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Evapotranspiration partitioning in semiarid shrubland ecosystems: a two-site evaluation of soil moisture control on transpiration

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ABSTRACT

Vegetation of dryland ecosystems is sensitive to precipitation pulses. Future climate scenarios suggest that the frequency and magnitude of precipitation events will change. How much and to what extent will these changes impact the hydrological cycle in creosotebush (*Larrea tridentata*) shrublands that dominate the three North American hot deserts? In this study, we examine the partitioning of precipitation inputs into bare soil evaporation (E) and transpiration (T) within creosotebush ecosystems at sites characterized by bimodal precipitation regimes: the Santa Rita Experimental Range (SRER) and the Walnut Gulch Experimental Watershed (WGEW). At both sites, during summer 2008, we measured evapotranspiration (ET) using eddy covariance, whole plant T using the heat-balance sap flow, and soil moisture at several depths. During the dry period preceding the summer monsoon, both ET and soil moisture were very low. With the onset of summer rains, E dominated ET; shrub transpiration did not respond to increases in soil moisture for approximately 3 more weeks. A series of large precipitation events increased moisture at deeper soil layers, and triggered T. Overall, ET was largely correlated to moisture levels in shallow soil layers typical of dryland ecosystems dominated by dry conditions, high evaporative demand, and poor soil infiltration. Under the current precipitation regime, characterized by many small storms and few large storms, soil moisture is low with most precipitation inputs lost as E. However, if climatic changes lead to less frequent but larger precipitation events, dryland communities could experience shifts in the partitioning of ET affecting the hydrologic budget of the ecosystem.

KEY WORDS sap flow; eddy covariance; creosotebush; *Larrea tridentata*; whitethorn acacia; *Acacia constricta*; Santa Rita Experimental Range; Walnut Gulch Experimental Watershed; dryland; desert

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INTRODUCTION

In dryland ecosystems, which account for over a third of the Earth's land surface, productivity is particularly sensitive to precipitation inputs delivered as discrete pulses (Huxman *et al.*, 2004a,b; Ogle and Reynolds, 2004; Fay, 2009). The result is a precipitation regime characterized by frequent small precipitation events (<5 mm) interspersed with infrequent larger events (>20 mm). The nature of this regime supports the great diversity and healthy ecosystem functioning characteristic of these semiarid ecosystems (Sala and Lauenroth, 1982; Golluscio *et al.*, 1998; Fay, 2009).

Most global climate models predict changes in the intra-annual variability of precipitation (IPCC, 2007; Knapp *et al.*, 2008). Given that average annual precipitation in semiarid areas worldwide is expected to experience major fluctuations (IPCC, 2007), the associated changes in timing, frequency, and magnitude of precipitation events will have ecological implications for semiarid ecosystems (Heisler-White *et al.*, 2008). A better understanding of how dryland vegetation currently uses water resources is critical to predicting and understanding the ecological consequences of precipitation changes.

Because most precipitation events in dryland ecosystems are relatively small (<5 mm, Sala *et al.*, 1992), often only the top few centimeters of the soil are wetted. As a result of high evaporative demand and the large amount of bare soil, more than 90% of all precipitation input to the system in semiarid environments returns to the atmosphere via evapotranspiration (ET) (e.g. Carlson *et al.*, 1990; Wilcox *et al.*, 2003; Huxman *et al.*, 2005; Scott, 2010), where ET is the sum of soil evaporation (E) and transpiration (T). Owing to the shallow nature of the moisture reservoir created from these small rainfall events, surface soil moisture is typically depleted rapidly by E (Scott *et al.*, 2006a; Kurc and Small, 2007; Moran *et al.*, 2009). In contrast to E, T is associated with the soil moisture deeper in the root zone. Usually only large precipitation events (e.g. $>\sim 5$ mm) are capable of wetting the root zone beyond the depth of evaporative demand (Kurc and Small, 2007), and these events are likely to occur during the growing season, when T/ET is larger than E/ET.

While ET in dryland ecosystems has been successfully estimated using Bowen ratio (e.g. Dugas *et al.*, 1998; Kurc and Small, 2004; Scott *et al.*, 2006a;) and open

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path eddy covariance techniques (e.g. Scott *et al*., 2006b, Kurc and Small, 2007; Scott, 2010), alterations of the ecohydrological processes, including the partitioning of ET in these systems, associated with isolated, episodic precipitation events, or pulses remain poorly understood (Loik *et al*., 2004; Potts *et al*., 2006). The frequency and intensity of pulses have been shown to influence soil moisture and thus the partitioning of E and T within the system (Potts *et al*., 2006); yet, information about how and when the vegetation uses this soil moisture is still needed.

The objectives of this study are to understand water use of the dominant vegetation of dryland systems under different environmental conditions within the southwestern United States and to gain a better understanding of the hydrologic control on ET partitioning in semiarid shrublands. Two study sites were chosen for this objective, which differ in soil type and vegetation structure. While both the sites experience bimodal precipitation patterns, these sites experience distinctly different precipitation events, including both small (<5 mm) and large (>10 mm) events or series of events. We compare ecosystem transpiration losses from the dominant vegetation at these two sites using the heat balance method (HBM) of sap flow measurement. Because both of these sites have extensive soil moisture measurements, we are able to examine the role of soil moisture in ET partitioning at creosotebush-dominated ecosystems. In particular, we address the following three hypotheses regarding ET partitioning: (1) following small storms, evaporation (E) losses would dominate ET; transpiration (T) losses would be minimal; (2) following large rainfall events or series of events E will dominate ET for the first few days, after which T would increase and dominate; and (3) the ratio of T to total ET (T/ET) would differ between the sites based on differences in soil and ecosystem structure.

MATERIALS AND METHODS

Site description

Our study was conducted at two locations in semiarid southeastern Arizona: the Santa Rita Experimental Range (SRER) and Walnut Gulch Experimental Watershed (WGEW) (Figure 1). The SRER lies entirely within the Sonoran Desert, whereas WGEW is in the transition zone between the Sonoran and Chihuahuan Deserts. Annual precipitation in the region is dominated by a bimodal precipitation pattern with the majority falling during the summer monsoon season (July through September).

