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Partitioning of evapotranspiration and its relation to carbon dioxide exchange in a Chihuahuan Desert shrubland

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Abstract:

Key to evaluating the consequences of woody plant encroachment on water and carbon cycling in semiarid ecosystems is a mechanistic understanding of how biological and non-biological processes influence water loss to the atmosphere. To better understand how precipitation is partitioned into the components of evapotranspiration (bare-soil evaporation and plant transpiration) and their relationship to plant uptake of carbon dioxide (CO₂) as well as ecosystem respiratory efflux, we measured whole plant transpiration, evapotranspiration, and CO₂ fluxes over the course of a growing season at a semiarid Chihuahuan Desert shrubland site in south-eastern Arizona. Whole plant transpiration was measured using the heat balance sap-flow method, while evapotranspiration and net ecosystem exchange (NEE) of CO₂ were quantified using the Bowen ratio technique.

Before the summer rainy season began, all water and CO₂ fluxes were small. At the onset of the rainy season, evapotranspiration was dominated by evaporation and CO₂ fluxes were dominated by respiration as it took approximately 10 days for the shrubs to respond to the higher soil moisture content. During the growing season, periods immediately following rain events (<2 days) were dominated by evaporation and respiration while transpiration and CO₂ uptake peaked during the interstorm periods. The surface of the coarse, well-drained soils dried quickly, rapidly reducing evaporation. Overall, the ratio of total transpiration to evapotranspiration was 58%, but it was around 70% during the months when the plants were active. Peak respiration responses following rain events generally lagged after the evaporation peak by a couple of days and were better correlated with transpiration. Transpiration and CO₂ uptake also decayed rather quickly during interstorm periods, indicating that optimal plant soil moisture conditions were rarely encountered. NEE of CO₂ was increasingly more negative as the growing season progressed, indicating a greater net uptake of CO₂ and greater water use efficiency due mainly to decreases in respiration. Copyright © 2006 John Wiley & Sons, Ltd.

KEY WORDS woody plant encroachment; evapotranspiration; net ecosystem exchange; Chihuahuan Desert; shrubland; evaporation; transpiration; respiration; gross ecosystem exchange

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INTRODUCTION

Arid and semiarid biomes cover a large portion of the Earth's terrestrial surface (Branson *et al.*, 1972), and the regulation of hydrological and biogeochemical processes by biological, geomorphic, environmental, and climatic factors in these regions has long been an important research topic (Noy-Meir, 1973; Dunne *et al.*, 1991; Whitford, 2002; Reynolds *et al.*, 2004). Patterns of soil water availability exert overwhelming control over biogeochemistry in these regions, not only by filtering potential vegetation type but also by determining specific temporal windows during which biologically-mediated chemical transformations can occur

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(Noy-Meir, 1973; Austin *et al.*, 2004; Huxman *et al.*, 2004a). In turn, vegetation type and geomorphology interact to affect how water is partitioned following precipitation in different hydroclimatic zones. In these regions, the response of the biological component of the system to climatic forcing such as rising CO₂ or temperature are mediated through variation in soil water availability (Hamerlynck *et al.*, 2000; Smith *et al.*, 2000). As such, there has been an important push to understand how ecological and hydrological cycles are coupled in both time and space for these regions (Huxman *et al.*, 2004a; Scott *et al.*, 2006).

In water-limited systems, large-scale changes in vegetation are an important component of global change. One example of these vegetation changes is the increase of woody plant density, as has been seen in the western US and much of the Earth's semiarid areas (e.g. Archer, 1994; McPherson, 1997), which has potential large-scale ramifications for both carbon (Archer *et al.*, 2001; Pacala *et al.*, 2001; Jackson *et al.*, 2002) and water cycling (Wilcox, 2002; Huxman *et al.*, 2005). A crucial issue in understanding how this change in vegetation type will alter water and carbon cycling in ecosystems is how evapotranspiration (ET) may be differentially partitioned into its biological (transpiration) or non-biological (evaporation) component fluxes (Huxman *et al.*, 2005; Reynolds *et al.*, 2000). Woody plant encroachment often results in a decrease in vegetation cover and increase in bare-soil surfaces. Thus, it has been hypothesized that there will be an increase in evaporation relative to transpiration that may be associated with changes in plant productivity and soil carbon processes following precipitation events (Huxman *et al.*, 2005). These processes combine to affect the ecosystem carbon budget. Unfortunately, data on the partitioning of ET coupled with carbon exchange characteristics at a sufficient temporal and spatial scale are lacking in order to better understand this challenging question of global change.

Using a combination of micro-meteorological (e.g. a Bowen ratio or eddy covariance system), hydrological (e.g. micro-lysimeters), and eco-physiological techniques (e.g. sap-flow measurements, stable isotopes), it is possible to determine the partitioning of the above-canopy water vapour exchange into its component fluxes for some ecosystems. Ecosystem ET has been partitioned into bare-soil evaporation, interception reservoir evaporation, and transpiration from the overstory and understory vegetation (e.g. Barbour *et al.*, 2005; Dugas *et al.*, 1996; Ham *et al.*, 1990; Scott *et al.*, 2003; Williams *et al.*, 2004; Yezzer *et al.*, 2003). Often, these studies have been over relatively short time periods (days to weeks) and data for woody plant encroached areas are sparse.

Despite the importance of ET partitioning data for determining the ecohydrological dynamics, only a few empirical studies have quantified T/ET in semiarid shrublands over limited time periods, and the results yield a wide range (7–80%) of estimates (as summarized by Reynolds *et al.*, 2000). This wide range of results is likely attributable to differences in methodologies and the inherent seasonal and inter-annual variability of the fluxes in these regions. As an alternative, Reynolds *et al.* (2000) determined annual T/ET over a 100-year period using a mechanistic ecosystem model for a Chihuahuan Desert shrub-dominated community and found that it varied greatly from year to year (6–60%, mean of 34%) because of seasonal patterns of precipitation, differential water use by different plant types, and the varying ET contribution of annual plants. Not only is there a lack of studies that have examined the components of ET, but also there have been few studies that have tried to understand how water exchanges are linked to ecosystem processes (canopy photosynthesis and ecosystem respiration) that underlie the net CO₂ exchange.

