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Year-Round Transpiration Dynamics Linked With Deep Soil Moisture in a Warm Desert Shrubland

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Key Points:

- Shallow and deep soil moisture are isotopically distinct at this warm semiarid shrubland
- Deep moisture tends to be isotopically similar to precipitation from previous season
- Shrubs use deep moisture all year round

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Abstract Ecohydrological processes in semiarid shrublands and other dryland ecosystems are sensitive to discrete pulses of precipitation. Anticipated changes in the frequency and magnitude of precipitation events are expected to impact the spatial and temporal distribution of soil moisture in these drylands, thereby impacting their ecohydrological processes. Recent field studies have shown that in dryland ecosystems, transpiration dynamics and plant productivity are largely a function of deep soil moisture available after large precipitation events, regardless of where the majority of plant roots occur. However, the strength of this relationship and how and why it varies throughout the year remains unclear. We present eddy covariance, soil moisture, and sap flow measurements taken over an 18-month period in conjunction with an analysis of biweekly precipitation, shallow soil, deep soil, and stem stable water isotope samples from a creosotebush-dominated shrubland ecosystem at the Santa Rita Experimental Range in southern Arizona. Within the context of a hydrologically defined two-layer conceptual framework, our results support that transpiration is associated with the availability of deep soil moisture and that the source of this moisture varies seasonally. Therefore, changes in precipitation pulses that alter the timing and magnitude of the availability of deep soil moisture are expected to have major consequences for dryland ecosystems. Our findings offer insights that can improve the representation of drylands within regional and global models of land surface atmosphere exchange and their linkages to the hydrologic cycle.

1. Introduction

The soil depth at which plants uptake soil moisture is commonly linked with the root distribution of the plant. Walter's two-layer hypothesis of niche partitioning (Walter, 1939), in which deeper-rooted plants such as trees use deep soil moisture and shallower-rooted plants such as grasses use shallow soil moisture, has dominated ecohydrological thinking (e.g., Germino & Reinhardt, 2014; Holdo, 2013; Ogle & Reynolds, 2004). However, Walter's hypothesis may not apply in warm water-limited environments where soil moisture distribution, and therefore transpiration dynamics and plant productivity, is strongly controlled by the frequency and intensity of precipitation pulses. Many water-limited ecosystems experience pulses of moisture that drive plant productivity (Huxman et al., 2004; Loik et al., 2004). Pulse size and frequency vary, and these variations affect biological and physical processes in the drylands such as potential for biomass production (Sala & Lauenroth, 1982), net ecosystem exchange (Kurc & Small, 2007), and soil evaporation (Raz Yaseef et al., 2010). Climate models project long-term changes in the frequency and magnitude of precipitation events in water-limited ecosystems (Easterling et al., 2000; Seager et al., 2007). These changes are expected to have an effect on moisture distribution in the soil profile (Loik et al., 2004; Weltzin et al., 2003), which will likely exacerbate changes in vegetation dynamics and partitioning of water resources (e.g., Potts et al., 2006) and affect the water supply in water-limited ecosystems (e.g., Knapp et al., 2008).

Stable water isotopes are a common ecohydrological tool for understanding the source waters for plants (e.g., Brooks et al., 2010; Dawson et al., 1993; Ehleringer et al., 1991; Ehleringer & Dawson, 1992; Ellsworth & Sternberg, 2015; Goldsmith et al., 2012; Schwendenmann et al., 2015; Schwinning et al., 2002; Snyder & Williams, 2000; Williams & Ehleringer, 2000). Using this technique, isotopically distinct source water end-members such as groundwater or shallow soil moisture can be combined in a linear function to determine the contribution of each end-member to the isotopic composition of the mixed plant component (Corbin et al., 2005; Dawson, 1998; Dawson et al., 2002; Phillips & Gregg, 2001). However, quantifying from where in the soil profile roots extract moisture has been challenging due to limitations in monitoring technologies (e.g., Zarebanadkouki et al., 2013) and confounding physical processes such as hydraulic redistribution (Burgess et al., 1998; Nadezhdina et al., 2010). In a highly cited study, Ehleringer et al. (1991) make use of Walter's hypothesis to support that deep-rooted desert plants make use of deep soil moisture and shallow-rooted desert plants make use of shallow soil moisture. Their analysis assumed that because deep-rooted desert plants look isotopically similar to winter rains, deep-rooted plants use winter moisture available from the deep soil layers; conversely, because shallow-rooted desert plants look isotopically similar to summer rains, shallow-rooted plants use summer moisture available from the shallow soil layers. However, their study did not measure the isotopic composition of the moisture in the shallow and deep soil layers and only assumed the use of water at specific depths based on root profiles.

Recent research has demonstrated that in semiarid ecosystems the density profile of plant roots does not necessarily correspond to the depth of soil moisture that the plants are actively using for photosynthesis and transpiration (Cavanaugh et al., 2011; Kulmatiski et al., 2010; Kurc & Small, 2007). For example, regardless of their rooting profile, in shallow-rooted desert grassland and deep-rooted desert shrublands, plant response was most strongly associated with moisture deep in the soil profile (i.e., >37.5 cm; Cavanaugh et al., 2011; Kurc & Benton, 2010; Kurc & Small, 2007). Stable isotope research has illustrated that roots can be hydraulically isolated from the soil; that is, root water was isotopically different from that of the surrounding soil (Thorburn & Ehleringer, 1995). Plant roots can hydraulically redistribute soil water along a moisture gradient (Richards & Caldwell, 1987), for example, to increase resilience against drought stress (Beyer et al., 2016; Kulmatiski et al., 2010). Furthermore, plant rooting strategies may be driven by other limiting growth factors such as nutrients (Brantley et al., 2017). Clearly, the presence of roots alone does not indicate where plants are extracting water from in the soil profile, so understanding plant water use strategies must go beyond the physical distribution of plant roots to understanding where in the soil profile plants are most dependent on soil moisture and how this dependence varies throughout the year.

Based on previous ecohydrological research in water-limited ecosystems, Sanchez-Mejia and Papuga (2014) proposed working within a hydrologically defined two-layer framework in which shallow soil moisture (0-20 cm) is primarily lost to evaporation (Gowing et al., 2006; Kurc & Small, 2004), while deep soil moisture (20-60 cm) is primarily used for transpiration (Cavanaugh et al., 2011; Kurc & Small, 2007). In this conceptual framework (Figure 1a), four soil moisture cases are always possible (Sanchez-Mejia & Papuga, 2014): Case 1 with a dry shallow layer and a dry deep layer, Case 2 with a wet shallow layer and a dry deep layer, Case 3 with a wet shallow layer and a wet deep layer, and Case 4 with a dry shallow layer and a wet deep layer (Figure 1a). We expect to see Case 1 (dry/dry) when there is no rain or a few days after a small storm (<5 mm; Cavanaugh et al., 2011; Sala & Lauenroth, 1982), Case 2 (wet/dry) after a small storm; Case 3 (wet/wet) after a large (>20 mm; Cavanaugh et al., 2011) storm or a small storm following Case 4, and Case 4 (dry/wet) a few days after a large storm. This framework shifts the focus of the two layers from the physical location of the plant roots such as in Walter's hypothesis to the location of soil moisture availability and the physical processes dominating the movement of soil moisture.

Within the context of this hydrologically defined two-layer conceptual framework, one can make the assumption that there are measurable isotopic differences between the shallow and deep soil because of evaporative isotopic fractionation (Figure 1b). Evaporation will deplete shallow soil moisture and preferentially evaporate isotopically lighter water molecules, thus leaving water with relatively higher $\delta^{18}O$ and $\delta^{2}H$ values in the shallow soil layer (e.g., Kulmatiski et al., 2006; Newman et al., 2010). Through time, evaporation is expected to shape a soil profile that has isotopically distinct shallow and deep soil moisture layers, with shallow soil moisture tending to be more enriched in ^{18}O and ^{2}H than deep soil moisture. If indeed shallow soil moisture and deep soil moisture differ in their water isotopic signatures, the soil layer from which semiarid plants are drawing their moisture can be identified. Further, the source of soil moisture can be potentially linked to summer or winter precipitation (Ehleringer et al., 1991; Ingraham et al., 1991; Williams & Ehleringer, 2000).

