

**Hydrologic control of the oxygen isotope ratio**

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# Hydrologic control of the oxygen isotope ratio of ecosystem respiration in a semi-arid woodland

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## Abstract

We conducted high frequency measurements of the  $\delta^{18}\text{O}$  value of atmospheric  $\text{CO}_2$  from a juniper (*Juniperus monosperma*) woodland in New Mexico, USA, over a four-year period to investigate climatic and physiological regulation of the  $\delta^{18}\text{O}$  value of ecosystem respiration ( $\delta_{\text{R}}$ ). Rain pulses reset  $\delta_{\text{R}}$  with the dominant water source isotope composition, followed by progressive enrichment of  $\delta_{\text{R}}$ . Transpiration ( $E_{\text{T}}$ ) was significantly related to post-pulse  $\delta_{\text{R}}$  enrichment because leaf water  $\delta^{18}\text{O}$  value showed strong enrichment with increasing vapor pressure deficit that occurs following rain. Post-pulse  $\delta_{\text{R}}$  enrichment was correlated with both  $E_{\text{T}}$  and the ratio of  $E_{\text{T}}$  to soil evaporation ( $E_{\text{T}}/E_{\text{S}}$ ). In contrast, soil water  $\delta^{18}\text{O}$  value was relatively stable and  $\delta_{\text{R}}$  enrichment was not correlated with  $E_{\text{S}}$ . Model simulations captured the large post-pulse  $\delta_{\text{R}}$  enrichments only when the offset between xylem and leaf water  $\delta^{18}\text{O}$  value was modeled explicitly and when a gross flux model for  $\text{CO}_2$  retro-diffusion was included. Drought impacts  $\delta_{\text{R}}$  through the balance between evaporative demand, which enriches  $\delta_{\text{R}}$ , and low soil moisture availability, which attenuates  $\delta_{\text{R}}$  enrichment through reduced  $E_{\text{T}}$ . The net result, observed throughout all four years of our study, was a negative correlation of post-precipitation  $\delta_{\text{R}}$  enrichment with increasing drought.

## 1 Introduction

Terrestrial ecosystems play an important role in global carbon cycling, and atmospheric oxygen isotope composition of  $\text{CO}_2$  ( $\delta_{\text{a}}$ ) has emerged as a promising tool to detect biosphere-atmosphere  $\text{CO}_2$  fluxes at tissue, ecosystem, regional and global scales (Francey and Tans, 1987; Yakir and Wang, 1996; Tans and White, 1998; Farquhar et al., 1993; Buenning et al., 2011; Cuntz et al., 2003a; Welp et al., 2011).  $\delta_{\text{a}}$  has been used to distinguish the contributions of photosynthesis and respiration (Tans and White, 1998; Yakir and Wang, 1996) and of nocturnal foliar and soil respiration (Bowling et al., 2003a) to net ecosystem exchange. The  $\delta^{18}\text{O}$  value of terrestrial  $\text{CO}_2$  fluxes ( $\delta_{\text{R}}$ ) may

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provide a stronger terrestrial signal than  $\delta^{13}\text{C}$  in some ecosystems (Fung et al., 1997; Ogee et al., 2004), but prediction of  $\delta_{\text{R}}$  is complex (Still et al., 2009) because it depends on prediction of both ecosystem water and C dynamics (Riley et al., 2003, 2005; Lai et al., 2006). The utility of oxygen isotopes in carbon cycle research can be improved, however, by a better understanding of plant physiological effects on the gross and net leaf fluxes of  $\text{C}^{18}\text{O}^{16}\text{O}$  (Flanagan et al., 1997; Gillon and Yakir, 2000; Cernusak et al., 2004).

$\delta_{\text{R}}$  depends on the  $^{18}\text{O}$  composition of the net  $\text{CO}_2$  effluxes from foliage, stem, and soils. These effluxes are strongly influenced by the  $^{18}\text{O}$  compositions of their respective water pools through oxygen atom exchange between  $\text{CO}_2$  and  $\text{H}_2\text{O}$  after equilibrium and diffusive fractionation (Brenninkmeijer et al., 1983; Tans, 1998; Farquhar et al., 1993). Carbonic anhydrase (CA) catalyzes this  $\text{CO}_2$ - $\text{H}_2\text{O}$  isotopic equilibration inside foliage (Flanagan et al., 1997) and soil (Riley et al., 2002; Seibt et al., 2006; Wingate et al., 2009).