Micro-meteorological measurements are also used to quantify the net ecosystem exchange (NEE) of CO₂. Using a variety of methods, NEE can be separated into its component respiratory (R) and gross ecosystem production (GEP) terms:

$$NEE = R - GEP \quad (1)$$

where the sign convention adopted here is that *R* and *GEP* are always positive and *NEE* less than zero indicates a net uptake of CO₂ by the land surface. *GEP* is the photosynthetic activity of plants in the ecosystem, and thus should be at least proportional to water loss to the atmosphere through transpiration (Enquist, 2002; Huxman *et al.*, 2004a). Ecosystem respiration quantifies plant (autotrophic), microbial (heterotrophic), and possibly, inorganic carbonate dynamics. The relationship of respiration to evaporation and transpiration is not well

known, but it is likely to be correlated with near-surface soil water status. This is especially true for systems dominated by wet–dry cycles where a substantial contribution of soil micro-organisms to the CO₂ efflux is expected (Austin *et al.*, 2004; Huxman *et al.*, 2004a). However, some fraction of efflux should be related to the respiratory activity of plants and correlated with deeper, rooting zone soil moisture and transpiration (Franzluebbers *et al.*, 2002; Chimner and Welker, 2005), and another fraction could be related to the release of CO₂ from the precipitation of carbonates in the soil profile during drying cycles (Emmerich, 2003).

In this paper, we report on the results of a study conducted over the summer and fall rainy season in a Chihuahuan Desert shrubland in south-eastern Arizona, USA, in order to better understand the relationship between key ecosystem component fluxes on the water and carbon balance of a spatially extensive semiarid ecosystem. In this study, we measured ecosystem-scale ET and NEE and simultaneously quantified the plant transpiration. By measuring plant transpiration and total ET, we partitioned daily total water vapour fluxes to determine evaporation and transpiration separately following different sized rainfall events. We then analysed the coupled response of evaporation and transpiration and their covariation with respiration and GEP using this unique dataset. Owing to the high degree of seasonal and inter-annual rainfall variability in this region, the specific magnitude of the ET and NEE partitioning that we found is likely to be unique (Reynolds *et al.*, 2000; Emmerich, 2003). Thus, we emphasize the importance of the general patterns of how ET was partitioned and how this was related to CO₂ uptake and release over a complete growing season.

METHODS

Using Bowen ratio and sap-flow methods, we monitored evapotranspiration, NEE, and transpiration through the end of the 2003 summer rainy season for a Chihuahuan Desert shrubland community. In addition to these fluxes, basic hydrometeorologic measurements were also made to determine the relationship between environmental forcing variables and states on ecosystem carbon and water fluxes.

Site description

This study took place at the Lucky Hills study site on the USDA-ARS Walnut Gulch Experimental Watershed in south-eastern Arizona. This site has been described in some detail elsewhere (Kustas and Goodrich, 1994; Scott *et al.*, 2000; Emmerich, 2003) as it has been the focus for numerous surface hydrology studies. Briefly, the site is a Chihuahuan Desert shrubland, dominated by a diverse stand of mainly Chihuahuan Desert shrub species. As determined by a 2003 survey of stem basal area, the dominant shrubs in order of decreasing abundance were: creosotebush (*Larrea tridentata*), mariola (*Parthenium incanum*), whitethorn acacia (*Acacia constricta*), littleleaf sumac (*Rhus microphylla*), and tarbush (*Flourensia cernua*). The shrub heights range from ~0.3–1.0 m. Most of the ground between the shrub canopies consists of bare and rocky soil (39% bare-soil cover of which 47% is composed of rock) with very small amounts of herbs and grasses. About 10% of the surface is covered with plant litter, and the canopy coverage is 51% (data collected on 19 Oct 2004, B. Emmerich, unpublished data). On average, 70% of the total fine root mass in the soil is confined within 0.15 m of the surface, with exponentially decreasing amounts down to about 1 m (Cox *et al.*, 1986). The soils are gravelly-sandy loams with a high percentage of rock fragments. Average 1970–1999 annual rainfall is 322 mm, with about 60% average fall during the months of July–September as part of the North American Monsoon (Adams and Comrie, 1997).

Instrumentation

Ecosystem water vapour and carbon dioxide fluxes were monitored using Bowen ratio methods. From 1997 to date, Bowen ratio data have been collected at the site as a part of the USDA-ARS rangeland carbon initiative (Emmerich, 2003; Svejcar *et al.*, 1997). In order to better understand how the water and carbon fluxes were influenced by key forcing parameters, a host of additional hydrometeorologic measurements are

continuously monitored at this site. They are (1) net radiation (Q7, REBS, Seattle, WA, USA¹), (2) average soil heat flux from five soil heat flux plates (HFT3, REBS) and soil thermocouples above each heat flux plate, (3) wind speed and direction (Wind Sentry, R.M. Young Company, Traverse City, MI, USA), (4) air temperature and relative humidity (HMP35c, Vaisala, Inc., Woburn, MA, USA), and (5) incoming and reflected photosynthetically active radiation, PAR (LI-190, LI-COR, Inc. Lincoln, NE, USA). Also, precipitation was monitored using an ARS weighing-type recording raingage and run-off from the small 4.4 ha watershed that the study took place in was measured using a super critical flow flume (Renard *et al.*, 1993). Volumetric soil moisture was measured under bare ground and shrub-covered profiles at 0.05, 0.15, 0.30, 0.50, 0.75, 1.0 and 2.0 m depths using time domain reflectometry (TDR100, Campbell Scientific Inc.) and a dielectric-soil moisture calibration curve was developed for the site-specific soils.

Bowen ratio. Continuous, 20-min average carbon and water vapour flux measurements were made using a Bowen ratio energy balance (BREB) system at the Lucky Hills site (Model 023/CO₂ Campbell Scientific Inc.). The system was located in an area with a fetch of >1 km in all directions. The theory and procedures used to calculate the fluxes has been presented in detail by Dugas (1993) and Dugas *et al.* (1999). Briefly, atmospheric gradients of air temperature, moisture, and CO₂ were measured every 2 s and averaged every 20 min. Gradients were measured between 1.5 m and 3.0 m above the soil surface. Atmospheric carbon dioxide and moisture concentrations were measured with an infrared gas analyser (IRGA) (LI-6262, LI-COR, Inc.). Temperature and water vapour gradients were used to calculate the Bowen ratio.