The objective of our study was to illustrate that dryland ecosystems tend to prefer deep soil moisture for their ecohydrological processes year-round, but that the strength of these relationships vary throughout the year and that the reason for these differences is also variable. To do this, we looked at the differential use of shallow and deep soil moisture of the semiarid *Larrea tridentata* (creosotebush), a widespread evergreen shrub that dominates the three North American warm deserts. As an evergreen shrub, creosotebush has

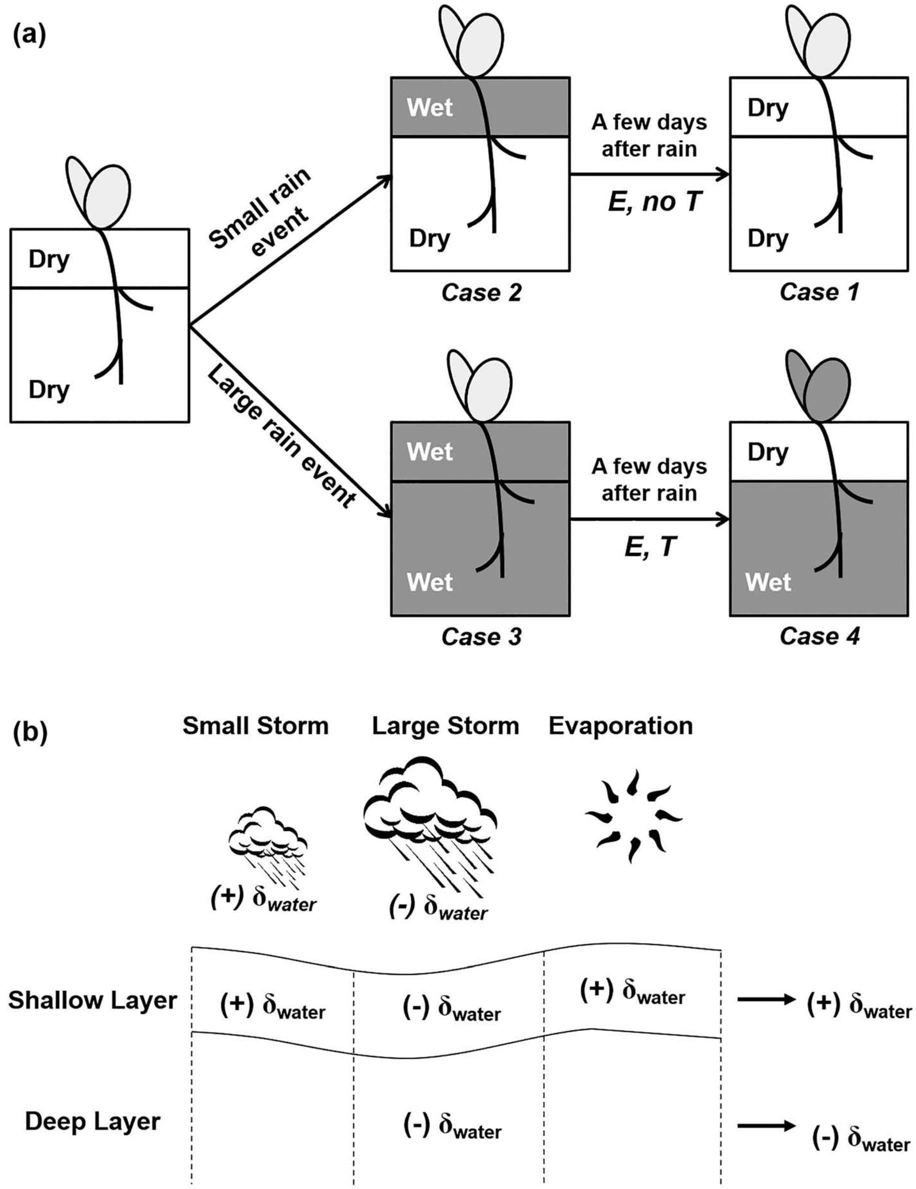

Figure 1. (a) An example of when the four Cases may occur relative to rain events: Case 1 (dry/dry) with dry shallow and dry deep soil layers; Case 2 (wet/dry) with wet shallow and dry deep soil layer; Case 3 (wet/wet) with wet shallow and wet deep soil layers; Case 4 (dry/wet) with dry shallow and wet deep soil layers. (b) Conceptualization of how the hydrologically defined shallow and deep soil layers might become isotopically distinct through precipitation and evaporation.

the potential to be actively transpiring throughout the year (Sharifi et al., 1988), allowing for the quantification of year-round differences in plant water use. We combined discrete isotopic sampling with continuous measurements of transpiration and soil moisture through the rooting zone over an 18-month period in a semiarid creosotebush-dominated shrubland of southeastern Arizona.

We made use of the hydrologically defined two-layer conceptual framework to address the following hypotheses: (1) shallow and deep soil moisture are isotopically distinct and that the reason behind these differences varies throughout the year and (2) year-round transpiration is limited to periods when deep soil moisture is available, regardless of how or when the moisture got there. Preliminary work support that in semiarid ecosystems, root density distribution does not necessarily correspond to the depth from which plants are primarily using. Again, this is contrary to the widely used two-layer paradigm where root distributions are assumed to govern resource partitioning (Ehleringer et al., 1991; Walter, 1939; Ward et al., 2013). Other studies have highlighted the value of a hydrologically defined two-layer soil conceptual framework in understanding how deep soil moisture affects land surface-atmosphere interactions (Sanchez-Mejia & Papuga, 2014; Sanchez-Mejia & Papuga, 2017). Here we use this simple guiding conceptual framework to isotopically isolate hydrologic conditions to better understand plant water use strategies in a semiarid ecosystem.

2. Methods

2.1. Study Site: Santa Rita Experimental Range

The Santa Rita Experimental Range (SRER) is located 60 km south of Tucson, Arizona. Our research was conducted at The Santa Rita Creosote (US-SRC) AmeriFlux Site (31.9083°N, 110.8395°W), located in the northern portion of SRER. Creosotebush has been the dominant species near the northern border of SRER (Humphrey & Mehrhoff, 1958). An eddy covariance tower provided half-hourly micrometeorological measurements (Sanchez-Mejia & Papuga, 2014). The SRC experiences cool winters and warm summers, with an average annual temperature of about 20 °C (Sanchez-Mejia & Papuga, 2014). The SRC has an average annual precipitation of about 133 ± 38 mm (1923-2013, Northeast Station; http://ag.arizona.edu/SRER/data.html), which falls in a bimodal precipitation pattern, with about 52% of the precipitation falling during the North American Monsoon (July through September) and about 23% of the precipitation falling during the winter rainy season (December through February; Sanchez-Mejia & Papuga, 2014). Vegetation cover is about 22%, of which creosotebush is 14% cover, and 10% are small grasses, forbs, and cacti (Kurc & Benton, 2010). Creosote canopy patches had the highest root densities (1-1.5 g root/kg soil) at 25 cm, while bare patches had highest root densities (~1 g root/kg soil) at 10 and 35 cm (Figure 2 in Sanchez-Mejia & Papuga, 2014). The soil type is sandy loam with no caliche layer within the first 1-m depth (Kurc & Benton, 2010). The estimated depth to groundwater near our site is greater than 70 m (Eastoe et al., 2004).

2.2. Soil Moisture

At SRC, six soil moisture profiles are located within the eddy covariance tower footprint. Three profiles are located under creosotebush canopy and three are located in the inter-canopy “bare” soil to account for different wetting and drying processes under the canopy and in the intercanopy patches (Newman et al., 2010). Soil moisture was measured every 30 min with water content reflectometers (precision < 0.1%; CS616, Campbell Scientific, Inc., Logan, UT, USA).