The  $\delta^{18}\text{O}$  value of near-surface soil water ( $\delta_{\text{SW}}$ ) is often reset to the isotopic content of precipitation, which varies strongly with condensation temperature, storm origin, and storm tracks (Rozanski et al., 1982; Wingate et al., 2010). Subsequently, a vertical gradient in  $\delta_{\text{SW}}$  is often established because soil evaporation leads to isotopic enrichment (increasing  $\delta^{18}\text{O}$  value; Sharp, 2005) in the upper layers (Walker et al., 1988; Mathieu and Bariac, 1996). Soil water that is taken up by plant roots is transported through the xylem unfractionated in most terrestrial ecosystems (Dawson and Ehleringer, 1991). Leaf water becomes enriched relative to xylem water because of fractionation during evapotranspiration (Wang and Yakir, 1995; Roden and Ehleringer, 1999; Flanagan et al., 1997). Slow turnover of water within leaves can cause a significant time lag in the isotopic equilibration of leaf and xylem water at night such that leaf water is even more enriched above stem water (Cernusak et al., 2002; Farquhar and Cernusak, 2005). Cuntz et al. (2003b) incorporated such a lag into a global model of  $\delta^{18}\text{O}$  value in atmospheric  $\text{CO}_2$ . They concluded that leaf respired  $\delta^{18}\text{O}$  value becomes further enriched above source water due to  $\text{CO}_2$  retro-diffusion (the process where  $\text{CO}_2$  enters foliage

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through stomata, equilibrates with leaf water, and escapes from the leaf without altering the net CO<sub>2</sub> flux, Cernusak et al., 2004). Lastly, assuming an accelerated soil hydration rate from soil surface CA activity improved agreement between predicted and observed <sup>18</sup>O composition of atmospheric CO<sub>2</sub> (Wingate et al., 2009).

$\delta_R$  is impacted by evaporative enrichment of ecosystem water pools. Evapotranspiration drives greater isotopic enrichment in foliage than in soils due to the much smaller water pool of foliage. This enrichment results in foliar respiration being more <sup>18</sup>O enriched than soil respiration, and the isotopic disequilibrium between the  $\delta^{18}\text{O}$  values of soil and leaf respired CO<sub>2</sub> is enhanced during dry periods (Wingate et al., 2010). For example, the  $\delta^{18}\text{O}$  values of branch and soil respiration increased during a post-precipitation dry period by 170‰ and 18‰ (VPDB-CO<sub>2</sub>), respectively, in a Pinus dominated ecosystem in Europe (Wingate et al., 2010). Thus,  $\delta_a$  may carry a strong signal of drought impacts on the hydrology of terrestrial systems.

A reasonable hypothesis is that  $\delta_R$  increases during seasonal droughts when precipitation ( $P$ ) minus potential evapotranspiration ( $E_P$ ; Ellis et al., 2010) is most negative. Testing this hypothesis requires long-term datasets to capture a large range of  $P - E_P$ . A further reasonable hypothesis is that drought imparts a  $\delta_R$  enrichment dependent on the ratio of canopy transpiration to soil evaporation ( $E_T/E_S$ ) because of their differential responses to drought (Wingate et al., 2010).  $E_T$  and  $E_S$  represent the two main fluxes of water from the ecosystem to the atmosphere. The  $E_T/E_S$  ratio is fundamentally important because it is mechanistically linked to vegetation and ecosystem water balance processes and is sensitive to disturbances such as climate extremes and woody encroachment (Huxman et al., 2005). Therefore, the magnitude of  $\delta_R$  enrichment over the several days after pulse events should be linked to  $E_T$  and  $E_S$  because these fluxes impact the  $\delta^{18}\text{O}$  values of source water pools (i.e. leaves and soil water) with which CO<sub>2</sub> interacts.

To our knowledge, no study has combined long-term  $\delta_R$ ,  $P - E_P$ , and  $E_T/E_S$  observations with an analysis of terrestrial ecosystem drought response.  $E_T/(E_S + E_T)$  has been estimated from observations for a relatively small number of locations in water-limited

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regions, and those field estimates vary greatly in methodology (Reynolds et al., 2000; Wilson et al., 2001). There have been a few high resolution, continuous monitoring studies of  $\delta_R$  (Griffis et al., 2005; Welp et al., 2006; Wingate et al., 2010), but none from arid ecosystems that would be expected to strongly exhibit drought signals. Semi-arid woodlands in the southwestern USA are dominated by pulse-driven precipitation patterns and prolonged and severe drought periods (Seager et al., 2007; Rauscher et al., 2008), thus a logical expectation is that these woodlands exhibit large variation in  $\delta_R$ ,  $P - E_P$ , and  $E_T/E_S$ .

We measured  $\delta_R$  in a juniper (*Juniperus monosperma*) woodland over a four year period to investigate precipitation pulse-driven eco-hydrological responses. Along with direct measurements of  $E_T$ , we improved and applied ISOLSM (Riley et al., 2002), an isotope enabled land-surface model, to estimate  $E_S$  and interpret  $\delta_R$  observations. We hypothesized that (1)  $\delta_R$  would be related to  $P - E_P$ ; however, (2) this relationship would be moderated by rainfall pulse-driven changes in  $E_T$  or  $E_T/E_S$ . Our overarching goal is to move towards better understanding of the mechanisms determining the  $\delta^{18}O$  compositions of terrestrial  $CO_2$  fluxes and the atmosphere, allowing for potential use of these signatures for monitoring the impacts of drought on terrestrial ecosystems.