Sap-flow. Shrub transpiration was measured using the constant heat balance sap-flow technique (Kjelgaard *et al.*, 1997). This method employs a heater to input energy into the stem and thermocouples to measure the heat lost to conduction up and down the stem and radially through the insulation around the stem. The remaining component in the heat balance is the heat lost through convection due to transpiration, which is calculated as the difference between the heat inputs and outputs. The convection component (transpiration) of the heat balance can then be converted to a mass flow using the specific heat of water (Kjelgaard *et al.*, 1997). We instrumented 16 individual stems (13 creosote and 3 littleleaf sumac) using homemade sensors and insulated them with pipe insulation and reflective bubble wrap. The sensors were measured every 5 s with a datalogger and multiplexer (CR10X and AM416, Campbell Scientific Inc.) and averages were output every 30 min. A voltage regulator was used to control the amount of heat applied to the stems. Radial conductance was calculated daily between 2:00 and 4:00 am (local time) as it tended to drift slightly throughout the season. These sensors have been shown to work successfully on similar types of shrubs (Pataki *et al.*, 2000), and we compared sap flow-derived canopy stomatal conductances with leaf-level stomatal conductances using a portable photosynthetic gas exchange system (LI-COR 6400, LI-COR, Inc.). Using three days of gas exchange measurements, we found a good agreement between the two conductances ($R^2 = 0.82$), with estimates derived from sap-flow measurements being slightly less than leaf-level ones due probably to the boundary-layer effects not accounted for in the leaf-level estimates. This result was very similar to that of Pataki *et al.* (2000) and confirmed the ability of the sap-flow sensors to capture the diurnal dynamics of canopy water loss.

Calculations

Evapotranspiration and net ecosystem exchange. Bowen ratio, net radiation, soil heat flux, and soil temperature were used to calculate sensible heat flux. Eddy diffusivity was calculated from sensible heat fluxes and temperature gradients and assumed to be equal for heat, water vapour, and CO₂. Eddy diffusivity could not be calculated when sensible/latent heat flux was in the opposite direction of temperature/water vapour gradients, or when Bowen ratio approached -1.0 (Ohmura, 1982). Under these conditions, eddy

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diffusivity was calculated by using wind speed, atmospheric stability, and canopy height (Dugas *et al.*, 1999). This alternative method for calculating eddy diffusivity was used about 12% of the time, primarily at night when gradients and fluxes were small, hence any errors from the alternative method would have minimal impact on the calculated flux values. For short periods of time, usually at sunset and sunrise and when Bowen ratio was near -1.0 , fluxes were estimated by linear interpolation, with less than 5% of the data interpreted in this way. Normally, fluxes were calculated as the product of the eddy diffusivity and CO_2 gradient corrected for vapour density gradients at the two heights (Webb *et al.*, 1980). Temperature corrections for the two heights were not applied, as Angell *et al.* (2001) have shown the temperature differences to be insignificant as the air enters the IRGA for analysis.

We examined the NEE data to determine whether there were problems with its under-estimation due to poor turbulent mixing in more quiescent periods (Goulden *et al.*, 1996). Although such problems are not typically reported for studies using the Bowen ratio technique, many studies using eddy covariance have reported that fluxes, even over short vegetation, are likely under-estimated during periods of poor turbulence (e.g. Flanagan *et al.*, 2002; Xu and Baldocchi, 2004). Similar conditions should present problems for Bowen ratio measurements as well, especially owing to the two different sampling heights. Following a methodology similar to Gu *et al.* (2005), we computed the average night-time CO_2 flux over increasing values of wind speed thresholds using several ten-day periods when soil moisture and temperature were fairly uniform and night-time respiration was expected to be constant. Wind speed was used as a surrogate for turbulent intensity since the commonly used friction velocity (u^*) was not quantified by the Bowen ratio system. Results were inconclusive, with slightly increasing, decreasing (all non-significant at $P = 0.25$), or non-changing fluxes with increasing wind speeds. Thus, we did not employ a low turbulence filter on the fluxes.

Transpiration and evaporation. We first determined the stem-level sap-flow per unit cross-sectional area of stem, J_i [L/T], for all functioning sensors (maximum of 16). From these 30-min data we computed the average sap-flow velocity, $\langle J \rangle$, for all stems that were measured. We then scaled this stem-level average to derive a shrub transpiration, T [L/T], that was commensurate in scale to the micro-meteorological measurements using

$$T = \alpha \langle J \rangle \quad (2)$$

where α is a scaling factor that represents the area of branches per area of land surface. α was determined at the end of the study period by a stem-survey of the shrub branches around the tower site, conducted by estimating the amount of stem area within three 1×100 m belt transects, and then computing the amount of stem area per unit land surface area. This assumes that all shrubs transpired similarly, independent of shrub type, and that sap-flow scales with the branch cross-sectional area.

Bare-soil evaporation was not measured independently in this study owing to our lack of recording micro-lysimeters and the difficulties in obtaining a spatially-representative estimate for an entire growing season from small-scale micro-lysimeters. Nevertheless, it is a common practice to estimate a component flux as a residual (Barbour *et al.*, 2005; Dugas *et al.*, 1996; Scott *et al.*, 2003; Williams *et al.*, 2004), and we can check whether the independent estimates of T and ET are compatible. As the time from the last precipitation event increased in an interstorm period, it is reasonable to expect that T increasingly dominates an ET signal because surface soil rapidly dries, increasing the resistance to water flux from deeper layers despite a large demand from the atmosphere (Wythers *et al.*, 1999). The magnitude of T , derived from the scaled sap-flow data (Equation (2)), and ET agreed well during these interstorm periods (Figure 1), providing some confidence for our scaling approach and the subtractive method for determining E from micro-meteorological and eco-physiological techniques.

After computing T , we computed daily averages and calculated a daily evaporation, E , by subtraction from daily ET . This procedure produced a number of days where E was slightly less than zero and they showed a small positive linear trend (less negative values) in time. This trend may be attributable to an over-estimation of α toward the beginning of the study, which is arguably consistent with shrub stem growth or increases

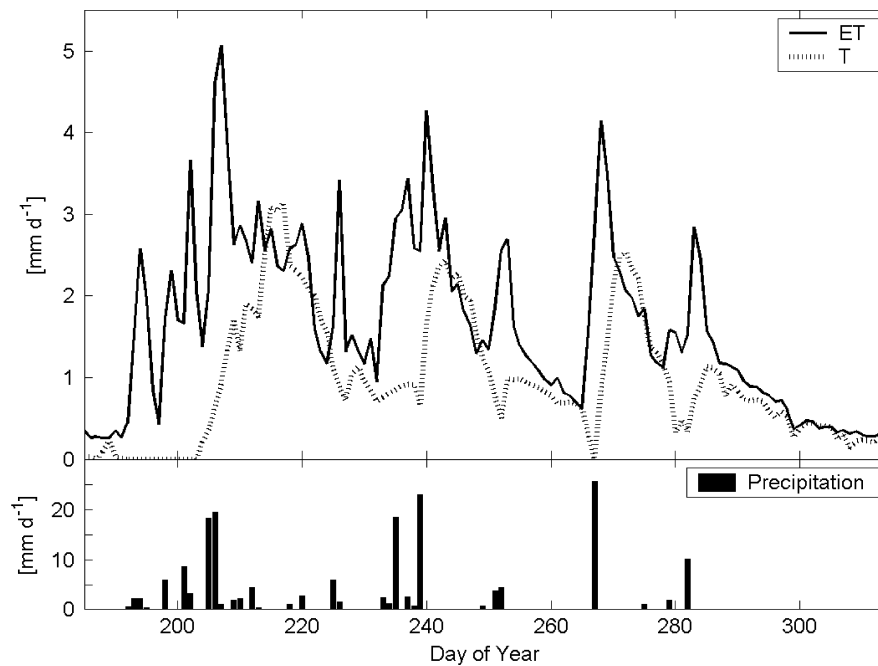


Figure 1. Daily evapotranspiration (ET), shrub transpiration (T), and precipitation. Shrub transpiration in this plot has not yet been corrected for days when $T > ET$