The Creosote site at SRER (31·9083N and 110·8395 W) (Table I) is at an elevation of about 1000 m. Laser diffraction particle size analyses (Arriaga *et al*., 2006) conducted in 2008 indicated an Agustin sandy loam with 5–15% surface gravel to at least 1 m; no caliche layer could be identified (Table I). Mean annual precipitation at the SRER is 345 mm (1971–2008) and mean annual temperature is 20 °C (WRCC, 2007). Between 1971 and 2008, the field site received approximately 50% of all annual precipitation during the summer monsoon season (June–September) and 45% during the winter (October–February). A vegetation survey in autumn 2008 indicated total percent cover of vegetation was 24%, the dominant vegetation being creosotebush (14%) with grasses, forbs, and cacti accounting for the remaining 10% of total cover. On the basis of the findings of Ogle and Reynolds (2004), roots of creosotebush at this site are expected to be most dense at 20–40 cm. Mean (± SE) plant area index (PAI; Bréda, 2003) for June–November was 0·45 ± 0·4 with a maximum PAI of 0·55 ± 0·24 occurring in September (Table I).

The Lucky Hills site at WGEW (31·7438N, 110·0522 W; 1375 m elevation) (Table I) is dominated by the Lucky Hills soil series with very-gravelly sandy loams and noncontinuous caliche layers at depths of

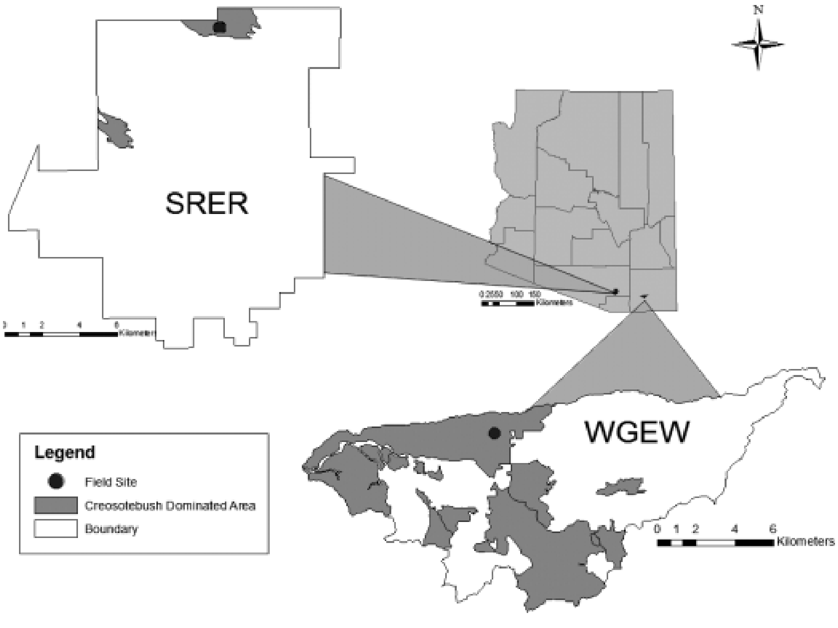

Figure 1. Map of study sites at SRER and WGEW in southern Arizona.

Table I. Differences in site characteristics between the shrublands at SRER and WGEW.

	SRER	WGEW
Average annual precipitation (mm)	345	322
Percent vegetation cover	24%	27%
Percent shrub cover	14% Creosotebush	9% Creosotebush; 9% Acacia
Average shrub height (m)	1·7	0·9
Average number of stems per plant	24	8
Average stem diameter (mm)	10	7
PAI	0·45 ± 0·4	0·46 ± 0·4
Soil texture	Agustin sandy loam	Lucky Hills series coarse-loamy
Depth to caliche layer	>100 cm	>30 cm
Root depth	Undetermined	70% in upper 0·15 m

30 cm or more (Table I; Breckenfeld *et al.*, 2000). Mean annual temperature is 17 °C and mean annual precipitation is 340 mm (Goodrich *et al.*, 2008). From 1964 to 2007, the WGEW received approximately 60% of annual precipitation in the summer and 25% in the winter months (Goodrich *et al.*, 2008). A vegetation survey conducted in the fall of 2008 indicated that total canopy cover at the site (27%) was dominated by creosotebush (9%) and acacia (*Acacia constricta*; 9%) and then other shrubs and some forbs (10%). Approximately 70% of the total fine root mass is located in the upper 15 cm of the soil with exponentially decreasing amounts to 1 m (Cox *et al.* 1986). The mean (± SE) PAI for June–November was 0·46 (±0·4) with a maximum PAI of 0·66 (±0·2) in September (Table I).

Micrometeorology

Both the SRER and WGEW sites are instrumented with standard eddy covariance systems (Moncrieff *et al.*, 2000). The SRER flux instrumentation is mounted at 3·75 m height and at 6·4 m at WGEW. Both sites record 30-min-averaged CO_2 and H_2O fluxes calculated using 10-Hz measurements from a LiCor 7500 (LI-COR Inc.) and Campbell Scientific CSAT 3-D Sonic Anemometer (Campbell Scientific Inc.). Flux data were filtered to screen points associated with rain events, outlier spikes, periods of low turbulence, and other noise. To calculate daily ET, using filtered 30-min data over the course of a day, an average ET in mm 0·5 h^{-1} was calculated and multiplied by 48 to obtain units of mm day^{-1}. Given that much of the missing data is likely associated with nighttime when ET is low, it is important to note that this averaging scheme likely results in a slight overestimate of ET at the daily scale.

Precipitation at SRER was measured with a Texas Electronics TE525-L tipping bucket rain gage. A digital weighing rain gage developed by the United States Department of Agriculture (USDA) Agricultural Research Service measured precipitation at WGEW. At SRER, volumetric soil water content (θ) was estimated using Campbell Scientific CS616 water content reflectometers (Campbell Scientific Inc.) in six profiles: three profiles under creosote canopies and three profiles in bare areas. In each profile, probes were placed at depths of 2·5, 12·5, 22·5, 37·5, 52·5, 67·5, and 82·5 cm. At each depth, the three sensors located under canopy as well as the three sensors in bare space were averaged together. Average soil moisture for each depth was calculated by combining the canopy and bare averages using a weighted average based on percent cover. Similar to SRER, at WGEW, soil moisture was estimated using a weighted average of soil moisture from profiles both under canopies and in bare areas based on percent cover using Campbell Scientific TDR100 (Campbell Scientific Inc.) time domain reflectometry sensors installed at depths of 5, 15, 30, 50, 75, 100, and 200 cm.