## 2 Methods

### 2.1 Field site

The field site is a piñon pine-one-seed juniper (*Pinus edulis-Juniperus monosperma*) woodland located in northern New Mexico at Los Alamos National Laboratory (35.85° N, 106.27° W, elevation 2140 m). Approximately 97 % of the mature piñon trees died in October 2002 (Breshears et al., 2005; McDowell et al., 2008a) resulting in a large necromass component to the ecosystem. The understory is dominated by  $C_3$  forbs that have increased substantially since the piñon mortality, with a minor component (< 10% cover) of native  $C_4$  grass (*Bouteloua gracilis*). Average leaf area index

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of the understory during the growing season is  $\sim 0.25 \text{ m}^2 \text{ m}^{-2}$  and juniper leaf area index is  $\sim 1.1 \text{ m}^2 \text{ m}^{-2}$ ; Maximum canopy height is  $\sim 5.5 \text{ m}$  and stand density is about  $371 \text{ trees ha}^{-1}$  (McDowell et al., 2008a). The site is located on a  $\sim 200 \text{ m}$  wide mesa with a slope of  $\sim 5\%$ . The soils are a Hackroy clay loam derived from volcanic tuff, with depths ranging from 30 to 130 cm. The climate is continental with warm summers and cold winters. Mean annual precipitation is 400 mm and exhibits a bimodal distribution between winter snowfall and summer monsoon showers. This has been the site of extensive research on ecology and hydrology (Lajtha and Barnes, 1991; Breshears et al., 1997; Newman and Robinson, 2005; Rich et al., 2008) and on the isotopic fluxes associated with photosynthesis and respiration at leaf, soil, and ecosystem scales (McDowell et al., 2008b; Bickford et al., 2009, 2010; Powers et al., 2010; Shim et al., 2011).

## 2.2 Micrometeorology and $E_c$ calculation

We collected meteorological measurements at 30 s and recorded averages every 30 min including air temperature, relative humidity (RH), soil water content (SWC) at 2 cm depth, and rainfall (Texas Electronics, Texas, USA). Soil water content was also measured at depths of 20–100 cm twice per month using neutron probes (503-DR Hydrophobe Neutron Moisture Probes, Campbell Pacific Nuclear, Inc., Pacheco, CA, USA). Pre-dawn leaf water potential ( $\Psi_{pd}$ ) was measured once per month using a Scholander-type pressure chamber (PMS Instruments Co., Corvallis, OR, USA) on six mature juniper trees.

Canopy scale transpiration,  $E_T$ , was estimated by measuring sap flux density with Granier heat dissipation probes (Granier, 1987; Phillips and Oren, 2001). A detailed description of sap flux methodology is described in Shim et al. (2011). Transpiration was scaled to the canopy level as

$$E_T = J_s A_s A_g \quad (1)$$

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Where  $J_s$  is sap flux ( $\text{g m}^{-2} \text{s}^{-1}$ ),  $A_s$  is sapwood area ( $\text{m}^2$ ), and  $A_g$  is the ground area ( $\text{m}^2$ ). Site-specific  $A_s/A_g$  was from McDowell et al. (2008a) and did not change considerably during the study due to the low growth rate of these trees.

### 2.3 Incorporation of the Isotope Land-Surface Model ISOLSM

The use of isotope-enabled land models to interpret  $^{18}\text{O}$  values of ecosystem water and  $\text{CO}_2$  fluxes at the site level is fraught with potential uncertainties (Ogee et al., 2004) stemming from challenges in (1) simulating the underlying bulk water and  $\text{CO}_2$  fluxes (Schwalm et al., 2010; Tang and Zhuang, 2008); (2) equilibrium and kinetic fractionations (Cappa et al., 2003); (3) above-canopy isotopic forcing (Welker, 2000); (4) vertical soil distributions of  $^{18}\text{O}$  and  $\text{CO}_2$  production (Riley et al., 2002; Riley, 2005); and (5) leaf water  $^{18}\text{O}$  and interactions with  $\text{CO}_2$  (Cernusak et al., 2003; Farquhar and Cernusak, 2005). The problem becomes even more acute when isotope-enabled land models are integrated into global models (e.g. Buening et al., 2012, Wingate et al., 2009). Despite these complications, we contend these models can be helpful to investigate relationships between forcing and net isotope exchanges with the atmosphere, as long as an awareness of these uncertainties is maintained.

With that philosophy in mind, we applied ISOLSM (Riley et al., 2002) to investigate land-to-atmosphere  $\text{C}^{18}\text{O}$  exchanges in the period immediately following precipitation events. ISOLSM has been used in a number of studies to evaluate controls on the  $^{18}\text{O}$  composition of ecosystem  $\text{C}$  and  $\text{H}_2\text{O}$  exchanges at site, regional, and global scales (Riley et al., 2002, 2003; Riley, 2005; Buening et al., 2011; Henderson-Sellers et al., 2006; Lai et al., 2006; McDowell et al., 2008b; Still et al., 2005, 2009).