in shrub leaf area throughout the growing season. To minimize these cases with $E < 0$ we added the linear trend, computed by a least squares fit, to E and subtracted this same amount from T . The result left only a few values of E that were less than zero and these small values were set equal to zero.

Respiration and gross ecosystem production. Daily respiration (R) was determined by

$$R = f_{\text{night}}R_{\text{night}} + (1 - f_{\text{night}})R_{\text{day}} \quad (3)$$

where f_{night} is the daily fraction of night-time hours, and R_{night} is average night-time NEE. The daytime respiration, R_{day} , was derived by using the relationship

$$R = b_1 e^{b_2 T_s} \quad (4)$$

where b_1 and b_2 are two fitting parameters and T_s is the average soil temperature at 2 and 6 cm depths. The fitting parameters in Equation (4) were derived using R_{night} and night-time averages of T_s . Owing to the dependency of respiration on volumetric water content at 5 cm ($\theta_{5 \text{ cm}}$), parameters for Equation (4) were determined for each decile of $\theta_{5 \text{ cm}}$. Then, R_{day} was computed using the parameters appropriate for the value of $\theta_{5 \text{ cm}}$ and daytime average of T_s . Following the determination of R , we computed GEP using Equation (1).

Using Equation (4) to develop a relationship with R_{night} , T_s , and $\theta_{5 \text{ cm}}$ resulted in only a marginal fit of the data (RMSE = $0.66 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $R^2 = 0.49$). Several other approaches were also tried, but the results were worse. Consequently, we caution that the computed R and GEP presented below likely contain considerable error. This uncertainty is not unexpected owing to the myriad of processes, not accounted for in the standard respiration models, that may influence total CO_2 efflux in semiarid areas and which include (1) the physical displacement of CO_2 following rainfall event, (2) the biological activity of both aboveground and belowground autotrophic biomass, (3) the microbial activity in close association with roots and the microbial

activity associated with 'slower' pools of carbon, and (4) physical transformations (Huxman *et al.*, 2004b; Fisher and Whitford, 1995; Emmerich, 2003).

RESULTS AND DISCUSSION

Evapotranspiration partitioning

The increasing dew point temperatures, beginning around DOY 190, reflected the onset of the summer rainy season (Figure 2a). Monsoon rains began on DOY 192 at the site, following the long, and typical, period of hot and dry weather associated with the fore-summer drought in this region (Adams and Comrie, 1997). The rainy season was characterized by numerous small events and several larger ones. The 2003 July–September total rainfall of 160 mm was slightly less than the 1970–to-1999 monsoon average of 188 mm. The diurnal air temperature swing was typically 20 °C, with air temperatures gradually decreasing throughout the study period.

Most of the soil moisture dynamics were confined to depths shallower than 15 cm (Figure 2(b)). There was little difference in the general behaviour of the soil moisture dynamics for the shrub- and bare-cover profiles with the exception that the bare-cover profile had larger increases in soil moisture for a given event (data not shown), which was consistent with the influence of canopy interception in shrub-cover micro-sites (Loik *et al.*, 2004). Only large rain events (one day with >25 mm or back-to-back days each with >15 mm rainfall) generated considerable wetting at 15 cm and little changes were seen at 30 cm (Figure 2(b)). The shallowness of infiltration was due, in part, to the frequent dry antecedent conditions, high evaporation demand, and the high intensity and short duration convective rainfall that quickly overwhelms infiltration rates and then runs off. These are typical characteristics of the region, and for this site in particular (Cable, 1980; Andraski, 1997; Scott *et al.*, 2000; Kurc and Small, 2004). Following all rain events, the increase in soil moisture at both 5 and 15 cm declined to near pre-event levels within ~10 days of rain-free weather.

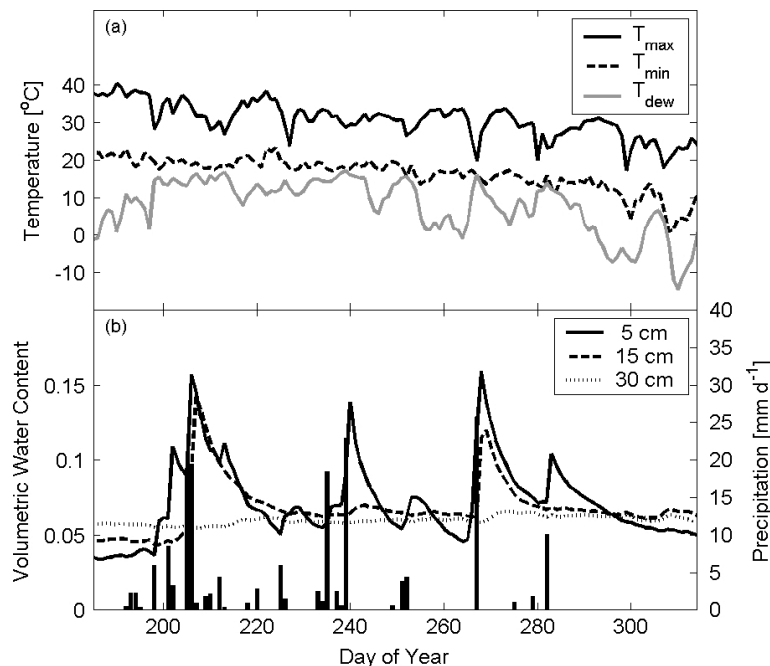


Figure 2. (a) Daily maximum and minimum air temperatures, and mean dew point temperature. (b) Daily average volumetric soil moisture and precipitation. Soil moisture values were computed by averaging TDR readings under bare and shrub-covered profiles

Total ecosystem ET, shrub transpiration (T), and bare-soil evaporation (E) reflected the pattern of rainfall pulses and drying; interstorm periods that are typical of the monsoon in this region (Figure 3). In semiarid ecosystems ET is strongly coupled to precipitation and soil moisture (Unland *et al.*, 1996; Kure and Small, 2004; Mielnick *et al.*, 2005). Before the monsoon season began, both E and T were essentially zero (Figure 3). At the onset of the monsoon rains, E dominated ET as it took approximately 10 days for the plants to recover from their down-regulated, dormant state and respond to the precipitation. Later, during interstorm periods, T was dominant and E was small. For the remainder of the growing season, E was high only on, and shortly after, days with rainfall. After 1–2 days of drying, evaporation was minimal as the soil surface and depression storage (rainfall captured on the surface of rocks, leaves, and limbs) dried quickly.