Sap flow

Sap flow was estimated using the HBM (Senock and Ham, 1993; Kjelgaard *et al.*, 1997). In the HBM, thermocouples are placed along a plant stem—one at the heating element, one upstream of the heating element, and one downstream. A second set of thermocouples wired in series are wrapped around the stem on top of the first set of thermocouples. The thermocouples measure the heat lost by conduction along the stem as well as radially away from the stem (Kjelgaard *et al.*, 1997). The HBM uses the principle of energy balance to interpret heat fluxes in sap flow, defined as:

$$Q = Q_f + Q_{\mathrm{rad}} + Q_{\mathrm{up}} + Q_{\mathrm{dn}} \qquad (1)$$

where the heat input (Q) is equal to the sum of heat transported by convection in the sap flow (Q_f), heat lost radially away from the stem (Q_{rad}), and heat lost up (Q_{up}) and downstream (Q_{dn}) through the plant stem (see Kjelgaard *et al.* (1997) for a more complete discussion of HBM sensor theory). Traditionally, thermocouple sensors are installed just under the bark for the best estimates of conductive heat flow. However, we found that for creosotebush and acacia, their very thin bark was severely damaged using this procedure. As a result, thermocouples were placed on top of the bark, perpendicular to the branch and secured to ensure contact and heat transport. Gravimetric comparisons (e.g. Senock and Ham, 1993) performed in a greenhouse setting in May 2008 showed that this modification improved the reliability and accuracy of T measurements.

HBM sensors were installed during the first week of June 2008 prior to the onset of the summer monsoon and data were collected from mid-June to mid-October

2008. We installed 15 sap flow sensors at each site. At SRER, nine creosotebush shrubs were randomly selected within the footprint of the eddy covariance tower to include a variety of stem diameters ranging from 5·3 to 16·0 mm. Six of the shrubs had two sap flow sensors installed on two separate stems; the remaining three plants had a single sensor. At WGEW, eight sensors were installed on four creosotebush shrubs, and seven sensors were installed on four acacia plants. Stem diameters ranged from 6·5 to 11·8 mm for creosotebush and from 5·5 to 9·7 mm for acacia. All sensors were installed on stems 10 cm from the ground. Temperature was recorded at 5-min intervals, then was averaged and stored at 30-min intervals on dataloggers (Campbell Scientific CR10X). Data was downloaded and general maintenance performed every 2 weeks. Monitoring sap flow on the small woody stems of shrub species in semiarid environments is not trivial (e.g. Allen and Grime 1995), and dry, hot, and monsoon conditions resulted in frequent sensor malfunction. At any given time during the study, approximately half of all sensors were working properly; data were not analysed from sensors which were malfunctioning or broken. This resulted in shrub-averaged sap velocities in some half-hour periods with large standard errors. The overall relationship between mean sap velocity of working sensors and the standard errors for those means was heteroskedastic; standard error of the means tended to increase with increasing mean velocity. As function of mean sap velocity, the standard error of the mean was $\sim$24% at SRER and $\sim$46% at WGEW where there were fewer sensors per species. Still, the relative trends of transpiration are evident.

Sap flow velocity was expressed per cross-sectional stem area at the location of heat input. In the fall 2008, an estimate of stems per unit area was determined through a survey of twenty 35-m line transects at each site. Average 30-min sap flow velocity was calculated using data from sensors functioning correctly and then scaled up using average stem density and species percent cover to estimate shrub-level transpiration. At SRER, creosotebush was assumed to account for total T at the site. At WGEW, ecosystem T was assumed to be composed of three components—creosotebush, acacia, and other woody plant species. The T from other woody plant species at WGEW was calculated as an average of T from creosotebush and acacia.

Ancillary measurements

Supplementary measurements included monthly measurements of pre-dawn plant water potential (Ψ_{pd}) and PAI at both sites. Average PAI was determined monthly from 22 PAI measurements taken at 6-m intervals along a 150-m East-West (E-W) transect using a LiCor 2000 (LI-COR Inc.) between civil twilight and sunrise. Each measurement consisted of two above canopy readings and three ground level (below canopy) readings. Pre-dawn water potential was determined for creosotebush (SRER and WGEW) and acacia (WGEW) using a Plant Moisture Stress (PMS) 1000 pressure chamber. We used 10 clipped ends of branches from 10 individual plants to determine a representative the Ψ_{pd} of the ecosystem. Samples were placed in a cooler to preserve them until placed in the pressure chamber at the site.

RESULTS

Precipitation and soil moisture

Both sites received small, infrequent storms prior to the onset of the summer monsoons. Subsequent to Day of Year (DOY) 176 and extending to DOY 285, precipitation events were recorded on 33 days with daily rainfall ranging from 0·25 to 40·4 mm (259·6 mm total) at SRER (Figure 2a). At WGEW summer rains began on DOY 174 and lasted until DOY 285 (Figure 2b) with rain on 48 days ranging from 0·25 to 38·6 mm/day (211·8 mm total).