Five depths were used for each soil moisture profile: 2.5, 12.5, 22.5, 37.5, and 52.5 cm. At each depth, canopy soil moisture sensor measurements were averaged together, and bare soil moisture sensor measurements were averaged together. The site-wide soil moisture measurement at each depth was then calculated by combining the average canopy and average bare measurements with weights based on surveyed fractional cover of canopy and inter-canopy spaces (Cavanaugh, unpublished data). Average root zone soil moisture (θ_{root}) was calculated by averaging volumetric water content from all five depths. Then, the profiles were divided into shallow (0-20 cm) and deep (20-60 cm) soil moisture layers per the two-layer soil moisture conceptual framework (Sanchez-Mejia & Papuga, 2014). To calculate soil moisture in the two different soil moisture layers, we used weighted averages based on the relative contribution of each sensor in the shallow or deep layers of the soil layer (Sanchez-Mejia & Papuga, 2014); for example, the soil moisture sensor at 22.5 cm represents soil moisture between 15.5 cm and 29.5 cm and therefore contributes to both shallow and deep soil moisture equation. Average soil water content in the shallow and deep layers was calculated with the following equations (Sanchez-Mejia & Papuga, 2014):

$$\theta_{\mathbf{shallow}} = \mathbf{0.33}\theta_{2.5} + \mathbf{0.5}\theta_{12.5} + \mathbf{0.17}\theta_{22.5} \tag{1}$$

$$\theta_{\mathbf{deep}} = \mathbf{0.25}\theta_{22.5} + \mathbf{0.375}\theta_{37.5} + \mathbf{0.375}\theta_{52.5} \tag{2}$$

$\theta_{2.5}$ is the soil water content at 2.5 cm, $\theta_{12.5}$ is the soil water content at 12.5 cm, etc.

Soil moisture Cases for the conceptual framework are defined by soil moisture thresholds set in Sanchez-Mejia and Papuga (2014; 0.1229 % for $\theta_{shallow}$ and 0.1013 % for θ_{deep}). Because shallow soil moisture is primarily lost through evaporation, the shallow soil moisture threshold was based on soil moisture drydown curves (Sanchez-Mejia & Papuga, 2014). In comparison, deep soil moisture is lost primarily through

Figure 2. Our creosote-dominated site had precipitation collected at both inter-canopy and canopy locations.

transpiration, so the deep soil moisture threshold was based on site-specific carbon dynamics via net ecosystem exchange of CO_2 measured from an eddy covariance tower (Sanchez-Mejia & Papuga, 2014). Further, we divided each year into soil moisture seasons. Following Sanchez-Mejia and Papuga (2014), we defined two distinct seasons: winter (December–February) and summer (July–September) to focus on the distinct bimodal precipitation regime at our study site.

2.3. Stable Water Isotopes

From July 2014 through March 2015, precipitation samples, plant tissue, and soil samples were collected approximately every 2 weeks at three collection sites within the footprint of the eddy covariance tower. These three collections sites were co-located with three permanently installed time-lapse phenological cameras (Kurc & Benton, 2010), and all isotopic samples were collected within 10 m of the phenological camera at each collection site.

We placed four precipitation collection bottles within the tower footprint: two bottles under the creosotebush canopy and two bottles in the intercanopy space (Figure 2). The collection bottles (250-ml high-density polyethylene bottles with a funnel inserted into the cap) were prepped with a 5-mm layer of mineral oil to minimize isotopic enrichment through evaporation (e.g., West et al., 2007; Williams & Ehleringer, 2000). On each collection date, if there had been rain since the previous collection date, we collected the four bottles and replaced them with new collection bottles prepared with fresh mineral oil. All isotopic samples collected were placed immediately in a cooler with ice until transported back to the lab where they were stored in a refrigerator until analysis (e.g., Hopkins et al., 2014). In the lab, approximately 20 ml of precipitation from each high-density polyethylene collection bottle was filtered through a cellulose filter into a 20-ml glass vial with polycone cap. The vial was wrapped with parafilm and stored in the lab refrigerator.

On each collection date, we sampled three plants of an intermediate size class (height between 1.5 and 2 m). We clipped a mature, suberized stem to minimize effects of stem-water evaporation (Dawson & Ehleringer, 1993). Since this was a destructive sampling technique, different plants were chosen on each collection date. Soil samples were collected at every 5 cm down to a 45-cm depth, using a 5-cm diameter split-core soil sampler (AMS, Inc., American Falls, ID, USA; e.g., Williams & Ehleringer, 2000). Two soil cores were sampled on each collection date, one under the canopy and one in the intercanopy space. The stem and soil samples were immediately sealed in a 20-ml glass vial with a polycone cap, and the vial was wrapped with parafilm.

We analyzed the precipitation, stem, and soil samples for stable water isotopes using an isotope ratio infrared spectroscopy water analyzer (L2130-i cavity ring-down spectrometer, Picarro Inc., Santa Clara, CA) that was calibrated against the primary isotopic standards of Vienna Standard Mean Ocean Water 2 and Standard Light Antarctic Precipitation 2 (precision: ±0.35‰ for $\delta^{18}O$, ±1.5‰ for $\delta^{2}H$). This analyzer was used with an integrated peripheral (A0213 Induction Module, Picarro Inc., Santa Clara, CA) that vaporizes the water from the environmental matrix-bound sample and passes it into the analyzer by a zero-gas carrier. Stem and soil subsamples were loaded directly into a metal sample holder, and precipitation subsamples were injected onto a small piece of glass filter paper, which was then clamped into a metal sample holder. For all samples, the sample holder was loaded into a vial with a septa cap and then quickly loaded into the Induction Module vaporizer. The samples were heated in the Induction Module, and the vaporized water was passed into the analyzer. An online Micro-Combustion Module (Picarro Inc., Santa Clara, CA) oxidized some organic contaminants that could cause spectral interference (Berkelhammer et al., 2013; Martín-Gómez et al., 2015). Although some isotopic errors may still be present because of spectral interference (Johnson et al., 2017), for our objectives we were interested in the relative rather than the exact isotopic values. To correct for memory effects common to gas analyzers, each sample was injected 10 times, and the sample result was calculated from the average of the last three injections. Three stem, two shallow soil (from ~10-cm depth), two deep soil (from ~40-cm depth), and four precipitation samples were analyzed from each day and averaged together to calculate a mean daily isotopic value for stem, shallow soil, deep soil, and precipitation samples.

The detailed methodology for analyzing samples with the Induction Module-cavity ring-down spectrometer system is described by Johnson et al. (2017).

2.4. Transpiration and Evaporation

Heat balance sap flow sensors (thermocouple precision 0.1 °C; Dynagauge, Dynamax Inc., Houston, TX, USA) were used to measure half-hourly sap flow rate and to estimate transpiration. These sensors use an energy budget to interpret heat fluxes from a constant heat source (Senock & Ham, 1993). Eight sap flow sensors were installed on four randomly chosen creosotebush shrubs within 10 m of the eddy covariance tower and of the soil moisture profiles. The sensors were installed on separate branches of the shrub at 1-m height. To reduce the effect of irradiation heat on the sensors, the sensors were covered with reflective bubble wrap, and the length of trunk below the sensor were wrapped with several layers of heavy-duty aluminum foil (J. Ji, personal communication Sept. 2013; Langensiepen et al., 2012). The sizes of the sensors were 5, 9, and 16 mm (designed to be installed on stems with the respective diameters). Two shrubs had two 16-mm sensors each, and the other two shrubs each had one 5 mm and one 9-mm sensor. Sap flow velocity was calculated as per cross-sectional stem area. The average sap flow velocity was scaled up with a site-specific average stem density and percent cover to estimate shrub-level transpiration (Cavanaugh et al., 2011). Evaporation was estimated by subtracting transpiration measured from the sap flow system from evapotranspiration measured by the eddy covariance tower (Rana & Katerji, 2000). We made the assumption that creosotebush water use was a proxy for ecosystem plant water use because creosotebush comprised the majority of vegetation biomass at the site (Kurc & Benton, 2010). We also assumed that our measurements of transpiration represented the same source area as the eddy covariance tower. As such, our results should be considered with these assumptions in mind.

2.5. Data Analysis

Daily averages of shallow and deep soil moisture were calculated from 30-min means of soil moisture using equations (1) and (2). Daily sums were calculated from the 30-min measurements of sap flow transpiration, evapotranspiration, and evaporation. To test for differences among normally distributed soil moisture and transpiration data, we used unpaired *t* tests assuming unequal variance (MATLAB 2013b). To test for differences among isotopic data, we used the nonparametric Mann-Whitney *U* test because of nonnormal distributions and low sample numbers (e.g., Newman et al., 2010). Linear regression and other statistical analyses were performed in MATLAB 2013b (The Mathworks, Inc., Natwick, MA).

3. Results

3.1. Precipitation

Our site received 237 mm of precipitation during the summer (July 2014 through August 2014), nearly double the long-term annual average precipitation received at the site. Our observation period included two winter seasons (December 2013 through February 2014; December 2014 through February 2015). These two winter seasons had different precipitation patterns. In winter 2013-2014, the total precipitation was about 25 mm, distributed across 3 days of precipitation, but in winter 2014-2015, the total precipitation was about 115 mm, distributed across 18 days of precipitation (Figure 3a). Winter 2014-2015 had more frequent rain events with an average smaller magnitude (Figure 3a). Vapor pressure deficit (VPD) was low during and immediately following rainfall and was generally higher in the summer than in the winter (Figure 3a), which was expected because higher temperatures in the summer raised the saturation vapor pressure.