In 2003, most of the rain fell during July and August (Table I). In July, only about 21% of the monthly ET was transpiration, since it took time for the shrubs to become active (develop leaf area and fine roots) and extract water from the soil volume (Figure 3). For the rest of the months, the shrubs were the major source of evaporative loss to the atmosphere, $\sim 70\%$. Thus, the shrubs were very capable of accessing much of the available soil moisture despite the shallow infiltration and the large amount of bare soil. This result fits well with the data collected by Cox *et al.* (1986) who found that an average of 70% of the total fine root mass in the soil at this site is confined within 0–15 m of the surface.

Overall, plant transpiration comprised 58% of the total ET for the study period (Table I). On an annual basis this ratio would decrease owing to the dormancy of the shrubs in the colder winter months. Following several rain events, Dugas *et al.* (1996) found that average T/ET ranged from 40–70% over several different Chihuahuan shrub sites in New Mexico. Kemp *et al.* (1997) simulated the annual ET partitioning of several different Chihuahuan Desert communities and found that annual T/ET was about 40% for a creosote community with 30% peak cover, but T/ET increased to 60% in a mixed community with about 60% cover. Again, we expect that seasonal T/ET is highly variable even at one site because of climate variability and differential plant functional responses (Reynolds *et al.*, 2000). For example, the greatest monsoon intensity

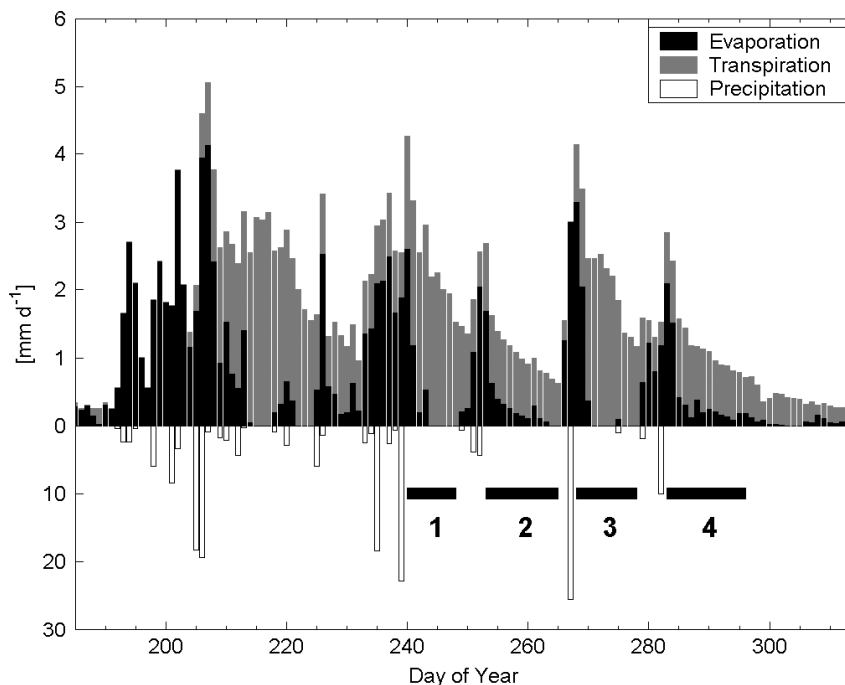


Figure 3. The partitioning of daily evapotranspiration (total bar height) into evaporation, shrub transpiration, and total daily precipitation. The four interstorm periods are also identified

Table I. Monthly water and carbon flux totals. P, ET, and T in units of mm. NEE, GEP, and R in units of g Cm^{-2}

	P	ET	T	T/ET	NEE	GEP	R
July	70	50	11	0.21	35	14	49
August	59	73	49	0.68	-8	79	72
September	34	52	36	0.70	-23	59	36
October	13	35	25	0.71	-26	49	23
July–October	176	210	121	0.58	-21	201	180

during this study was in July, when the shrubs were not able to fully respond to all of the available moisture, suggesting that years with a greater density of rainfall events in the months of August and September would have a higher growing season T/ET.

Total ET exceeded precipitation for the study period by 34 mm or 119% (Table I). Considering the change in total soil moisture ($\Delta\theta = 4$ mm) and run-off ($Q = 9$ mm) during the same period, total ET exceeded precipitation excess (i.e. $P - \Delta\theta - Q$) by 129%. Half of this imbalance was arguably due to the precipitation measurement, which probably under-estimated true rainfall by $\sim 10\%$ because of gage under-catch errors (Hanson *et al.*, 2004). The different scale of water balance measurements may also be a factor in the imbalance. P and ΔS were all measured on top of a gently sloping hill where the micro-meteorological instrumentation was located, but numerous small drainage channels that receive considerable run-on bisect this region. The denser and larger shrubs located along these small ephemeral channels give evidence for this lateral redistribution of moisture. However, the scale of the run-off measurements for the small watershed that this study took place in was 4.4 ha and likely comprises a region where much of the flux source area was located.

Four interstorm periods were delineated to assess the response of evaporation and transpiration to rainfall pulses when the vegetation was active (Figure 3). interstorm events were characterized by breaks in monsoon rainfall of 10 days or more with little rainfall accumulation (< 2 mm). For each event, evaporation peaked on either the day of or the day following the rain pulse (Figure 4) and rapidly declined in the following days. After 3 or more days, it was essentially negligible (< 0.5 mm d^{-1}). Interestingly, the peak transpiration rate was lagged compared to the evaporation peak, and the length of the lag increased with larger evaporation responses. Thus, transpiration rates remained suppressed on days with significant evaporation. This preferential response of ET may be indicative of the greater resistance in the transpiration pathway due to roots-shoot-stomata resistances that have developed from dry antecedent conditions (Shuttleworth and Wallace, 1985).