Here, we briefly describe the methods used in ISOLSM; details of the model formulation can be found in Riley et al. (2002). In addition to simulating fluxes of  $\text{CO}_2$ ,  $\text{H}_2\text{O}$ , radiation, sensible heat, and latent heat, ISOLSM predicts separately each component of the ecosystem  $\text{CO}_2$  and  $\text{H}_2\text{O}$  isotope effluxes. Site-level climate observations sufficient to force ISOLSM continuously for the three years of this study were unavailable.

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Therefore, the necessary inputs (wind speed, humidity, temperature, pressure, solar and long-wave radiation) to drive ISOLSM were obtained from the North American Regional Reanalysis product (NARR; <http://www.emc.ncep.noaa.gov/mmb/rrean/>). The NARR is a meteorological assimilation framework designed to produce a consistent climate data for the North American region. It assimilates, at a 3-h time step, a suite of high-resolution meteorological observations into a coupled atmosphere (Eta) and land (NOAH) model. ISOLSM interpolates the resulting climate forcing to its half-hour internal time step, so no gap filling of climate forcing was required.

As with almost every other long-term C and H<sub>2</sub>O isotope modeling exercise ever performed, we did not have continuously observed  $\delta^{18}\text{O}$  values of precipitation or above-canopy atmospheric humidity. For this study, as in Still et al. (2009), we used the monthly mean precipitation  $\delta^{18}\text{O}$  values averaged over 2–5 yr from analyses of archived water samples collected by the EPA National Atmospheric Deposition Program (NADP) network (Lynch et al., 1995) between 1980 and 1990 and interpolated across the US (Welker, 2000). Many factors affect the  $\delta^{18}\text{O}$  value of vapor ( $\delta^{18}\text{O}_v$ ; Lee et al., 2006; Helliker et al., 2002; Lai et al., 2006; White and Gedzelman, 1984). We set  $\delta^{18}\text{O}_v$  to be in a temperature-dependent isotopic equilibrium with the most recent precipitation event (Still et al., 2009). We note that the sensitivity of ecosystem-atmosphere CO<sup>18</sup>O exchanges to diurnal variations in  $\delta^{18}\text{O}_v$  is relatively small (Riley et al., 2003). Accelerated CO<sub>2</sub>-H<sub>2</sub>O isotopic exchange (by carbonic anhydrase CA) in soils and foliage is an important factor impacting  $\delta_R$ . We set the CO<sub>2</sub>-H<sub>2</sub>O isotopic hydration to 100% (Wingate et al., 2009; also see Farquhar and Cernusak, 2012) because seasonal and temporal variability in hydration activity is unknown. We set the soil setting point depth to 0–2.5 cm soil depth and applied a 7.2‰ diffusive offset reflecting disequilibrium between CO<sub>2</sub> and water near the surface (Miller et al., 1999).

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We incorporated the one-way flux model proposed by Cernusak et al. (2004) to calculate the  $\delta^{18}\text{O}$  value of leaf  $\text{CO}_2$  fluxes ( $\delta_{\text{LR}}$ ):

$$\delta_{\text{LR}} = \frac{\theta [\delta_{\text{cw}} (1 + \varepsilon_w) + \varepsilon_w] + (1 - \theta) \delta_{\text{C0}} - \frac{C_a}{C_c} (\delta_a - \bar{a}) - \bar{a}}{(1 + \bar{a}) \left(1 - \frac{C_a}{C_c}\right)} \quad (2)$$

where  $\theta$  is the proportion of chloroplast  $\text{CO}_2$  that is isotopically equilibrated with chloroplast water (assumed to be 1 for the simulations here);  $\delta_{\text{cw}}$ ,  $\delta_{\text{C0}}$ , and  $\delta_a$  are the  $\delta^{18}\text{O}$  values of chloroplast water (‰) of  $\text{CO}_2$  in the chloroplast that has not equilibrated with local water, and the  $\text{CO}_2$  mole fractions in the ambient atmosphere, respectively;  $C_a$  and  $C_c$  are the  $\text{CO}_2$  in the ambient air and in the chloroplasts ( $\mu\text{mol mol}^{-1}$ ), respectively; and  $\varepsilon_w$  is the equilibrium  $^{18}\text{O}$  fractionation between  $\text{CO}_2$  and water that is dependent on temperature (Brenninkmeijer et al., 1983).  $\bar{a}$  is the weighted mean discrimination against  $\text{C}^{18}\text{OO}$  for diffusion from the chloroplast to the atmosphere (Farquhar and Lloyd, 1993):

$$\bar{a} = \frac{(C_c - C_i) a_w + (C_i - C_s) a + (C_s - C_a) a_b}{C_c - C_a} \quad (3)$$

where  $a_w$  is the summed discriminations against  $\text{C}^{18}\text{OO}$  during liquid phase diffusion and dissolution (0.8‰);  $a$  and  $a_b$  are the discriminations against  $\text{C}^{18}\text{OO}$  during diffusion through the stomata and the boundary layer (8.8 and 5.8‰, respectively); and  $C_i$  and  $C_s$  are  $\text{CO}_2$  in the leaf intercellular spaces and at the leaf surface ( $\mu\text{mol mol}^{-1}$ ), respectively.