The overall average of precipitation samples (n=16) had a δ^{18}O value of -5.4 ± 0.8‰ (mean ± standard error) and a δ^2H value of -46 ± 7‰. We collected isotopic samples from the summer season and one winter season (the "wetter" winter of 2014-2015). The average of summer precipitation samples ($n = 9$) had a δ^{18}O value of -4.6 ± 1.1‰ and a δ^2H value of -44 ± 9‰, and the average of winter precipitation samples ($n = 4$) had a δ^{18}O value of -7.6 ± 1.8‰ and a δ^2H value of -55 ± 18‰ (volume-weighted averages of summer precipitation samples had a δ^{18}O value of -4.6‰ and a δ^2H value of -49‰ and winter precipitation had a δ^{18}O value of -7.2‰ and a δ^2H value of -53‰). Average summer precipitation was more enriched in ^{18}O than average winter precipitation (Mann-Whitney p=0.20; Figure 4). These averages are consistent with other published values of long-term (1981-2000) Tucson precipitation: May-September δ^{18}O averages of -6.0‰ and δ^2H averages of -43, and October-April δ^{18}O averages of -8.9‰ and δ^2H averages of -56‰ (Wright, 2001). There were no

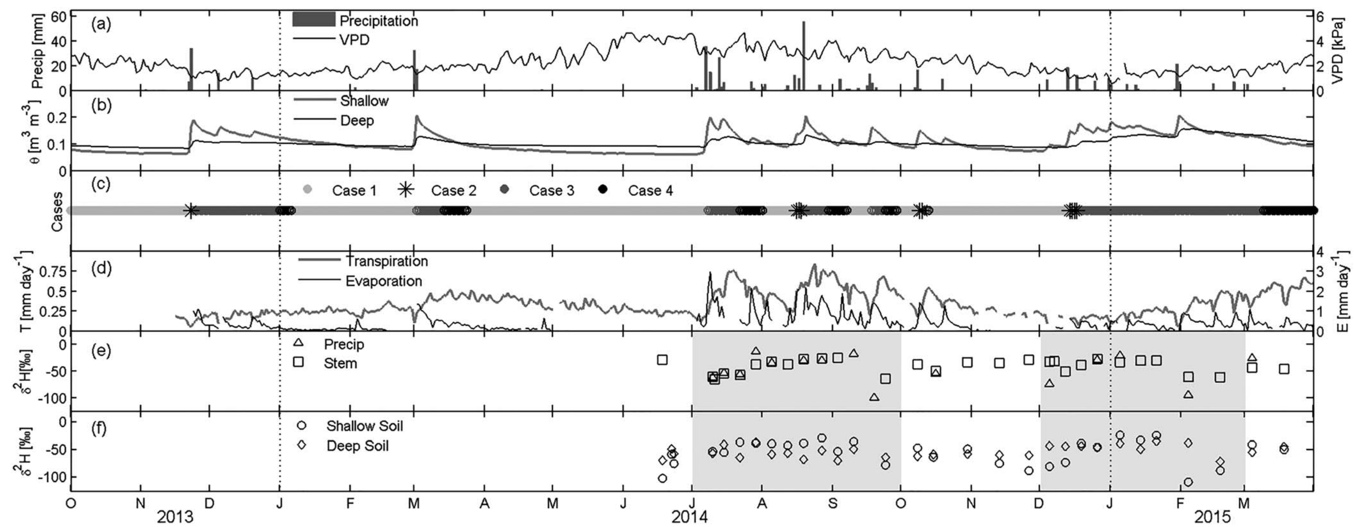

Figure 3. Time series of (a) daily precipitation [mm], vapor pressure deficit (VPD) [kPa]; (b) shallow and deep volumetric soil moisture (θ, [m3/m^3]); (c) soil moisture cases; (d) transpiration (T) [mm/day], evaporation (E) [mm/day]; (e) δ^2H values [‰] of precipitation and stem samples; (f) δ^2H values [‰] of shallow and deep soil samples; the shaded area highlight winter and summer seasons when isotope samples were collected.

statistically significant differences in δ^2H or δ^{18}O values between canopy and intercanopy precipitation samples (Mann-Whitney p>0.5).

3.2. Soil Moisture

Shallow soil moisture over our study period ranged from 0.06 to 0.21 m^3/m^3, and deep soil moisture ranged from 0.08 to 0.16 m^3/m^3. Shallow soil moisture increased with different magnitudes after both small and large rain events (Figure 3b; see November and December 2013), but deep soil moisture increased only after large rain events (Figure 3b; see March 2014) or after a series of small rain events (Figure 3b; see January 2015). However, differences in precipitation resulted in very different ranges of soil moisture between the two winter seasons themselves: winter 2013-2014 had a maximum shallow and deep soil moisture of 0.16 and 0.11 m^3/m^3, respectively, whereas winter 2014-2015 had a higher maximum shallow and deep soil moisture of 0.21 and 0.16 m^3/m^3 (Figure 3b).

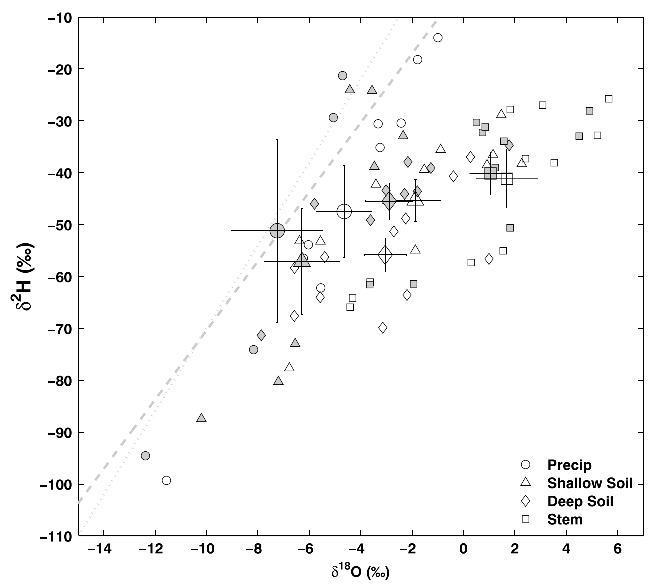

Figure 4. Daily precipitation, shallow soil, deep soil, and stem samples plotted with the global meteoric water line (GMWL; gray dotted line; Clark & Fritz, 1997), and the local meteoric water line (LMWL; gray dashed line, **δ^2H = 6.67 * δ^{18}O – 3.7‰**; Gallo et al., 2012). The gray symbols represent summer samples, the white symbols represent winter samples, and the large icons represent the seasonal averages with standard error bars.

The overall average of shallow soil samples (n=31) had a δ^{18}O value of -4.8 ± 0.9‰ (mean ± standard error) and a δ^2H value of -55 ± 4‰. The averages of summer and winter shallow soil samples, respectively, had δ^{18}O values of -1.9 ± 1.0‰ and -6.3 ± 1.5‰ and δ^2H values of -45 ± 4‰ and -57 ± 10‰ (Figure 4). Average summer shallow soil samples were more enriched in ^{18}O than average winter shallow soil samples (Mann-Whitney p=0.02; Figure 4) The overall average of deep soil samples (n=31) had a δ^{18}O value of -4.0 ± 0.5‰ and a δ^2H value of -53 ± 2‰. The averages of summer and winter deep soil samples, respectively, had δ^{18}O values of -3.1 ± 0.8‰ and -2.9 ± 0.9‰ and δ^2H values of -56 ± 3‰ and -45 ± 4‰, so average summer deep soil was more enriched in ^{2}H than average winter deep soil (Mann-Whitney p=0.06; Figure 4). There was no statistically significant difference in δ^2H or δ^{18}O values between canopy and intercanopy shallow soil and deep soil samples (Mann-Whitney p>0.5).