For both evaporation and transpiration, the size of the rainfall pulse was positively related to the magnitude of the subsequent flux (Figure 4). However, in contrast to evaporation, which decreased rapidly following a rainfall event, the decay in transpiration following its peak occurred more slowly for relatively larger rainfall event sizes. Transpiration rarely sustained maximal rates, indicating that the plant performance was almost always water-limited. The smallest rainfall pulse (actually, two ~ 4 mm events) preceded Period 2, and the plant response scaled to the ecosystem (i.e. ecosystem transpiration, not individual plant transpiration) was quite limited. Such an event may not be of a size that is important for sustaining much transpiration, but may be important for the alleviation of leaf water stress, allowing for continued functioning throughout the periods between large rainfall events (Sala and Lauenroth, 1982).

Net ecosystem exchange

The arrival of the North American Monsoon dramatically affected how incident radiation acted as a driver of material and energy fluxes. The average diurnal patterns of the water and carbon dioxide fluxes over a five-day, cloud-free period in the pre-monsoon and late-monsoon period illustrate the increase in shrub activity following the availability of water in the soil (Figure 5). Prior to the monsoon, ET was minimal and NEE was slightly positive with a diurnal respiration response due to changes in air/soil temperature, despite dry soils. Soil CO_2 efflux during the dry times of the year have been reported at a Chihuahuan Desert grassland in New

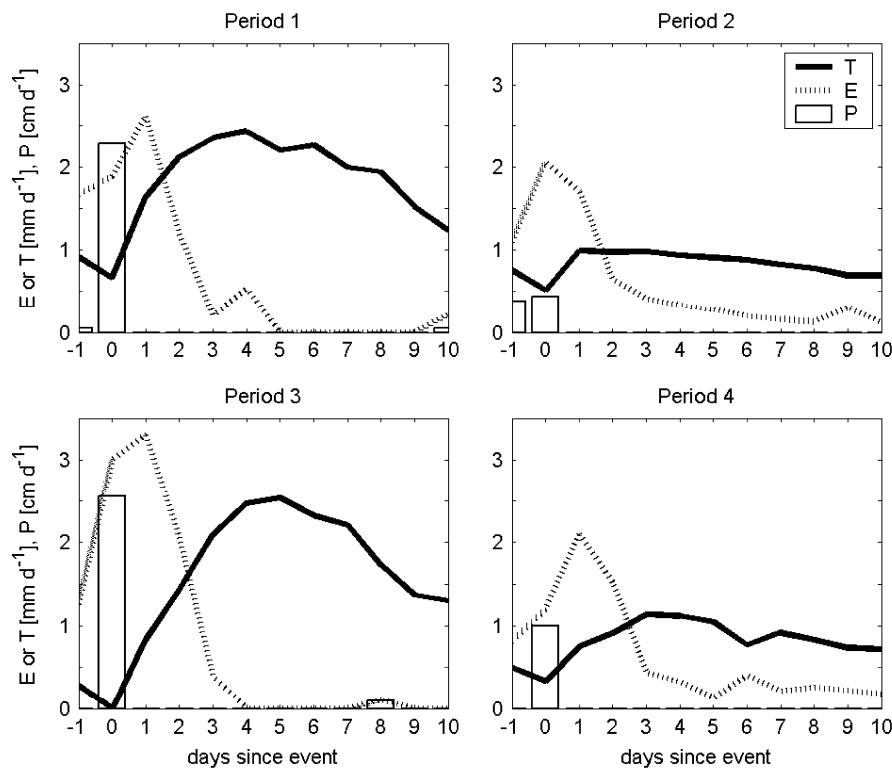


Figure 4. Rainfall pulse (P), response of soil evaporation (E), and transpiration (T) for the interstorm events identified in Figure 3

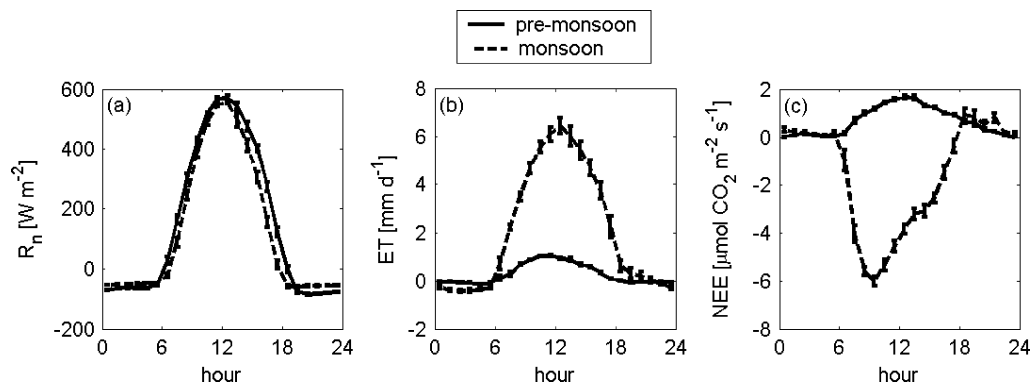


Figure 5. Average diurnal patterns of (a) net radiation, (b) evapotranspiration, and (c) net ecosystem exchange for pre-monsoon (DOY 185–190) and peak monsoon period (DOY 270–275). Error bars indicate ± 1 standard error

Mexico by Mielnick *et al.* (2005) and at this site by Emmerich (2003), who speculated that this transport is due to precipitation of carbonates in semiarid soils. During the peak of shrub activity in the monsoon, ET had increased and followed the course of the net radiation. NEE showed a net carbon uptake by the ecosystem in the day, with a peak just prior to that of incident radiation. The change in NEE prior to peak radiation is most likely a result of depressions in leaf photosynthesis from partial stomatal closure owing to midday declines in leaf water potential; a situation often seen in these desert shrub species (Smith *et al.*, 1997).

Carbon efflux was enhanced by the onset of summer rains (Figure 6). As the shrubs ended their dormancy and began to transpire, NEE was driven downwards and eventually reflected a net uptake ($NEE < 0$). As the monsoon progressed, rainfall events had the effect of increasing NEE temporarily, but there was a trend toward increased uptake as the growing season progressed until the shrubs began to senesce deciduous leaves or initiate seasonal dormancy (\sim DOY 290). Interstorm periods following large rain pulses showed the largest amount of CO_2 uptake from the atmosphere.