Soil moisture (θ) near the surface fluctuated more than θ at deeper depths, peaking after large precipitation events and showing a distinct dry down after individual events as well as at the end of the summer rains (Figure 2). At SRER (Figure 2a), with the onset of the summer monsoon on DOY 176, $\theta_{2\cdot5\ \mathrm{cm}}$ and $\theta_{37\cdot5\ \mathrm{cm}}$ increased markedly, whereas deeper in the soil profile, $\theta_{52\cdot5\ \mathrm{cm}}$ and $\theta_{67\cdot5\ \mathrm{cm}}$ increased only slightly. Later in the monsoon, e.g. DOY 237–244, precipitation events elicited a similar

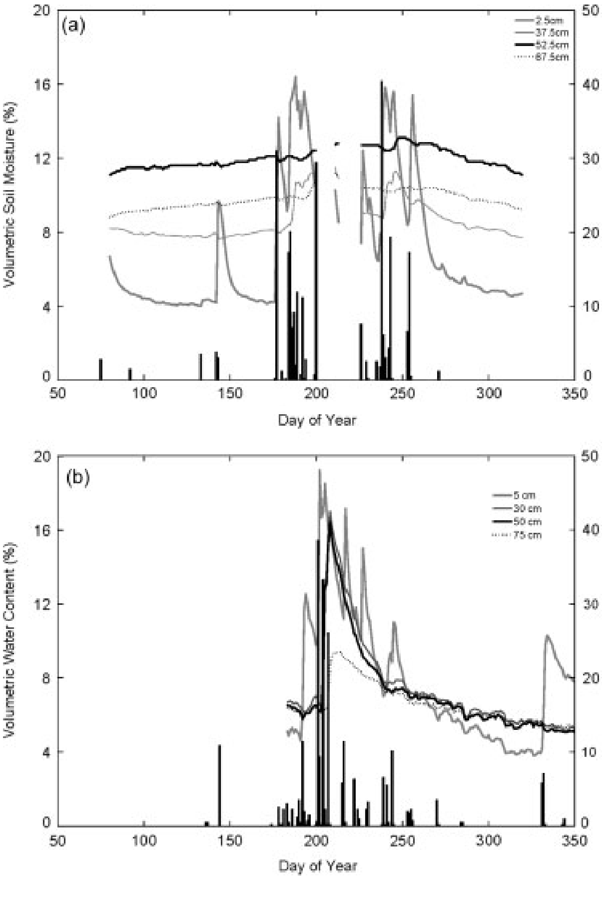

Figure 2. Time series of precipitation (bars) and volumetric water content (θ) at various depths for SRER (a) and WGEW (b) in summer 2008.

increase in $\theta_{2\cdot5\ \mathrm{cm}}$ and $\theta_{37\cdot5\ \mathrm{cm}}$, but unlike early in the monsoon, $\theta_{52\cdot5\ \mathrm{cm}}$ and $\theta_{67\cdot5\ \mathrm{cm}}$ remain unchanged. At WGEW (Figure 2b), $\theta_{5\ \mathrm{cm}}$ increased in response to precipitation events starting on DOY 191. However, increases in soil moisture at deeper soil profiles ($\theta_{15\ \mathrm{cm}}$, $\theta_{30\ \mathrm{cm}}$, $\theta_{70\ \mathrm{cm}}$) were not seen until following a series of large precipitation events on DOY 201, 204, and 207. At all depths, a gradual dry down followed large storms with only $\theta_{5\ \mathrm{cm}}$ spiking after individual small events. Near the surface, $\theta_{5\ \mathrm{cm}}$ and $\theta_{30\ \mathrm{cm}}$ quickly dried down following large storms, whereas $\theta_{50\ \mathrm{cm}}$ remained elevated for a more extended period of time.

ET and ET Partitioning

Increased rates of ET followed most precipitation events at both sites (Figure 3). However, the relationship between T and precipitation was less clear. For instance, at the SRER, even though summer rains commenced on DOY 176, creosotebush plants did not respond to the available moisture until DOY 200 (Figure 3a); peak T occurred between DOY 205 and 216 during which time there was no rainfall. Maximum daily T (1·9 mm d^{-1}) occurred on DOY 210. The length of the SRER growing season was 85 days (DOY 200–285) based on the response of T. Total ET for the SRER over this time was 147·1 mm and total T was 54·7 mm. Peak T for both creosotebush and acacia at WGEW occurred between DOY 210 and 229 with a maximum ecosystem value of 1·5 mm d^{-1} on DOY 220 (Figure 3b). Shrubs began actively transpiring around DOY 205, about 25 days after the monsoon onset. The growing season at WGEW appeared to be shorter than at SRER, lasting 69 days (DOY 205–274). Total ET for the WGEW growing season was 102·2 mm and total T was 44·5 mm, 30% and 20% lower, respectively, than at SRER. Figure 4 illustrates the relationship between weekly T and ET at each site. At SRER (Figure 4a), the T/ET ratio was slightly higher (Slope $= 0\cdot38$, $R^2 = 0\cdot85$) with a weekly mean of 0·41, whereas at WGEW it was 0·23 (Figure 4b; Slope $= 0\cdot27$, $R^2 = 0\cdot78$). While these differences are not statistically significant, over a longer time scale, a clearer trend could be established.

Linear regressions were performed between the moisture fluxes (ET, T, and E) and soil moisture at all depths (Table II). For this analysis, E was calculated as the residual of ET and T. At SRER, the strongest correlation between ET and θ was at 37·5 cm ($R^2 = 0\cdot78$, Figure 5a, Table II). At this depth, T and θ were also most strongly correlated ($R^2 = 0\cdot65$, Figure 5b, Table II). The depth of greatest correlation for E and θ was 2·5 cm ($R^2 = 0\cdot57$, Figure 5c). At WGEW, ET and θ had the strongest correlation at depth 15 cm ($R^2 = 0\cdot58$, Figure 5d). T was most strongly correlated to $\theta_{75\ \mathrm{cm}}$ with an R^2 value of 0·78 (Figure 5e). At WGEW, both ET and E were most strongly correlated with surface soil moisture ($\theta_{15\ \mathrm{cm}}$).