Over our 18-month study period, we categorized each day as one of the four soil moisture Cases using the daily average shallow and deep soil moisture. We found that n = 306 days for Case 1 (dry/dry), n = 10 days for Case 2 (wet/dry), n = 164 days for Case 3 (wet/wet), and n = 68 days

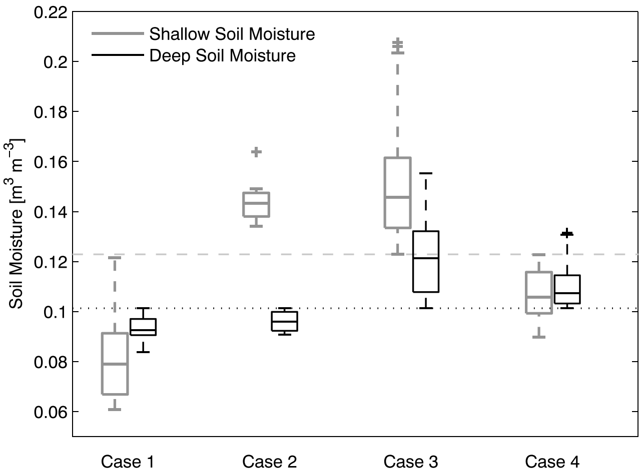

Figure 5. Daily average shallow and deep soil moisture in each soil moisture Case. The horizontal lines indicate wet/dry thresholds for the shallow soil layer (gray dashed line, determined by soil moisture drydown curves) and the deep soil layer (black dotted line, derived from site-specific carbon dynamics measured from an eddy covariance tower; Sanchez-Mejia & Papuga, 2014).

for Case 4 (dry/wet). Average daily shallow soil moisture was higher in Case 2 (0.14 m^3/m^3) and Case 3 (0.15 m^3/m^3) than in Case 1 (0.08 m^3/m^3) and Case 4 (0.11 m^3/m^3). Deep soil moisture was higher in Case 3 (0.12 m^3/m^3) and Case 4 (0.11 m^3/m^3) than in Case 1 (0.09 m^3/m^3) and Case 2 (0.10 m^3/m^3). Deep soil moisture had a much higher maximum and median in Case 3 than in Case 4 (Figure 5). Since Case 4 always follows Case 3 (Figure 3c), with transpiration supported by available deep soil water present in both these cases, the difference in deep soil moisture between these two cases could be a proxy for the amount of water that had been transpired away from the deep soil layer.

All four soil moisture cases were found in both winter and summer seasons. In the winter, most of the days were either Case 3 (wet/wet) or Case 1 (dry/dry), but again, the different precipitation dynamics in the two winter seasons led to different soil moisture distributions. Case 1 made up 59% of the “drier” winter, but only 14% of the “wetter” winter, whereas Case 3 made up 34% of the “drier” winter and 81% of the “wetter” winter. The “drier” winter had no Case 2 (wet/dry) days and only six Case 4 (dry/wet) days; the “wetter” winter had four Case 2 days and no Case 4 days. In the summer (n=92 days), most of the days were evenly divided between Case 1 (32 days), Case 3 (31 days), and Case 4 (26 days), and only 3 days of summer fell into Case 2.

3.3. Stable Water Isotopes

Precipitation samples fell close to the local meteoric water line (LMWL); the samples that were to the right of the LMWL may have been affected by evaporation despite the precautions we took during sampling and analysis. In addition, the summer precipitation samples tended to be more to the right of the LMWL than winter precipitation samples (Figure 4), which we expect because precipitation arriving during the warmer summer months is more enriched in the heavy isotopes ^{18}O and ^2H relative to precipitation during the cooler winter months (Dansgaard, 1964). An overall precipitation regression line was $\delta^2H = 7.8^* \delta^{18}O$ -3.8 (Table 1). The shallow soil samples were similar to the precipitation isotope samples in that they fell along the LMWL, with the summer shallow soil samples tending more to the right of the winter shallow soil samples (Figure 4). Again, this is what we expect because the shallow soil undergoes more evaporative enrichment during the warmer summer months than during the cooler winter months (Gat, 1996). The deep soil isotope samples all fell to the right of the LMWL (Figure 4), a trend which seems to indicate that shallow and deep soil moisture are isotopically different and that deep soil moisture may be influenced by other fractionation processes such as plant discrimination against heavier isotopes (^{18}O and ^2H) during water uptake (e.g., Ellsworth & Williams, 2007; Lin & Sternberg, 1993).

Table 1
Linear Regression Between Precipitation, Soil, and Stem $\delta^{18}O$ and δ^2H Values

	All data		
Sample type	n	R^2	Slope
Precipitation	16	0.88	7.8**
Shallow soil	31	0.75	3.7**
Deep soil	31	0.29	2.0**
Stem	31	0.74	3.9**
	Summer		
Sample type	n	R^2	Slope
Precipitation	9	0.97	8.1**
Shallow soil	11	0.66	3.4*
Deep soil	11	0.37	2.4*
Stem	12	0.84	4.3**
	Winter		
Sample type	N	R^2	Slope
Precipitation	4	0.93	9.6*
Shallow soil	9	0.81	6.3**
Deep soil	9	0.74	3.3**
Stem	10	0.55	3.7*

*The slope is significantly different from 0 at α=0.05. **The slope is significantly different from 0 at α=0.01.

We analyzed seasonal patterns in precipitation and soil δ^2H and $\delta^{18}O$ values. During the winter, precipitation and shallow soil values were similar, whereas summer shallow soil samples were relatively enriched in ^{18}O than summer precipitation samples (Mann-Whitney p=0.15; Figure 4). On the other hand, summer precipitation δ^2H and $\delta^{18}O$ values were similar to winter deep soil values, and winter precipitation δ^2H values were similar to summer deep soil values (Figure 4). Unlike the average shallow soil samples, the summer deep soil samples were more depleted in ^2H than the winter deep soil samples (Mann-Whitney p=0.06; Figure 4). Because summer precipitation was more enriched in ^2H and ^{18}O than winter precipitation, summer deep soil moisture was likely recharged in

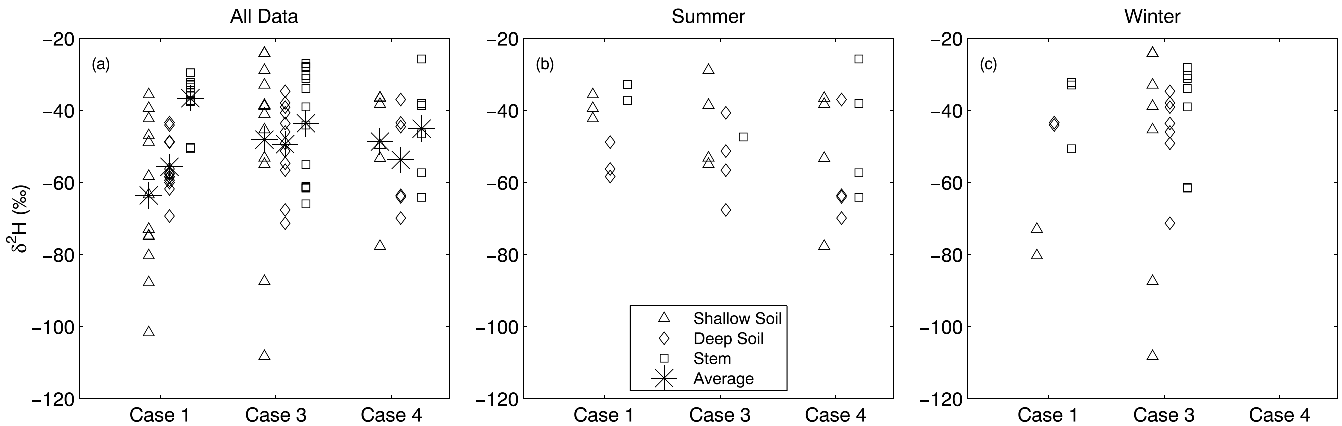

Figure 6. Daily average δ^2H values of shallow soil, deep soil, and stem samples in each soil moisture case for (a) all data, (b) summer, and (c) winter. Case 2 was excluded because of low sample numbers. We did not collect any isotope samples during winter Case 4 days.

part by winter precipitation and winter deep soil moisture was likely recharged in part by summer precipitation.