Relationships between components of ET and NEE

By disentangling NEE into GEP and R, the interpretation of NEE becomes easier (Figure 7). The shrubs were opportunistic with the available soil moisture as GEP increased after larger rainfall pulses. Peak rates were not maintained for long and began to decline rapidly, though not as quickly as the respiratory activity. Respiration was highest after the initial monsoon rains, and it increased and declined rapidly following subsequent rain events. Overall, the response seemed dampened as the rainy season progressed. Fisher and Whitford (1995) suggest that the first substantial rains following a drought period will induce a particularly strong soil respiration response as soil micro-organisms find a number of readily available energy sources (Austin *et al.*, 2004; Schwinning and Sala, 2004). Likewise, Fierer and Schimel (2002) found that frequent exposure to drying-rewetting events decreased the amount of CO_2 released upon rewetting. Respiration occurred throughout this study, even when the soil was very dry, most likely due to the continued activity of perennial plants (Huxman *et al.*, 2004b). Reflecting the plant activity alone, T and GEP had similar responses in time, though peaks in GEP appeared to precede T by a day or two. This likely derives from changes in the diurnal pattern of instantaneous photosynthetic gas exchange relative to maximum achievable photosynthetic rates of individual leaves within a canopy that influence different patterns of leaf water loss. Likewise, E and R both spiked in response to moisture pulses with a pattern of R peaking slightly after E. The slight differences in these processes in time could arguably be due to either increased resistance for CO_2 diffusion from the deeper soil layers as water infiltrates the surface soil immediately following rainfall (Conant *et al.*, 2004) and/or the added contribution of plant respiration to the total CO_2 efflux, which would show a peak

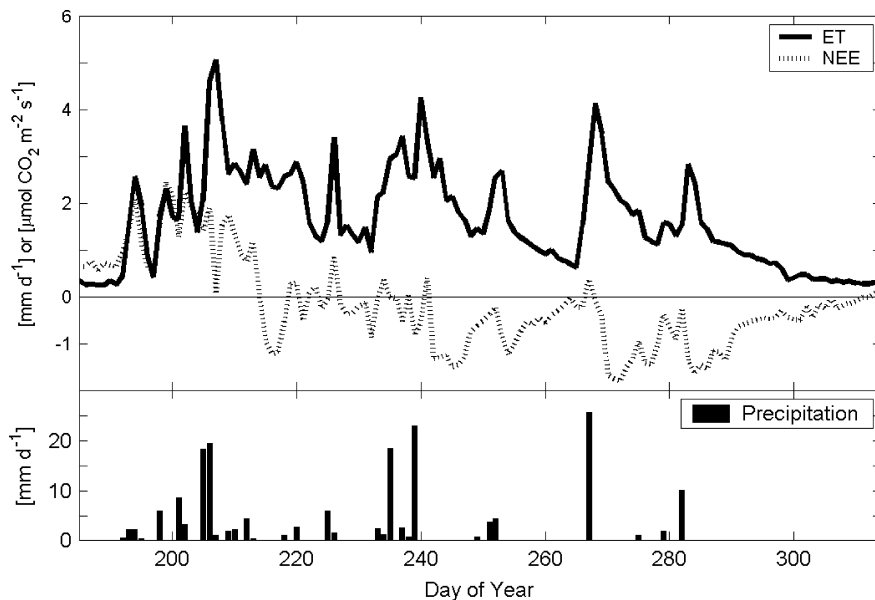


Figure 6. Daily average evapotranspiration (ET), net ecosystem exchange (NEE), and daily precipitation

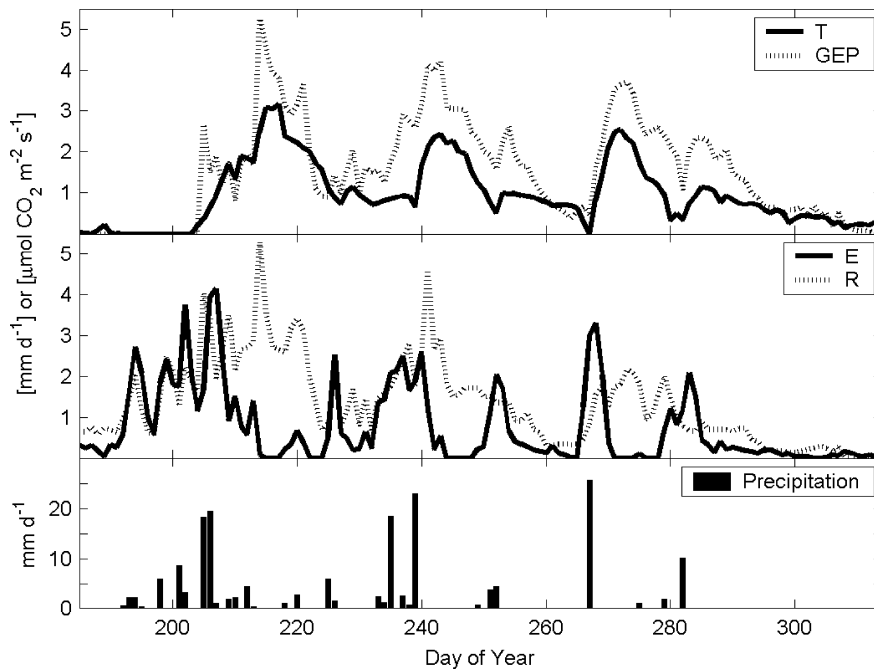


Figure 7. Daily components of the ecosystem water and carbon dioxide flux

in activity several days after the event, which is likely to be in some fairly constant proportion to the GEP response (Huxman *et al.*, 2004b).

Overall, GEP was well correlated with T, but R and E were not (Figure 8). While some of the disagreement between R and E is undoubtedly due to our calculation of R and the failure of Equation (4) to fully capture the dynamic influences on R, the good correlation between GEP and T gives some confirmation to our approach. It is possible that the lack of correlation between R and E is real because of how plant and carbonate equilibrium processes may be contributing to the patterns of efflux. The expected decreased respiration response in time due to the frequent drying–rewetting events (Fierer and Schimel, 2002) would diminish the correlation between R and E as well. For the case when evaporation was small ($E < 0.5 \text{ mm d}^{-1}$), there was a good linear relationship between T and R ($R^2 = 0.72$) and between GEP and R ($R^2 = 0.60$, data not shown), indicating that shrub respiration may be a large part of the total CO_2 efflux (Chimner and Welker, 2005).