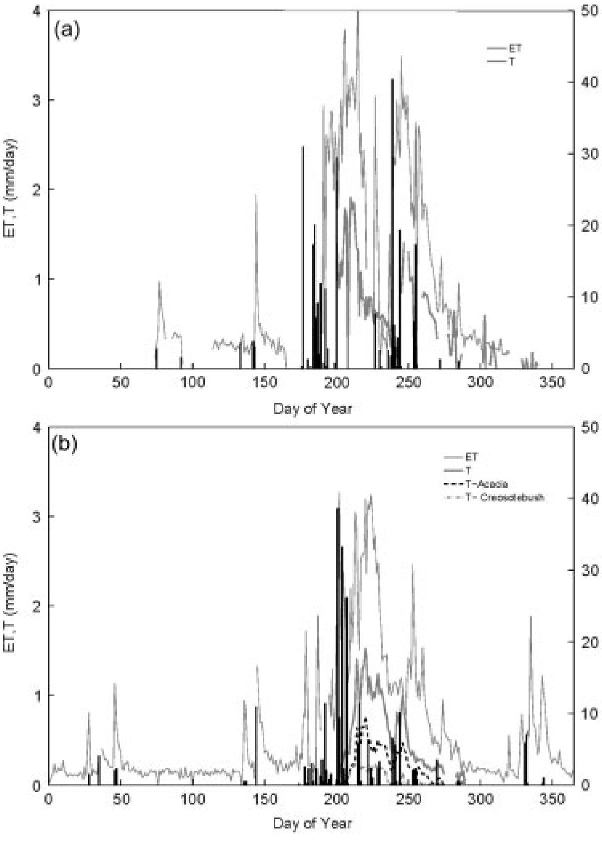

Figure 3. Time series of precipitation (bars), ET, and transpiration (T) at SRER (a) and WGEW (b) in summer 2008.

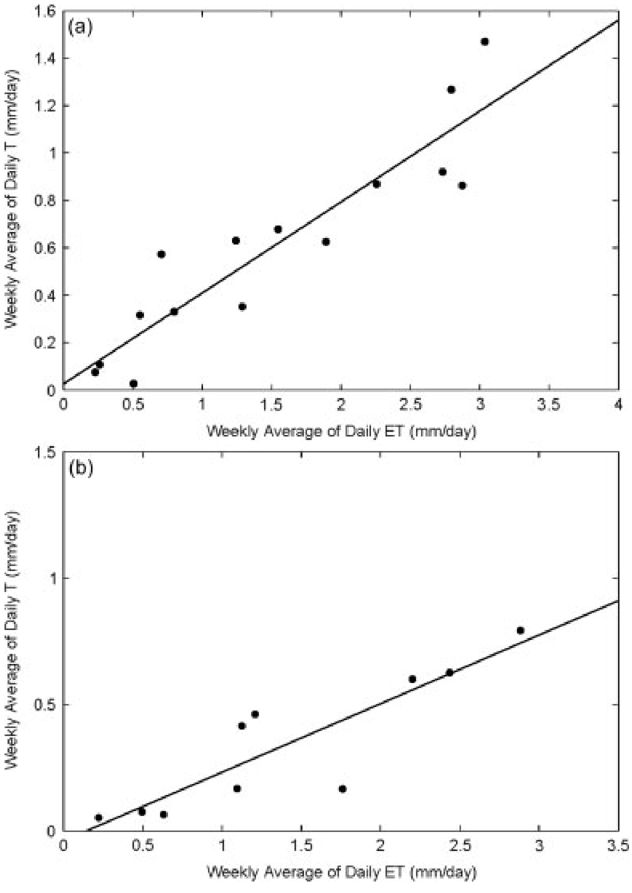

Figure 4. Linear regression of weekly averages of daily T versus weekly averages of daily ET at SRER (a) and WGEW (b).

Table II. R^2 resulting from linear regressions of ET, transpiration (T), and evaporation (E) versus all soil moisture depths at SRER and WGEW. Bolded values are largest R^2 values for each of ET, T, and E.

SRER				WGEW			
Depth (cm)	ET	T	E	Depth (cm)	ET	T	E
2.5	0·69	0·15	**0·57**	5	0·54	0·40	0·55
12.5	0·67	0·17	0·51	15	**0·58**	0·47	**0·68**
22.5	0·72	0·30	0·56	30	0·51	0·50	0·61
37.5	**0·78**	**0·65**	0·46	50	0·49	0·46	0·60
52.5	0·44	0·40	0·12	75	0·57	**0·70**	0·60
67.5	0·44	0·56	0·11	100	0·40	0·49	0·36
82.5	0·36	0·20	0·10	—	—	—	—

Timing of T

At SRER, no isolated precipitation events of 5 mm or less could be identified in the record. In fact, only a single isolated event which was not preceded or immediately followed by another precipitation event was found within the record (DOY 227, Figure 2a). Likewise, no isolated precipitation events at WGEW which were not preceded or followed by another event within 2 days (Figure 2b) were identified within the record. Figure 6a and c illustrates response to events or series of events$<$10 mm at SRER and WGEW, respectively. Following the precipitation event on DOY 227 (7·62 mm) at SRER, an immediate increase occurs in ET; however, T remained constant and low, not responding to small precipitation inputs. Similar to SRER, at WGEW following a series of two events totalling 5·64 mm, ET increases immediately following the storms and again there is no change in T.

Figure 6b and d illustrates the response to a series of larger rainfall events at SRER and WGEW, respectively. At SRER (Figure 6b), following a series of nine events totalling 78 mm of precipitation from DOY 236 to 245, ET begins to increase immediately following the first event and continues to increase for the next 10 days. T does not show a strong response to the inputs until approximately DOY 243, 7 days after the first precipitation event. T continues to increase for approximately 5 more days before decreasing along with ET. Similar to SRER, at WGEW (Figure 6d), a series of nine events from DOY 200 to 208 provided 110·7 mm of rain to the system at the beginning of the growing season. Following the first event, ET responded immediately dominated by E, whereas there is a lag in the T response by several days with a clear increase in T by DOY 209; T then began to decrease on DOY 214.