We imposed a two-hour turnover time to the leaf water pool to account for the delayed equilibrium of leaf water with xylem water after transpiration ceases (Cuntz et al., 2003a; Farquhar and Cernusak, 2005; Lai et al., 2006). We used the model default value of minimum nighttime stomatal conductance (Bonan, 1996), which was supported by limited direct measurements (data not shown). We discuss the uncertainty resulting from these assumptions in the Discussion section.

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We calculated the fractional contribution of each isoflux, i.e. leaf, soil, and stem, to the total ecosystem isoflux from the specific sources predicted by ISOLSM by multiplying the  $\delta^{18}\text{O}$  values of leaf, soil and stem  $\text{CO}_2$  fluxes by leaf, soil, and stem respiration rates, respectively.

## 2.4 Drought index

We used the difference between precipitation ( $P$ ) and estimated potential evapotranspiration ( $E_p$ ) as a hydroclimatic index. We employed the Hamon (1961) method for  $E_p$  estimation as

$$E_p = 13.97D^2P_t \quad (4)$$

where  $E_p$  is potential evapotranspiration ( $\text{mm d}^{-1}$ ),  $D$  is the number of daylight hours in units of 12 h for a given day, and  $P_t$  is the saturated water vapor density term calculated by

$$P_t = \frac{4.95e^{0.062T_a}}{100} \quad (5)$$

where  $T_a$  is daily mean air temperature ( $^\circ\text{C}$ ). This index is well suited for regions with high inter-annual variability and extremely warm seasons during which evaporative loss dominates the hydrologic budget despite significant precipitation (Ellis et al., 2010).

## 2.5 Tunable diode laser system

A description of the tunable diode laser absorption spectrophotometer (TDL, TGA100A, Campbell Scientific Instruments, Logan, UT, USA) operation and sampling system is provided in Shim et al. (2011). Briefly, air samples were continuously collected from the canopy airspace of the piñon-juniper woodland at 0.05, 1.0, 1.5 and 3.0 m height. The fetch for the sample area is representative of the local vegetation at our sampling location because the (dead) piñon-juniper ecosystem extends for approximately

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73 km<sup>2</sup> around the tower site. The lead salt laser within our TDL system was tuned to absorption lines of 2308.225 cm<sup>-1</sup>, 2308.171 cm<sup>-1</sup>, and 2308.416 cm<sup>-1</sup> for <sup>12</sup>CO<sub>2</sub>, <sup>13</sup>CO<sub>2</sub>, and C<sup>12</sup>O<sup>18</sup>O<sup>16</sup>, respectively. The TDL sampled two calibration cylinders for 35 s each followed by four sample inlets and one quality control cylinder for 34 s each resulting in a sample collected for each height every four minutes. The first 20 s of all samples were discarded to omit transients associated with valve switching and to ensure complete purging of the sample cell of the previous sample. To assess the net error associated with CO<sub>2</sub> and δ<sup>18</sup>O measurements, we sampled a quality control cylinder during each sample cycle. This cylinder was sampled with the piñon-juniper field inlets and treated as an unknown. Precisions (1σ standard deviation) for the unknown cylinders were 0.18 μmol mol<sup>-1</sup> for CO<sub>2</sub> and 0.16‰ for δ<sup>18</sup>O value (*n* = 6000).

A linear two point gain and offset correction was applied to the sample data as described by Bowling et al. (2003b). Working calibration cylinders were propagated from World Meteorological Organization (WMO) traceable gases obtained from the National Oceanic and Atmospheric Administration (NOAA) Earth System Research Lab (ESRL); [CO<sub>2</sub>] from 344.88 to 548.16 μmol mol<sup>-1</sup> and δ<sup>18</sup>O value from -8.16 to -16.42‰. The mole fractions of the isotopologues <sup>12</sup>CO<sub>2</sub>, <sup>13</sup>CO<sub>2</sub> and <sup>12</sup>C<sup>18</sup>O<sup>16</sup>O within our calibration gases spanned the range observed in the field samples. The secondary standards (Scott-Marín, Inc., USA) were propagated weekly from our two primary standards throughout 2006 and analyzed for drift in CO<sub>2</sub> and δ<sup>18</sup>O value within the cylinders. Cylinder drift was negligible, averaging 0.00001‰ d<sup>-1</sup>, with maximum drift of 0.00005‰ d<sup>-1</sup> (*n* = 12 cylinders). We switched to approximately monthly propagation of secondary cylinders beginning in 2007.