The shrubland acquired increasing amounts of carbon through the growing season mainly owing to the decrease in respiratory losses, but, overall, the ecosystem appeared to be only a very small sink of CO_2 for the study period (Table I). Rainfall-use efficiency (biomass production by plants as a function of precipitation) has been an important variable describing function in water-limited systems (Le Houerou, 1984; Paruelo *et al.*, 1999), but there have been difficulties relating the eco-physiological characteristics of vegetation to ecosystem processes owing to the fact that precipitation is not completely consumed by vegetation (Huxman *et al.*, 2004c). At the leaf scale, water use efficiency has been computed in many different ways (e.g. Ehleringer and Osmond, 1989). Here we define the ecosystem water use efficiency (EWUE) as

$$EWUE = \frac{-\sum NEE}{\sum ET} \quad (5)$$

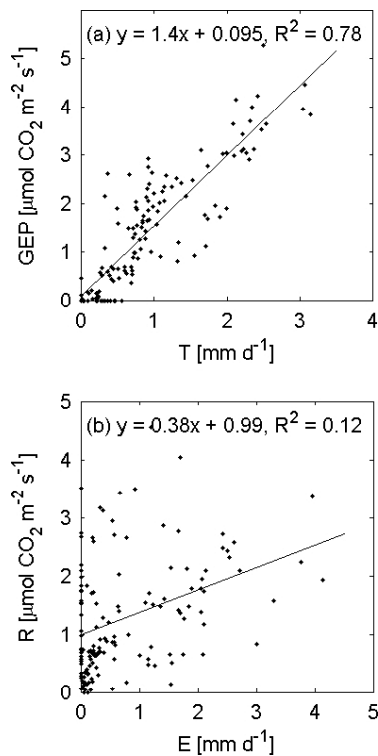


Figure 8. Regression plots of (a) daily transpiration (T) versus gross ecosystem exchange (GEP) and (b) daily evaporation (E) versus total respiration (R)

and plant canopy-scale water use efficiency ($PWUE$) as

$$PWUE = \frac{\sum GEP}{\sum T} \quad (6)$$

to highlight the functioning of the plants versus the total ecosystem in their ability to acquire CO_2 . Our definition of $PWUE$ lacks an accounting of the loss of CO_2 due to plant respiration and thus only represents an approximation for the photoautotrophic efficiency. However, it is reasonable to assume that the proportion of plant productivity that was lost to plant respiration is a constant function of GEP (Waring *et al.*, 1998).

Both $EWUE$ and $PWUE$ increased monotonically throughout the growing season with $EWUE$ having larger monthly changes (Figure 9). From July through September, increases in $EWUE$ were mainly due to the increasing dominance of canopy photosynthesis relative to ecosystem respiration reflected in the decreasing NEE (Table I) and only partially due to increases in $PWUE$ (Figure 9). From September to October, $EWUE$ continued to rise, but these gains were mainly attributable to increased $PWUE$. Thus, the ecosystem as a whole became more efficient in its carbon acquisition as the season progressed because of the decreasing respiration response and the increasing efficiency of the plants.

CONCLUSIONS

In this paper, we examined how ET was partitioned into evaporation and transpiration for the 2003 summer growing season of a Chihuahuan Desert shrubland, and we investigated how these components of ET were

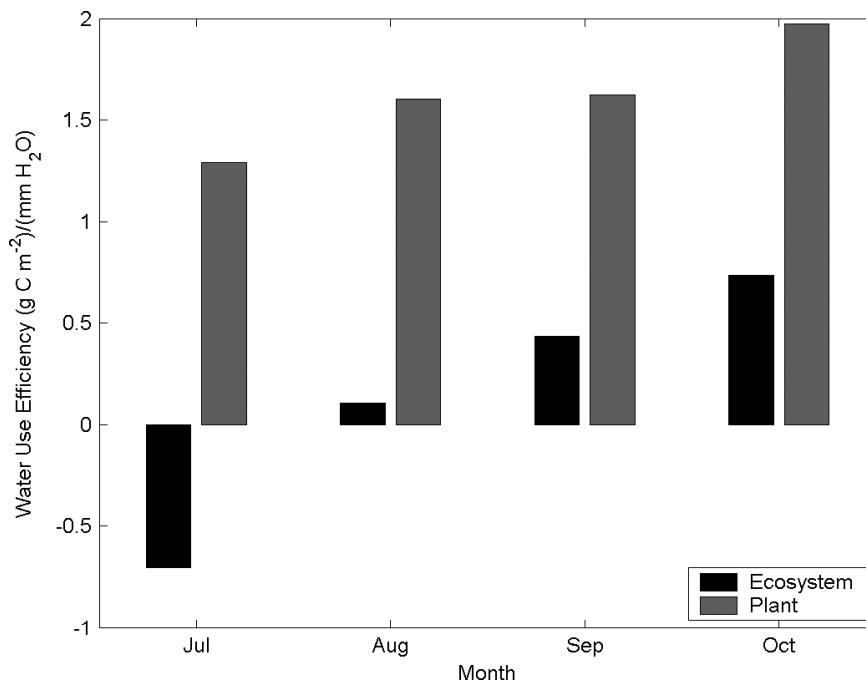


Figure 9. Monthly ecosystem and plant water use efficiency

related to NEE. We found that evaporation peaked and declined very rapidly (within a couple of days) following rainfall events, and there was a preferential response for evaporation over transpiration following larger rainfall events. The peak in transpiration usually followed the evaporation peak, and transpiration declined more gradually. The shrubs' transpiration was proportional to the size of the rainfall event, but they did show some response to even medium-sized events (~10 mm). Infiltration was confined to the upper 0–30 m of the soil and only twice did it reach past the 0–15 m depth. Thus, the shrubs were able to acquire moisture from shallow soil depths. For this growing season, about 58% of the total ET went through the biological pathway of the shrubs, but it was around 70% for August–October when the shrubs were not dormant for part of the time. Despite the large amount of bare soil in this ecosystem, the shrubs were very capable of accessing much of the available soil moisture.

Growing season NEE revealed that the ecosystem lost carbon when the shrubs were dormant and that these losses dramatically increased at the start of the rainy season. After about 10 days, the shrubs were able to transpire and acquire CO₂, and this resulted in decreasing NEE and an eventual net gain of CO₂ (NEE < 0) for the ecosystem as the growing season progressed. When the shrubs were actively transpiring, NEE continued to decrease through the study owing to the decreased respiration response to rainfall. Transpiration, photosynthesis, and respiration were closely linked, but evaporation and respiration were not. Finally, the water use efficiency of the ecosystem to acquire carbon monotonically increased throughout the months of the study. This was shown to be a function of both increases in photosynthesis relative to ecosystem respiration and the increased water use efficiency of the plants themselves as the study progressed.

The main issues presented in this paper are essential toward developing a mechanistic understanding of how woody plant encroachment alters water and carbon cycling in semiarid ecosystems. The disaggregation of the water and carbon dioxide fluxes into their respective components reveals the dynamical nature of the biological and non-biological response of the ecosystem and how they respond to environmental forcing. Once similar data has been collected for grasslands and shrub-invaded grasslands for this and other semiarid

ecological regions, then comparisons can be made to further our understanding of this important question of global change.

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