Vegetation parameters

At SRER, Ψ_{pd} (Figure 7a) and PAI (Figure 7b) generally tracked the monsoonal precipitation pattern with increased Ψ_{pd} and PAI during the period of greatest rainfall. The same trends are exhibited by plants at WGEW (Figure 7a and b). In comparing sites, there were no significant differences for the PAI values. However, Ψ_{pd}

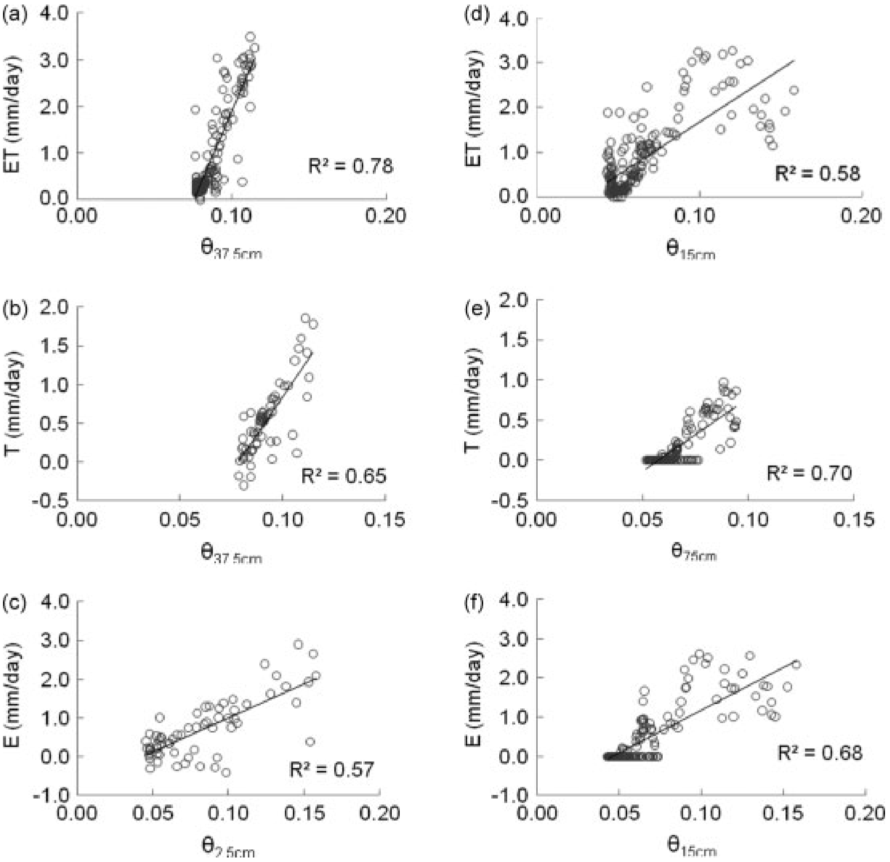

Figure 5. Linear regressions of ET, T, and E versus θ at various depths at SRER (a,b,c) and WGEW (d,e,f).

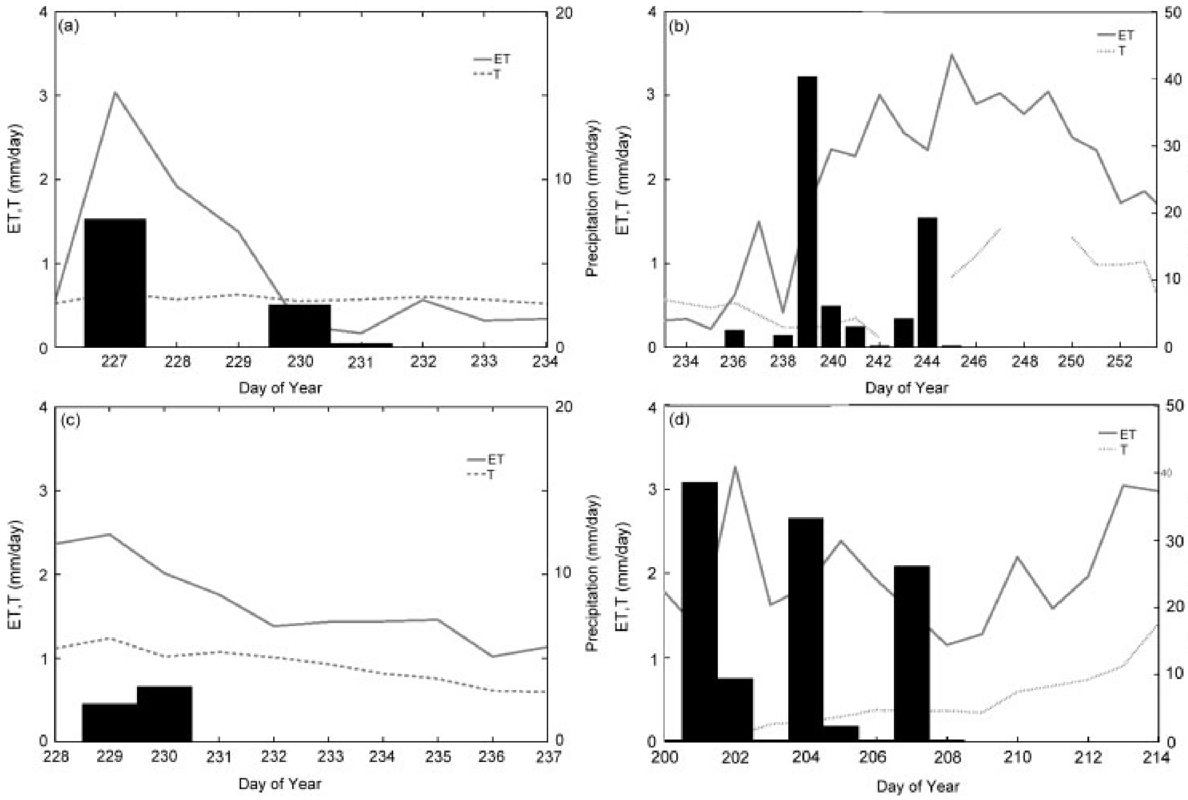

Figure 6. ET and T response to small storms at SRER (a) and WGEW (c). ET and T response to a large precipitation event or series of events at SRER (b) and WGEW (d).

values were statisically different. At both sites, Ψ_{pd} peaked during the month of July (DOY 209) following the onset of the summer rains. In August (DOY 236), Ψ_{pd} decreased back to pre-monsoon levels at the SRER, whereas there was only a slight reduction at WGEW. Then, in September (DOY 270) there was a slight increase at SRER and reduction to pre-dawn levels at WGEW. Finally at the end of the season (DOY 312), both sites' Ψ_{pd} values were reduced to seasonal lows.