In Case 1 (dry/dry), shallow soil samples tended to be more depleted in ^{2}H than deep soil samples, and the deep soil samples tended to be more depleted in ^{2}H than the stem samples (Figure 6a). The pattern was different in the summer, with the deep soil samples being the most depleted in ^{2}H (Figure 6b). Summer precipitation was relatively enriched in ^{2}H (Figure 4), and the higher evaporative demand of summer led to higher δ^2H values of shallow soil than deep soil samples. In Case 3 (wet/wet), deep soil samples were slightly more depleted in ^{2}H than shallow soil and stem samples (Figure 6a). In the winter, shallow samples were more depleted in ^{2}H than deep soil and stem samples (Figure 6c) because the winter shallow soil was recharged by winter precipitation, which was relatively depleted in ^{2}H compared to summer precipitation (Figure 4). Finally, Case 4 (dry/wet) was similar to Case 3 in that deep soil samples were more depleted in ^{2}H than shallow soil and stem samples both overall and in the summer (Figures 6a and 6b).

3.4. Transpiration

Transpiration averaged 0.3 mm/day, with a maximum of 0.8 mm/day (Figure 3c). Evapotranspiration averaged 0.5 mm/day over the observation period, with a maximum of 3.3 mm/day. While evapotranspiration always increased immediately following rain events, evaporation contributed most to this immediate increase in evapotranspiration, while the contribution of transpiration to evapotranspiration was low immediately following a rain event, only increasing a few days after the rain event (Figure 3d). As expected, summer averages of transpiration (0.5 mm/day) and evapotranspiration (1.2 mm/day) were higher than winter averages of transpiration (0.2 mm/day) and evapotranspiration (0.5 mm/day).

The different precipitation patterns and soil moisture content of our two winter seasons resulted in different average evapotranspiration but similar average transpiration. The "drier" winter in 2013-2014 had an average deep soil moisture of 0.10 ± 0.006 m^3/m^3 (mean $\pm$ standard deviation), while the "wetter" winter in 2014-2015 had a higher average deep soil moisture of 0.13 ± 0.02 m^3/m^3. In the drier winter, average evapotranspiration about 0.2 mm lower than the wetter winter, while the average transpiration was only about 0.01 mm lower. We also found that in the drier winter, increasing deep soil moisture was correlated with decreasing transpiration, while in the wetter winter, increasing deep soil moisture was correlated with increasing transpiration. This difference in dynamics could indicate an effect of air temperature on wintertime transpiration. In the drier winter, more variation in transpiration is explained by air temperature (R^2=55%) than by deep soil moisture (R^2=26%). In the "wetter" winter, only slightly more variation in transpiration is explained by air temperature (R^2=38%) than by deep soil moisture (R^2=33%). Our findings indicate that wintertime transpiration dynamics depend not only on deep soil moisture availability but may also be influenced by air temperature when deep soil moisture is not available (e.g., the drier winter). Further exploring the role of air temperature on wintertime transpiration should be an avenue for future research.

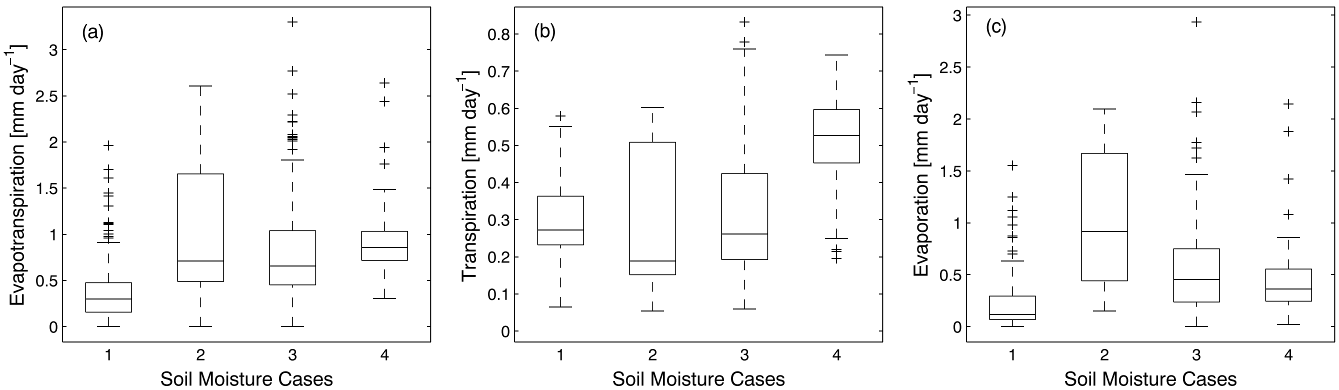

Figure 7. Daily sums of (a) evapotranspiration, (b) transpiration, and (c) evaporation in each soil moisture case.

The overall average of plant stem samples (n=30) had δ^{18}O value of 1.3 ± 0.5‰ (mean ± standard error) and δ^2H value of -41 ± 2‰. The averages of summer (n=11) and winter (n=10) stem samples, respectively, had δ^{18}O values of 1.0 ± 1.1‰ and 1.1 ± 0.8‰ and δ^2H values of -45 ± 5‰ and -40 ± 4‰ (Figure 4). Although these summer and winter averages were effectively the same number given our analysis precision, other patterns in the data indicate similarities between deep soil with stem samples and shallow soil with precipitation samples. The range of stem sample δ^2H values were -66 to -26‰, which was similar to the δ^2H range of deep soil samples (-71 to -35‰); both had a similar δ^2H range of about 38‰. The δ^2H range of both precipitation samples (-99 to -14‰) and shallow soil samples (-108 to -24‰) had a similar δ^2H range of about 85‰. The deep soil and stem samples did not display a consistent seasonal bias like the precipitation and shallow soil samples (Figure 4). Further, the average stem values of δ^{18}O and δ^2H did not fall between shallow and deep soil moisture as expected; although stem and soil δ^2H values were similar, average stem δ^{18}O values were higher than average shallow and deep soil δ^{18}O values. Summer and winter stem averages had similar δ^2H values as winter deep soil and summer shallow soil, but higher δ^{18}O values than deep and shallow soil averages (Figure 4). Our findings indicate that the plants appear to use deep soil water during period of high transpiration (summer) and that this deep soil water available in the summer was recharged by winter precipitation.

Our hydrologically defined two-layer soil moisture framework hypothesizes that shallow soil moisture is lost primarily to evaporation and that deep soil moisture is lost primarily to transpiration. We found that evapotranspiration was lower during Case 1 (dry/dry) than the other Cases (Figure 7a) because there is not much water available for either evaporation or transpiration. As expected, evaporation was lower in Case 1 than Case 2 and Case 3, although the median evaporation in Case 4 was similar to that in Cases 2 and 3 (Figure 7c). Transpiration was higher in Case 3 (wet/wet) and Case 4 (dry/wet) than Case 1 and Case 2 (wet/dry; Figure 7b); median transpiration in Case 4 was higher than the median transpiration in other Cases (Figure 7b). The low median transpiration in Case 3 can be explained by examining the relationship between $\theta_{shallow}$, VPD, and transpiration (Figure 8). Immediately following a rain event, the shallow soil moisture will be recharged (e.g., Figure 3b). However, in the following few days, as most of the shallow soil moisture is evaporated (Figures 3b and 3d), relative humidity increases and VPD decreases (Figure 3a): the linear regression between shallow soil moisture and VPD has a significantly negative slope of -10.7 (p <0.01; Figure 8a). As VPD increases, the rate of transpiration increases because there is greater atmospheric demand of water from the stomata. Transpiration increases with increasing VPD until about 3-4 kPa (Figure 8b), when stomatal conductance likely decreases and reduces transpiration (Aphalo & Jarvis, 1991). This relationship between $\theta_{shallow}$, VPD, and transpiration offers an explanation for the low transpiration amounts found in Case 3.

In both winter and summer seasons, more of the variation in transpiration is explained by θ_{deep} (R^2=0.20 in winter and R^2=0.36 in summer) than $\theta_{shallow}$ (R^2=0.02 in winter and R^2=0.08 in summer; Figures 9a and 9b) or θ_{root}. In addition, more of the variation in evaporation is explained by $\theta_{shallow}$ (R^2=0.37 in winter and R^2=0.45 in summer) than θ_{deep} (R^2=0.30 in winter and R^2=0.17 in summer; Figures 9c and 9d) or θ_{root}.

