iturbe (2001), The ecohydrological role of soil texture in a water-limited ecosystem, *Water Resour. Res.*, *37*(12), 2863–2872.
- Frank, A., et al. (2002), Soil carbon dioxide fluxes in northern semiarid grasslands, *Soil Biol. Biogeochem.*, *34*, 1235–1241.
- Franzluebbers, K., et al. (2002), Environmental controls on soil and whole-ecosystem respiration from a tallgrass prairie, *Soil Sci. Soc. Am. J.*, *66*, 254–262.
- Grunzweig, J. M., et al. (2003), Carbon sequestration in arid-land forest, *Global Change Biol.*, *9*, 791–799.
- Guswa, A., M. A. Celia, and I. Rodriguez-Iturbe (2002), Models of soil moisture dynamics in ecohydrology: A comparative study, *Water Resour. Res.*, *38*(9), 1166, doi:10.1029/2001WR000826.
- Gutmann, E., and E. Small (2005), The effect of soil hydraulic properties versus soil texture in land surface models, *Geophys. Res. Lett.*, *32*, L02402, doi:10.1029/2004GL021843.
- Hastings, S. J., et al. (2005), Diurnal, seasonal and annual variation in the net ecosystem exchange of a desert shrub community (Sarcocaulis) in Baja California, Mexico, *Global Change Biol.*, *11*, 927–939.
- Hibbard, K. A., et al. (2001), Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna, *Ecology*, *82*(7), 1999–2011.
- Huxman, T. E., et al. (2004), Precipitation pulses and carbon fluxes in semiarid and arid ecosystems, *Oecologia*, *141*, 254–268.
- Huxman, T., et al. (2005), Ecohydrological implications of woody plant encroachment, *Ecology*, *86*(2), 308–319.
- Jarvis, P. (1976), The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field, *Philos. Trans. R. Soc. London*, *273*, 593–610.
- Kimball, B. A., et al. (1976), Soil-heat flux determination: Temperature gradient method with computed thermal conductivities, *Soil Sci. Soc. Am. J.*, *40*, 25–28.
- Kurc, S., and E. Small (2004), Dynamics of evapotranspiration in semiarid grassland and shrubland ecosystems during the summer monsoon season, central New Mexico, *Water Resour. Res.*, *40*, W09305, doi:10.1029/2004WR003068.
- Laio, F., et al. (2001), Plants in water-controlled ecosystems: Active role in hydrologic processes and response to water stress: II. Probabilistic soil moisture dynamics, *Adv. Water Resour.*, *24*, 707–723.
- McClaran, M. (1995), Desert grasslands and grasses, in *The Desert Grassland*, edited by M. McClaran and T. Van Devender, pp. 1–30, Univ. of Ariz. Press, Tucson.
- Mielnick, P., and W. Dugas (2000), Soil CO₂ flux in a tallgrass prairie, *Soil Biol. Biogeochem.*, *32*, 221–228.
- Moncrieff, J., et al. (2000), Canopy fluxes, in *Methods in Ecosystem Science*, edited by O. Sala *et al.*, pp. 161–180, Springer, New York.
- Montaldo, N., R. Rondona, J. D. Albertson, and M. Mancini (2005), Parsimonious modeling of vegetation dynamics for ecohydrologic studies of water-limited ecosystems, *Water Resour. Res.*, *41*, W10416, doi:10.1029/2005WR004094.
- Nguyen, M. T. P., et al. (2005), Comparison of growth feature and drought tolerance between two high productive species, kenaf (*Hibiscus cannabinus*, C3-plant) and napiergrass (*Pennisetum purpureum*, C4-plant), *J. Fac. Agric. Kyushu Univ.*, *50*(2), 521–532.