DISCUSSION

Soil moisture controls on T and ET

In our study, soil moisture dynamics were mainly confined to the upper 37·5 cm of soil at SRER and 15 cm at WGEW (Figure 2), which is consistent with other studies in this region (Scott *et al*., 2000; Kurc and Small, 2004; Scott *et al*., 2004; Scott *et al*., 2006a; Kurc and Small, 2007). Overall, ET is correlated with soil moisture at relatively shallow depths; 37·5 cm at SRER and 15 cm at WGEW (Figure 5). The correlation of ET to shallow soil layers is typical of semiarid ecosystems which are dominated by the dry conditions, high evaporative demand, and poor infiltration (Scott *et al*., 2000; MacCracken *et al*., 2003; Kurc and Small, 2004). As such, at both locations, E is best correlated with surface moisture, which is expected in these sparse systems dominated by bare soil (Kurc and Small, 2004; Scott *et al*., 2006a; Kurc and Small, 2007). In contrast, regardless of differences between the sites, T at both sites is correlated with

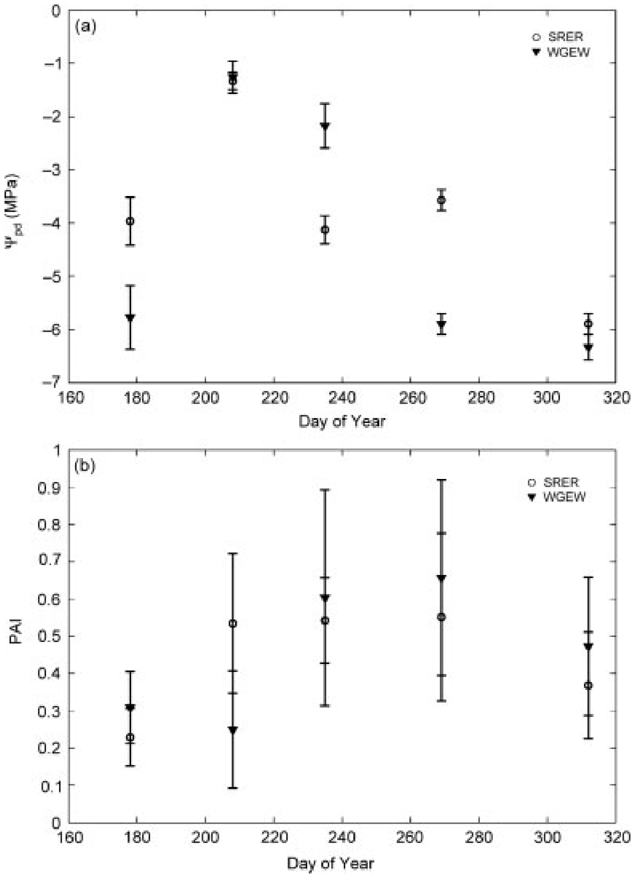

Figure 7. Time series of Ψ_{pd} (a) and *PAI* (b) at SRER (open circles) and WGEW (solid triangles).

moisture deeper in the soil profile (Figure 5). Since E has been shown to have the greatest influence on shallow surface soils (Yamanaka and Yonetani, 1999), leaving T only available to dominate at the deeper soil layers in these dryland systems (Kurc and Small, 2007), this is reasonable. Notably, T at SRER is best correlated at a shallower depth than at WGEW, 37·5 and 75 cm, respectively. This is likely due to the presence of the gravelly, coarse-loamy soils and caliche layer at WGEW which would presumably retard water movement to greater depths. The lack of a caliche layer and presence of sandier soils at SRER allows for better drainage and increased infiltration. While percent cover and PAI between the two sites were not significantly different, the shrubs at SRER were nearly twice as tall (Table I). Previous work has suggested that larger plants will have higher levels of T as compared to small plants of the same species (Tong *et al.*, 2008). However, we also note that acacia is co-dominant with creosotebush at WGEW, suggesting that acacia may use deeper soil moisture than creosotebush. Increased correlation between T and soil moisture below the surface soils at SRER could be due to larger average shrub size, physiological differences, species differences, soil differences, or a combination (Donovan and Ehleringer, 1992; De Soyza *et al.*, 1996; Ryel *et al.*, 2004).

A common model used to estimate ET and leakage losses from soil moisture uses averaged soil moisture for the entire soil profile (Rodriguez-Iturbe *et al.*, 1999; Rodriguez-Iturbe, 2000; Laio *et al.*, 2001). Vivoni *et al.* (2008) suggest that in semiarid sites, the relation between ET and θ is dependent upon seasonal precipitation and vegetation response. Our data show that a single averaged root zone soil moisture is likely not able to capture the dynamics of the ET in these systems, because it will not be able to parse out T or E. Precipitation rarely percolates below 10 cm in summer and therefore, roots below this depth are not wetted following most events (Kurc and Small, 2004). Surface soil moisture is the primary source of ET losses within the system with E from bare soil being a larger contributing factor than T losses from plants (Dugas *et al.*, 1996; Kurc and Small, 2004). If surface soil moisture (within the top 10 cm) were averaged across the entire root zone (within the top 1 m), the tight coupling between surface soil moisture and ET, in periods when E dominates ET, would be lost.

Partitioning of ET into E and T

As shown in similar studies (Kurc and Small, 2004; Scott *et al.*, 2006a), the ET and T trends at both SRER and WGEW reflect the precipitation pattern with increased ET and T following rainfall with near zero ET prior to the summer rains. When the plants are in a dormant or down-regulated state, E will dominate ET (Mielnick *et al.*, 2005; Scott *et al.*, 2006a). A T response was not seen until about 3 weeks following the commencement of summer rainfall as the plants began to respond to the available soil moisture. The initial plant response appears to have been driven by an accumulation of moisture from many events rather than a single large event. For the remainder of the season, T remained a large part of total ET at SRER, whereas at WGEW E continued to dominate the system. Likely, this can be attributed to soil differences between sites, where the noncontinuous caliche layers at WGEW may be confining the majority of soil moisture to the surface layers where it can also be used by evaporation. Alternatively, given the best relationship between T and soil moisture at 75 cm at WGEW, it is possible that the co-dominant acacia may need to access soil moisture deeper in the profile than creosotebush leading to the lower T response following the commencement of summer rain at WGEW.