We employed a two-ended mixing model to estimate δ<sub>R</sub> (Keeling, 1958; Flanagan et al., 1996; Zobitz et al., 2006). δ<sub>R</sub> represents the <sup>18</sup>O composition of the net ecosystem flux associated with respiration as well as abiotic invasion flux between leaves and the atmosphere (Francey and Tans, 1987) and soils and the atmosphere (Tans, 1998). We used measurements of CO<sub>2</sub> and <sup>18</sup>O taken between 20:00 and 04:00 h and data from four inlets located at 0.05, 1.0, 1.5 and 3.0 m together to examine nightly

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$\delta_R$ . Model I regressions were used to avoid negatively skewed intercepts (Zobitz et al., 2006). To assess the stability of isotopic sources for each night, we compared Keeling intercepts to the isotopic mixing line proposed by Miller and Tans (2003) (MT2003 hereafter). The MT2003 approach estimates  $\delta_R$  as the slope of a linear regression between the product of  $\delta^{18}\text{O}$  and  $[\text{CO}_2]$  versus  $[\text{CO}_2]$  and offers an advantage when the Keeling approach violates the assumption of a stable background (Miller and Tans, 2003; Lai et al., 2004). Determining  $\delta_R$  from a Keeling or a MT2003 regression from model I regressions gave similar results for our 4-yr data record ( $r^2 = 0.99$ , see Fig. A5), therefore we retained our analysis via the Keeling approach. An independent check on the assumption of stable source values was conducted using ISOLSM, which revealed that the sources were relatively stable (mean standard error (‰) = 1.5, 0.1, 0.1 for  $\delta^{18}\text{O}$  of foliar, soil and stem respiration, respectively; see Fig. A6). We screened the data to include only values with ranges of 10 ppm for  $\text{CO}_2$  and 2‰ for  $\delta^{18}\text{O}$  value (Schaeffer et al., 2008). Using this filter, 64 % of the nightly datasets were retained between April 2005 and October 2008.

## 2.6 Analyses of pulse responses

To determine the  $\delta_R$  response to precipitation pulses we compared the  $\delta_R$  prior to a rain event to the subsequent days after that event and lasting up to 11 days, but not including subsequent rain events. The number of days after precipitation pulses was not significantly different by seasons ( $F = 0.6$ ,  $P = 0.5$ , ANOVA). Analysis within individual pulse events avoids confounding multiple precipitation events when analyzing the coupling of  $\delta_R$  to meteorological or physiological parameters. Rain events differed in  $\delta^{18}\text{O}$  value due to varying  $\delta^{18}\text{O}$  values of source water, temperature, and storm tracks (Rozanski et al., 1982), thus we report  $\delta_R$  responses to pulse precipitation events as the maximum  $\delta_R$  change over the week following a rain event (see an inset in Fig. 2). This approach allows comparison of the rate and magnitude of  $\delta_R$  changes after each pulse event across the four years.

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We conducted correlation analyses of  $\delta_R$  with  $E_T$ , vapor pressure deficit (VPD), RH, and SWC for each pulse event to determine the degree and speed of coupling between  $\delta_R$  and hydrologic drivers (Bowling et al., 2002; Shim et al., 2011). We considered all possible subsets from day 1 after pulse event up to 11 days, for all four years. We considered correlations ranging from instantaneous (e.g.  $\delta_R$  from day  $x$  paired with  $E_T$  from day  $x$ ) to lagged responses (e.g.  $\delta_R$  from day  $x$  correlated with  $E_T$  from day  $x - 1$ ,  $x - 2$ , and so on). Responses of  $\delta_R$  lagged up to 11 days behind driving variables were considered. The number of days used in these analyses varied with the length of time between rain events. All correlations were conducted as linear regression models using the least squares method. We present all relationships with significance ( $p$ ) < 0.1 (Flanagan et al., 1996; McDowell et al., 2004; Shim et al., 2011).

## 2.7 $\delta^{18}\text{O}$ of precipitation, foliage, stem, and soils

Samples of precipitation, foliage, stem, and soil water were collected and analyzed for  $^{18}\text{O}$  composition in 2006 and 2007. Precipitation was collected from a sealed collection vial at the base of a rain funnel immediately after rain events. Foliage, stem and soil samples at 2, 7, and 10 cm were collected on a monthly basis as part of the Moisture Isotopes in the Biosphere and Atmosphere (MIBA) project.  $\delta^{18}\text{O}$  values of the soil water profile were measured at 5 depths: 2, 5, 7, 10 and 15 cm on DOY 151 in 2006. Samples were cryogenically extracted on a vacuum line and analyzed with a Thermo Delta Plus XL mass spectrometer at the UC Berkeley stable isotope laboratory where long-term external precision (over 5+ yr) is  $\pm 0.24\%$ . All oxygen isotope ratios in this paper for water and  $\text{CO}_2$  are referenced to the Vienna Standard Mean Ocean Water (V-SMOW) scale (Coplen, 1996) and are presented in dimensionless units of  $\%$ .

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### 3 Results

#### 3.1 Climate regimes over four years and associated patterns of $P - E_P$ , $E_S$ , $E_T/E_S$ and $\delta_R$

The pre-monsoon periods (~ April–June) typically had relatively wet soil at depth (20–40 cm) from snowmelt but dry soil near the surface due to small precipitation inputs and long inter-pulse durations (Fig. 1a, Table A1). There was substantial inter-annual variation, however, with a particularly dry pre-monsoon period in 2006 and relatively wet pre-monsoon period in 2007 (Fig. 1b, and Shim et al., 2011). The mid-summer monsoon seasons (typically July and August) were characterized by frequent rainfall events and subsequently dynamic SWC (Fig. 1). Again, there was substantial inter-annual variation, with relatively strong monsoon precipitation in 2006 characterized by an early onset of monsoon rains and particularly short (< 5 days) inter pulse duration (Table A1). 2007 was the driest monsoon season of the four years, with lowest SWC, highest VPD and  $T_{\text{soil}}$ , and longest inter-pulse durations.  $P - E_P$  declined rapidly after pulse events and was particularly low in 2007 and 2008. Post-monsoon periods were relatively similar between years and were characterized by decreasing rainfall and declining  $T_{\text{soil}}$ .