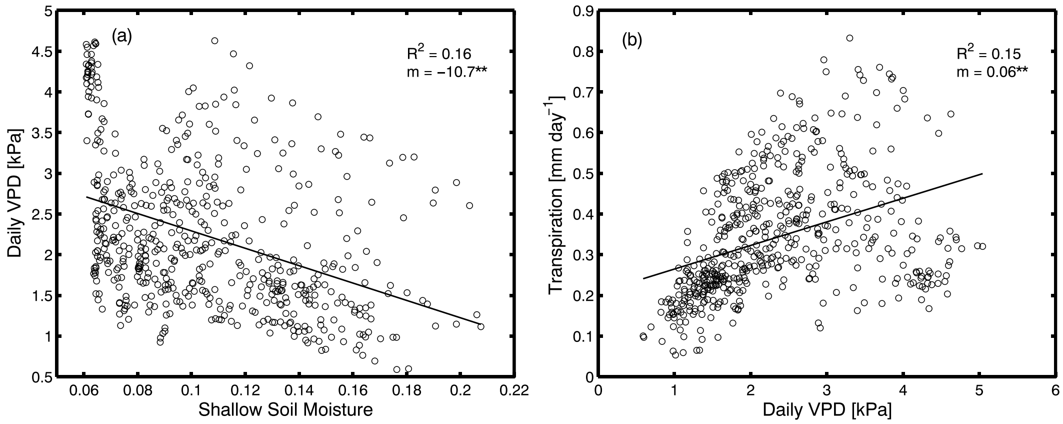

Figure 8. Linear regressions between (a) $\theta_{shallow}$ and vapor pressure deficit (VPD) and (b) VPD and transpiration. "**" indicates that the slope was significantly different from 0 at α=0.01.

However, the relationship between evapotranspiration and $\theta_{shallow}$ and evapotranspiration and θ_{deep} differ between winter and summer. In winter, more of the variation in evapotranspiration is explained by θ_{deep} (R^2=0.44) than $\theta_{shallow}$ (R^2=0.25); in summer, more of the variation in evapotranspiration is explained by $\theta_{shallow}$ (R^2=0.48) than θ_{deep} (R^2=0.29; Figures 9e and 9f). These results suggest that different processes are dominant at different times of the year, that is, in winter, transpiration could be the dominant process in evapotranspiration; we estimated that transpiration was 60% of evapotranspiration during the wetter winter and 44% of evapotranspiration during the drier winter. In summer, on the other hand, evaporation was the dominant process in evapotranspiration; we estimated evaporation to be 58% of evapotranspiration.

4. Discussion

4.1. Isotopic Distinction Between Shallow and Deep Soil Moisture

We hypothesized that shallow soil moisture and deep soil moisture would be isotopically distinct because evaporative fractionation of moisture in the shallow soil layer leads to higher $\delta^{18}O$ and δ^2H values in the shallow soil moisture than in the deep soil moisture. On most sampling days, we saw that the $\delta^{18}O$ and δ^2H values of shallow soil samples were more enriched than deep soil samples, with two types of exceptions (Figure 3f). The first exception was days when a large, isotopically depleted storm wet the shallow soil layer but had not yet infiltrated to the deep soil layer (Figure 3f; e.g., storm in early February 2015). The second exception was on dry days when there had been no rain for at least a few weeks (Figure 3f; e.g., June, November, and December 2014). One possibility for this second exception is overnight dew condensation or water adsorption into the shallow soil layer, which would lead to relatively higher $\delta^{18}O$ and δ^2H values (e.g., Zhu & Jiang, 2015); dew condensation would occur if the surface temperature was lower or equal to the dewpoint temperature, and water adsorption would occur if the relative humidity of the soil pores was less than the relative humidity of the air immediately above the soil surface (Agam & Berliner, 2006; Beysens, 1995).

We also expected the shallow and deep soil samples to be isotopically distinct between the winter and summer rainy seasons. However, during this particular study period, southern Arizona experienced four tropical storms during August, September, and October 2014 (Figure 3a), whereas tropical storms in this region usually average one every three years (C. Eastoe, personal communication Feb. 2015). Because tropical storm precipitation is generally depleted relative to the average summer precipitation (Miller et al., 2006), their $\delta^{18}O$ and δ^2H values tend to be more similar to winter precipitation than summer precipitation, which was the case for the tropical storms that fell during our study period (Figure 3e). Because these isotopically light tropical storms fell during the summer season, averages in winter and summer precipitation were not statistically isotopically distinct during our study period (Figure 4). With more samples during years with fewer tropical storms, winter and summer precipitation samples could be statistically isotopically distinct.

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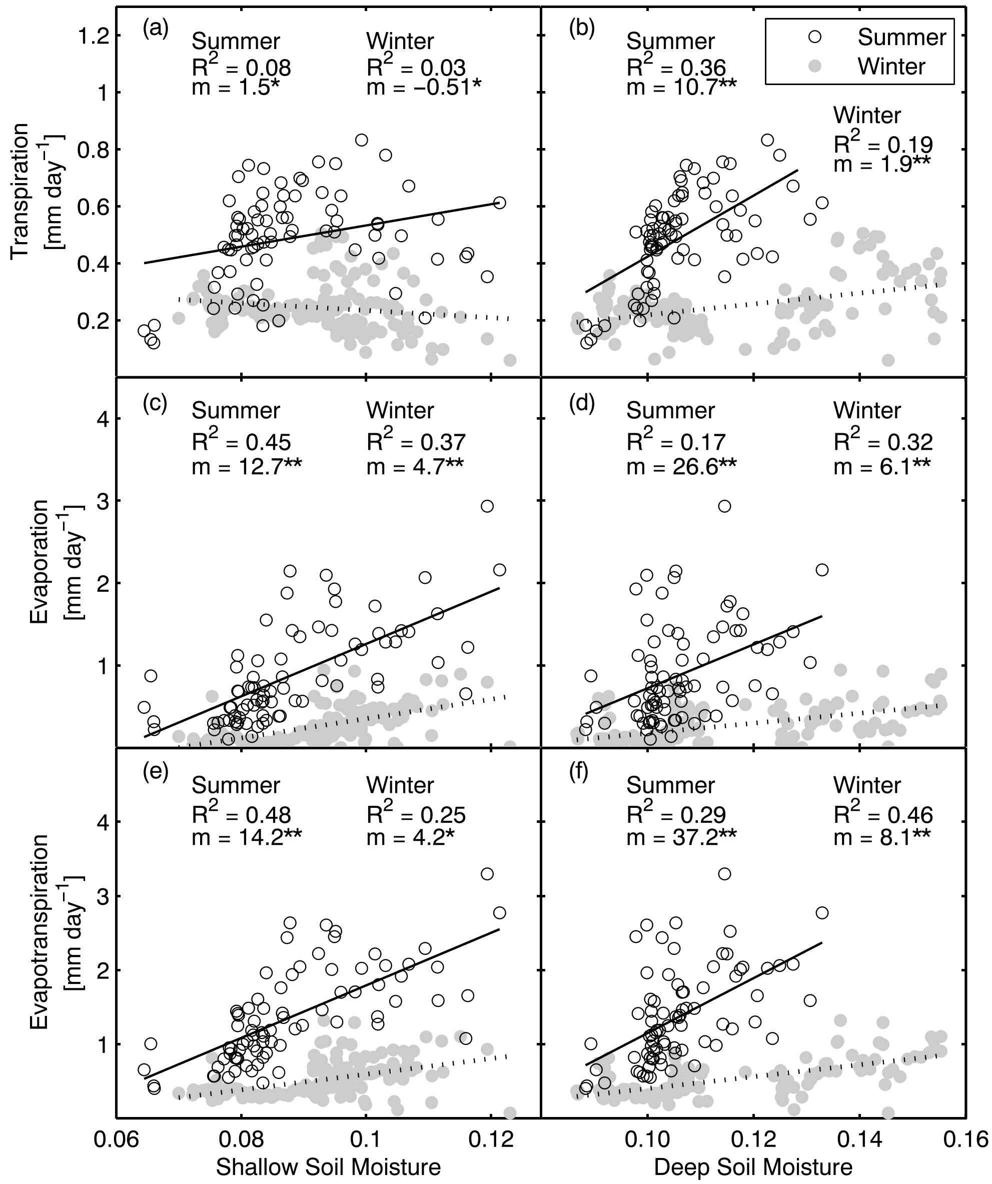

Figure 9. Linear regressions between (a) $\theta_{shallow}$ and evapotranspiration; (b) θ_{deep} and evapotranspiration; (c) $\theta_{shallow}$ and transpiration; (d) θ_{deep} and transpiration; (e) $\theta_{shallow}$ and evapotranspiration; and (f) θ_{deep} and evaporation. The solid lines represent summer regression, and the dotted lines represent winter regression. "*" and "**" indicate that the slope was significantly different from 0 at α=0.05 (*) and at α=0.01 (**).