- Ogle, K., and J. F. Reynolds (2004), Plant responses to precipitation in desert ecosystems: Integrating functional types, pulses, threshold, and delays, *Oecologia*, *141*, 282–294.
- Paruelo, J. M., et al. (2000), Long-term dynamics of water and carbon in semi-arid ecosystems: A gradient analysis in the Patagonian steppe, *Plant Ecol.*, *150*, 133–143.
- Pattey, E., et al. (2002), Measuring nighttime CO₂ flux over terrestrial ecosystems using eddy covariance and nocturnal boundary layer methods, *Agric. For. Meteorol.*, *113*, 145–158.
- Phillips, F. M. (1994), Environmental tracers for water movement in desert soils of the American Southwest, *Soil Sci. Soc. Am. J.*, *58*, 15–24.
- Porporato, A., et al. (2001), Plants in water-controlled ecosystems: Active role in hydrologic processes and response to water stress: III. Vegetation water stress, *Adv. Water Resour.*, *24*, 725–744.
- 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*, 999–1017.
- Reynolds, J. F., et al. (2004), Modifying the “pulse-reserve” paradigm for deserts of North America: Precipitation pulses, soil water, and plant responses, *Oecologia*, *141*, 194–210.
- Rodriguez-Iturbe, I., et al. (2001), Plants in water-controlled ecosystems: Active role in hydrologic processes and response to water stress: I. Scope and general outline, *Adv. Water Resour.*, *24*, 695–701.
- Sala, O., et al. (1992), Long-term soil water dynamics in the shortgrass steppe, *Ecology*, *73*(4), 1175–1181.
- Sala, O. E., and W. K. Lauenroth (1982), Small rainfall events: An ecological role in semiarid regions, *Oecologia*, *53*(3), 301–304.
- Saunders, C. J., et al. (2006), Comparison of belowground biomass in C-3- and C-4-dominated mixed communities in a Chesapeake Bay brackish marsh, *Plant Soil*, *280*(1–2), 305–322.
- Schenk, H. J., and R. B. Jackson (2002), Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems, *J. Ecol.*, *90*(3), 480–494.
- Schmidt, A. (2004), The effects of variable green fraction on land atmosphere fluxes and soil moisture in semi-arid environments, simulated using the Noah LSM, M.S. thesis, 83 pp., Univ. of Colo., Boulder.
- Scott, R., et al. (2004), Interannual and seasonal variation in fluxes of water and carbon dioxide from a riparian woodland ecosystem, *Agric. For. Meteorol.*, *122*, 65–84.
- Scott, R., et al. (2006), Partitioning of evapotranspiration and its relation to carbon dioxide exchange in a Chihuahuan Desert scrubland, *Hydrol. Processes*, *20*, 3227–3243.
- Shuttleworth, W. J. (1993), Evaporation, in *Handbook of Hydrology*, edited by D. Maidement, 4.1–4.53, McGraw-Hill, New York.
- Small, E. (2005), Climatic controls on diffuse groundwater recharge in semiarid environments of the southwestern United States, *Water Resour. Res.*, *41*, W04012, doi:10.1029/2004WR003193.
- Tate, R. L. (2000), Impact of individual soil properties on microbial activity, in *Soil Microbiology*, pp. 125–158, John Wiley, Hoboken, N. J.
- Turner, D. P., et al. (2005), Site-level evaluation of satellite-based global terrestrial gross primary production and net primary production monitoring, *Global Change Biol.*, *11*, 666–684.
- van Keulen, H., and D. Hillel (1974), A simulation study of the drying-front phenomenon, *Soil Sci.*, *118*, 270–273.
- Walter, H. (1971), *Ecology of Tropical and Subtropical Vegetation*, Oliver and Boyd, White Plains, N. Y.
- Williams, C. A., and J. D. Albertson (2004), Soil moisture controls on canopy-scale water and carbon fluxes in an African savanna, *Water Resour. Res.*, *40*, W09302, doi:10.1029/2004WR003208.
- Yamanaka, T., and T. Yonetani (1999), Dynamics of the evaporation zone in dry sandy soils, *J. Hydrol.*, *217*, 135–148.
- Yepez, E. A., et al. (2005), Dynamics of transpiration and evaporation following a moisture pulse in semiarid grassland: A chamber based isotope method for partitioning flux components, *Agric. For. Meteorol.*, *132*, 359–376.

S. A. Kurc, School of Natural Resources, University of Arizona, 325 BSE, P.O. Box 210043, Tucson, AZ 85721-0043, USA. (kurc@ag.arizona.edu)

E. E. Small, University of Colorado, 2200 Colorado Avenue, Campus Box 399, Boulder, CO 80309-0399, USA.