Pre-dawn leaf water potential ( $\Psi_{\text{pd}}$ ) tended to track SWC at 20 cm depth, with least negative values in spring, most negative values in August, and rebounded in early September (Fig. 1a;  $p < 0.001$ ,  $r^2 = 0.3$ ). SWC at 20 cm depth followed seasonal variation in  $P - E_P$  (Fig. 1b;  $p < 0.001$ ,  $r^2 = 0.3$ ).

Mean daily  $E_T$  ( $\text{mm d}^{-1}$ ) from days 100 to 304 were  $0.7 \pm 0.1$ ,  $0.5 \pm 0.1$ , and  $0.3 \pm 0.1$  in 2006, 2007, and 2008, respectively.  $E_T$  increased after rainfall events throughout the three years of sapflow measurements (Fig. 1c). Average maximum changes in  $E_T$  ( $\text{mm d}^{-1}$ ) after pulses were  $0.6 \pm 0.2$ ,  $0.4 \pm 0.1$  and  $0.4 \pm 0.2$  during pre-monsoon, monsoon, and post-monsoon periods, respectively.  $E_T$  did not exceed  $0.3 \text{ mm d}^{-1}$  when  $\Psi_{\text{pd}}$  was  $\leq -1 \text{ MPa}$  in monsoon and post-monsoon seasons, but did reach higher values for

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the same  $\Psi_{pd}$  during the premonsoon seasons (Fig. A1); this is consistent with the relatively anisohydric behavior of juniper trees (McDowell et al., 2008a). Similarly,  $E_T$  responses to VPD were only strong when  $SWC \geq 15\%$ , with relatively shallow responses when soil moisture was low (i.e.  $< 15\%$ ; Fig. 3a).

Modeled  $E_S$  generally showed rapid spikes and subsequent gradual decreases after rainfall events (inset in Fig. 1c). As  $E_S$  declined,  $E_T$  consistently increased resulting in increasing  $E_T/E_S$  (Fig. 1c, 59% of rain events) because soil evaporation responds rapidly to pulses, while the vegetation response was more gradual and long-lived because it takes longer for water to infiltrate, reach the rooting zone, transport through xylem, and transpire through the leaves (Reynolds et al., 2004). Strong positive responses of  $E_T$  to VPD became evident when  $SWC > 15\%$  (Fig. 3a). Average maximum changes in  $E_T/E_S$  after pulses were  $4.3 \pm 1.3$ ,  $1.4 \pm 0.4$  and  $5.5 \pm 2.5$  during pre-monsoon, monsoon, and post-monsoon periods, respectively.  $E_T/E_S$  peaks were associated with elevated soil moisture after snowmelt and during relatively wet monsoon periods due to high values of  $E_T$  (Figs. 1a, c, Table A1).

After filtering atmospheric  $CO_2$ - $\delta^{18}O$  ( $\delta_a$ ) by our QC criteria, 64% of the nights were retained for  $\delta_R$  calculation from April 2005 through October 2008 (547 nights). Nightly measured  $\delta_R$  averaged  $46.7\text{‰} \pm 0.6$ ,  $50.7\text{‰} \pm 0.7$ ,  $52.6\text{‰} \pm 1.2$ , and  $44.8\text{‰} \pm 2.3$  in 2005, 2006, 2007, and 2008, respectively.  $\delta_R$  generally became depleted immediately after rainfalls and subsequently enriched until the next rain event (Fig. 2). Average maximum  $\delta_R$  enrichment after pulses were 28.7, 18.9, and 25.6‰ during pre-monsoon, monsoon and post-monsoon periods, respectively.

### 3.2 Patterns of water pool $\delta^{18}O$ and relationships of $\delta_R$ and hydrologic drivers after pulses

Juniper foliage water consistently had the highest  $\delta^{18}O$  values (mean  $17.6 \pm 0.2\text{‰}$ ), followed by soil water (mean  $-2.2 \pm 1.0\text{‰}$ ) and juniper stem water ( $-8.7 \pm 0.6\text{‰}$ ) (Tukey's test,  $F = 225.1$ ,  $p < 0.001$ , Table 1). Foliar water  $\delta^{18}O$  value was positively correlated

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with VPD ( $r^2 = 0.7$ ,  $p < 0.001$ ); but there was no correlation of mean 0–15 cm soil water  $\delta^{18}\text{O}$  value with VPD (Fig. 2b).