In addition, precipitation falling during a small storm is enriched (more positive $\delta^{18}O$ and δ^2H values) relative to a large storm because of the "amount effect" (Dansgaard, 1964; Rozanski et al., 1993) caused by both evaporation (e.g., Lee & Fung, 2008) and exchange processes (e.g., Field et al., 2010; Friedman et al., 1962) and has been found to affect rainfall through dry air in other semiarid regions (e.g., Mayr et al., 2007). Therefore, we expect small storms to have moisture with relatively higher $\delta^{18}O$ and δ^2H values compared to large storms and that these small storms will wet only the shallow soil layer (Kurc & Small, 2007; Sala & Lauenroth, 1982). On the other hand, a large storm will wet both the shallow and deep soil layers (Raz Yaseef et al., 2010; Sanchez-Mejia & Papuga, 2014). There were both small and large storms in our winter and summer time periods (Figure 3a), but our sampling frequency could not differentiate isotopically between small and large events, so we expect that this in part led to the lack of statistically significant seasonal isotopic distinctions between averages in shallow and deep soil moisture (Figure 4).

The shallow soil moisture $\delta^{18}O$ and δ^2H values fell on or slightly to the right of the LMWL, and all the daily deep soil moisture $\delta^{18}O$ and δ^2H values fell to the right of the LMWL (Figure 4). The shallow soil δ^2H- $\delta^{18}O$ slope in summer was 3.4, while the slope in winter was 6.3. While precipitation usually has a slope close to 8, a slope between 2 and 6 indicate evaporative influence (Sprenger et al., 2016), and it is clear that the shallow soil is more influenced by evaporation in both summer and winter. The deep soil δ^2H- $\delta^{18}O$ slopes (2.4 in summer and 3.3 in winter) indicate surprisingly similar influences of evaporation. One explanation of this deep soil moisture isotopic characteristic in our sandy loam soil is that the deep soil moisture, rather than reflecting only the isotopic signature of large precipitation events, is instead a mix of precipitation with tightly bound soil water that could be relatively enriched in ^{18}O and ^2H (Robertson & Gazis, 2006; Sprenger et al., 2016). Another possibility is that this deep soil moisture reflects subsurface mixing of infiltrating precipitation with antecedent soil moisture (Barnes & Turner, 1998; Gazis & Feng, 2004); for example, precipitation from isotopically light, large storms infiltrates to the deep soil layer and mixes with shallow soil moisture that had been enriched in ^{18}O and in ^2H because of evaporative fractionation.

4.2. Complexities in Stable Water Isotopes for Understanding Shrub Plant Water Use

Stable water isotope values associated with plants are complex to interpret (Dawson et al., 2002; Meißner et al., 2013), especially as plant samples of stable water isotopes may be affected through both mixing processes and fractionation processes (Gessler et al., 2014). Notably, stem samples were on average more enriched in both ^{18}O and ^2H relative to the shallow and deep soil samples; that is, the stem samples did not fall between the expected sources of plant water use, shallow soil water, and deep soil water. This may have been because we did not consider all possible end-members (e.g., Brooks et al., 2010) or did not recognize the effect of fractionation processes between the soil water and the sampled plant water (e.g., Gessler et al., 2014). Recent research by Martín-Gómez et al. (2016) also found significant evaporative enrichment in xylem water from suberized stems on a subdaily temporal scale when sap flow was restricted through either leaf removal or shading.

Our soil sampling technique could also have contributed to these unexpected findings of stem samples having higher $\delta^{18}O$ and δ^2H values than soil samples. For instance, we know that soil moisture is spatially heterogeneous in dryland ecosystems (e.g., D'Odorico et al., 2007; Weltzin et al., 2003), in part because of soil differences related to pore distribution and soil microtopography (e.g., Brunel et al., 1995). Although we did not see statistically significant difference between the canopy and intercanopy soil sample isotopic values, our sampling design assumed that a single vertical soil core under the canopy and a single vertical soil core in the intercanopy space were representative of overall soil moisture conditions of the ecosystem. We also assumed that the uncertainty associated with time of sampling soil or stem water was negligible because the diurnal variation would be smaller than the seasonal variation (Zhao et al., 2014). Our study showed that although shallow and deep soil moisture were generally isotopically distinct on each sampling day, these distinctions did not necessarily follow our seasonal predictions, partly because there was no clear distinction between mean δ^2H values of summer and winter precipitation. Given these complexities in interpreting isotopic results, our study suggests that integrating stable isotope techniques with sap flow and soil moisture measurements offers a better understanding of how plant water use strategies than either technique could offer on its own.

4.3. Deep Soil Moisture Influence on Transpiration Dynamics

Our combination of continuous soil moisture and transpiration data and stable water isotope samples indicates that these warm semiarid shrubs depend on deep soil moisture for transpiration. Overall, periods of high deep soil moisture were associated with periods of high transpiration and periods of high shallow soil moisture were associated with periods of high evaporation (Figures 3 and 9). During periods associated with high transpiration (Figure 3d), shrubs appear to be dependent on moisture from the deep soil layer (Figure 9b), and this deep summer soil moisture is likely recharged by winter precipitation based on the similarity in isotopic composition of winter precipitation with those of deep soil and stem samples at during high transpiration: similar to how winter precipitation samples were more depleted in ^2H than summer precipitation, summer deep soil and stem samples were more depleted in ^2H than winter deep soil and stem samples, respectively (Figure 4). Because the shrubs are dependent on deep soil moisture for transpiration, a hypothetical decrease in large precipitation events would decrease deep soil moisture, which could reduce water available for transpiration and biomass accumulation, with major consequences for the health and functioning of these warm dryland ecosystems. Our results are consistent with other studies in warm dryland ecosystems (Beyer et al., 2016; Cavanaugh et al., 2011; Kurc & Small, 2004, 2007; Scott, Huxman, Cable, et al., 2006), although in a cold-desert semiarid shrubland, individual shrub growth was better predicted by shallow than deep soil moisture (Germino & Reinhardt, 2014), possibly because of nutrient availability or soil water storage capacity.

Previous studies have tended to emphasize summer transpiration dynamics (Cavanaugh et al., 2011; Scott, Huxman, Williams, et al., 2006; Yepez et al., 2003, 2005). However, our study suggests that under certain conditions, winter transpiration may be an important component of the water budget in desert shrubland ecosystems. Biederman et al. (2018) show that winter transpiration is an important contributor to wintertime carbon storage, although the authors assume that similar seasonal distributions of evapotranspiration and precipitation indicate that there is no seasonal lag between soil moisture recharged by precipitation and water used for evapotranspiration. Our results showed that evapotranspiration in the drier winter was dominated by evaporation, but in the wetter winter was dominated by transpiration. This suggests that transpiration can indeed occur in the winter, although the transpiration dynamics seemed to be affected by both deep soil moisture and by air temperature, depending on soil moisture availability.

5. Conclusions

Our results show how a hydrologically defined two-layer soil moisture conceptual framework may be more appropriate than other conceptual models based on average root zone soil moisture for understanding plant water use in semiarid shrublands. Results from both continuous sap flow transpiration data and discrete isotopic sampling of precipitation, soil, and stem samples suggest that plants are primarily using deep soil moisture for transpiration. From the isotopic samples, we found that the shallow and deep soils were isotopically distinct, with the shallow soil generally more enriched in ^{18}O and ^{2}H than deep soil. In particular, the δ^2H values of shallow soil samples on each sampling day tended to be more positive than the δ^2H values of deep soil samples, except on days where a large, isotopically depleted storm wetted the shallow soil layer. Using sap flow and soil moisture data, we showed that transpiration was generally more strongly correlated with deep moisture, whereas evaporation was more strongly correlated with shallow moisture. This was supported by analysis of our isotopic data, from which we show that stem samples were isotopically similar to deep soil samples. Using a combined approach to understand shrub plant water use in semiarid areas offers us more insights than simply using sap flow or isotopic techniques alone, in part because of the complexity of isotopic patterns in the rainfall and the conditions for fractionation. Contrary to what a root zone soil moisture model would predict, we found that this semiarid shrubland depends year-round on deep moisture for growth and is therefore vulnerable to shifts in precipitation.

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