At both SRER and WGEW, ET responded immediately to precipitation events. However, at both sites T showed a lagged response to these events of several days. The lagged response coincided with moisture reaching deep into the soil profile, i.e. 37·5 cm at SRER and 75 cm at WGEW. Scott *et al.* (2006a) found similar results stating that peak T rates were lagged compared with ET which peaks immediately after storms. Given that transpiration and plant carbon uptake are necessarily linked, these findings support recent conceptual models of pulse-driven carbon dynamics in water-limited systems (Huxman *et al.*, 2004b; Ogle and Reynolds, 2004; Fay, 2009) where plant carbon uptake lags behind initial microbial respiration (Kurc and Small, 2004; Scott *et al.*, 2006a, Williams *et al.* 2009). Additionally, similar to the findings of Scott *et al.* (2006a) peak T rates in our study were rarely sustained for more than a day. This suggests that the plants are almost always functioning in a water-limited state (Kolb and Sperry, 1999; Schwinning and Sala, 2004; Scott *et al.*, 2006a).

Over the course of the study, T comprised 42% of the total ET at SRER and 47% of total ET at WGEW. At WGEW, the creosotebush portion of this T was very small compared to the contribution of acacia (Figure 2b) given that they represented the same amount of overall cover. At SRER where creosotebush was the only woody species, creosotebush T was very high and in fact higher than the ecosystem T at WGEW. While the percent of creosotebush was just under twice as high at the SRER, these differences in creosotebush T at the two sites are large enough to have to be accounted for in other ways. For instance, the creosotebush at SRER were also almost twice as tall at SRER as at WGEW (Table I). This difference in size as well as the species composition between the two sites may have played a role in the differences in the T/ET partitioning (Donovan and Ehleringer, 1992; De Soyza *et al.*, 1996; Allen *et al.*, 2008). Also, because ecosystem T was estimated for WGEW based in part on an estimate of ‘other woody species’ calculated as an average T for creosotebush and acacia, this estimate is more uncertain and could be an under- or overestimate depending on whether other woody plant species were more or less active as compared to the species used for measurement.

Seasonal T/ET can be highly variable from year to year at the same site because of climate variability and differential plant responses (Reynolds *et al*., 2000; Knapp and Smith, 2001; Scott *et al*., 2006a). During our study, the majority of rainfall was received in July at both sites when the shrubs were not fully able to respond to and utilize the available soil moisture. This suggests that years with more precipitation events later in the summer (August and September) would have a higher T/ET ratio (Scott *et al*., 2006a). Furthermore, semiarid shrublands have also been shown to experience a spring green-up period apparently supported by deep infiltration of winter or early spring rain (e.g. Nagler *et al.* 2007; Kurc and Benton, 2010). Dugas *et al.* (1996) found that average T/ET values ranged from 40% to 70% in different desert sites in New Mexico. Given the results of studies like these, it is reasonable to suspect that occasional precipitation events that wet the deep soil layers, whether in winter or summer, may support plant growth beyond the current season, contributing to plant growth and water use. In fact, plant water use efficiency averaged over annual or longer cycles could be higher than what is observed during the summer monsoon. This is especially true of ecosystems with ephemeral plants whose transpiration rates that are typically not measured, as in our study, could significantly increase T/ET at various times during the year (e.g. Yuan *et al.* 2009).

Finally, in a comparative modelling study, Kemp *et al.* (1997) found that annual T/ET was approximately 40% for a site dominated by creosotebush with 30% cover. In their modelling study, the authors argue that field studies in semiarid environments that monitor the contribution of transpiration and evaporation to soil water loss are few, putting major limitations on the general understanding how plant, soil, and climate interactions control water loss in arid environments—and consequently the ability to predict soil water distributions (Kemp *et al.* 1997). While the amount of bare space and percent cover by woody plants will affect the T/ET ratio, the results of their modelling study are comparable to the results our field study with T/ET of 42% at SRER and 47% at WGEW and fall within the range of T/ET found in other field campaigns (Kemp *et al.* 1997). Now, with the results of our study, we can identify the depth at which moisture must reach before plants are able to transpire, enabling us to explore the ability of modelling frameworks with a daily time step that include multiple soil layers (e.g. Kemp *et al.* 1997; Guswa *et al.* 2002; Tietjen *et al.* 2009) to capture T/ET in these semiarid ecosystems.

Pulse dynamics and climate change

As a result of changes in global atmospheric conditions and hydrologic processes, it has been predicted that mean annual precipitation will be modified and that there will be increases in intra- and inter-annual variability in precipitation (Easterling *et al.*, 2000; IPCC, 2007). One of the key predictions of this shift is the increased probability of more intense precipitation events (Knapp *et al.*, 2008) and greater inter-annual variability in summer rain (Diffenbaugh *et al.*, 2008). These events could result in longer dry periods punctuated by larger individual events (Easterling *et al.*, 2000; IPCC, 2007) and lead to shifts in ET dynamics, reduced infiltration, and increased runoff (MacCracken *et al.*, 2003; Knapp *et al.*, 2008).

Rainfall in semiarid landscapes such as SRER and WGEW is characterized by infrequent large pulses and more numerous small precipitation events that wet only the soil surface (Loik *et al.*, 2004). This leads to rapid evaporation of the surface soil layers leaving the surface soil dry between events. Because the soil water content is low, small precipitation events are not big enough to increase water content to the point of reducing plant stress (Knapp *et al.*, 2008). If a more intense rainfall regime were to occur, water would be able to reach deeper soil layers past the zone of evaporation which could then be utilized by shrubs (Knapp *et al.*, 2008).

Under the current regime of smaller, less intense storms, soil moisture at SRER and WGEW will likely remain very low with most water lost to E. However, if climate predictions are accurate, SRER and WGEW as well as other creosotebush-dominated ecosystems in western North America will have a precipitation regime including more intense storms, resulting in increased volumetric water content within the soil. This increase in available moisture at deeper soil depths will likely favour creosotebush enabling them to thrive and persist in these systems.

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