$\delta_{\text{R}}$  showed progressive enrichments with increasing VPD and  $E_{\text{T}}$  and decreasing RH at the intra-seasonal scale (Table 2 and Fig. A2), indicating the importance of evaporative demand and transpiration on  $\delta_{\text{R}}$ . Despite the clear dependence of  $\delta_{\text{R}}$  on these drought-related parameters, there were no significant relationships between  $\delta_{\text{R}}$  and  $P - E_{\text{P}}$  when including all nights from DOY 100–273 over the four years (Fig. A3), though a clear pattern emerges of a wide  $\delta_{\text{R}}$  range during wetter periods and a limited range during drought. Thus,  $P - E_{\text{P}}$  by itself was not a good predictor of  $\delta_{\text{R}}$ , perhaps due to the variable  $\delta^{18}\text{O}$  of rainfall events.  $\delta_{\text{R}}$  on the day of rain events followed annual  $\delta^{18}\text{O}$  precipitation trends ( $r^2 = 0.4$ ,  $p = 0.001$ ). Indeed, pulse events induced an immediate decrease in  $\delta_{\text{R}}$  (Fig. 4b). Following these immediate depletions,  $\delta_{\text{R}}$  subsequently became enriched following nearly all pulse events (Fig. 4c). Similarly,  $E_{\text{T}}$  increased following rain events (Fig. 4a). The post-pulse  $\delta_{\text{R}}$  enrichment typically reached a plateau within five days after the rain event (Fig. 5a–c). The largest and smallest enrichments occurred in pre-monsoon and monsoon seasons, respectively (Fig. 5a–c). The normalized  $\delta_{\text{R}}$  enrichment was correlated with  $E_{\text{T}}$  (Fig. 5d–f).

The model accurately captured the temporal  $\delta_{\text{R}}$  dynamics of the post-pulse  $\delta_{\text{R}}$  enrichment ( $r^2 = 0.7$ ; Fig. 6). Simulated depletion in  $\delta_{\text{R}}$  immediately following precipitation events was often underestimated (mean underestimate of  $7.2 \pm 1.6\%$ ; Fig. A7). The  $\delta_{\text{R}}$  prediction accuracy improved greatly after the one-way flux model proposed by Cernusak et al. (2004) was incorporated to estimate leaf  $\text{C}^{18}\text{OO}$  fluxes ( $p < 0.001$  for all,  $r^2 = 0.2$  and  $0.5$  for net flux model and one-way flux model, respectively; Fig. A4). The higher accuracy of the one-way flux model is consistent with large enrichment of chloroplast  $\text{CO}_2$ . ISOLSM predicted that foliar  $\text{C}^{18}\text{OO}$  flux was the dominant contributor to post-pulse  $\delta_{\text{R}}$  enrichment during pre- and post-monsoon periods over the three years, whereas soil  $\text{C}^{18}\text{OO}$  flux was the dominant contributor during monsoon periods (Fig. 7).

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Consistent with our expectations,  $\delta_R$  enrichment was correlated with  $E_T/E_S$  (Fig. 8a). A stronger relationship between  $\delta_R$  and  $P - E_P$  emerged after accounting for precipitation effects on ecosystem water pools by calculating the maximum  $\delta_R$  change between the day of the rain event and the subsequent dry period (see methods,  $r^2 = 0.4$ ,  $p = 0.001$ , Fig. 8b).

## 4 Discussion

$\delta_R$  did not simply increase with larger values of  $P - E_P$  (Fig. A3). Rather, the relationship between  $\delta_R$  and  $P - E_P$  was heavily moderated by precipitation events (Fig. 8b). Further, the four year semi-continuous  $\delta_R$  observations exhibited strong coupling of  $\delta_R$  with hydrological attributes of local weather ( $P - E_P$ , VPD, and RH) and ecosystem physiology ( $E_T$  and  $E_T/E_S$ ) at daily (Figs. 3, 5, A2), seasonal (Figs. 5, A2) and inter-annual scales (Figs. 3, 5, A2). The wide  $\delta_R$  range at more positive  $P - E_P$  and narrow range at more negative  $P - E_P$  (Fig. A3) appears to be the result of multiple factors, most notably resetting of water pool  $\delta^{18}\text{O}$  values by rain (Fig. 5b), and regulation of subsequent enrichment by transpiration and soil evaporation (Figs. 1, 2, 5, 8). The magnitude of post-pulse  $\delta_R$  enrichment varied with seasonal and inter-annual climate (Figs. 1, 5) due in part to constraints on the  $E_T$  response (Figs. 1, 2, 4, 8 and A1) and changes in  $E_T/E_S$  (Fig. 8a). These patterns support the contention of strong hydrological regulation of ecosystem function in semi-arid regions (Weltzin and Tissue, 2003) and suggest that long-term monitoring of  $\delta_R$  has promise for understanding drought responses and detecting drought induced eco-physiological changes. Below, we explore the potential mechanisms driving the drought signal of  $\delta_R$ .

Rain reset near-surface soil and source (i.e. xylem water)  $\delta^{18}\text{O}$  values, causing immediate  $\delta_R$  depletions followed by subsequent enrichment as the ecosystem dried (Figs. 1, 4, 5), consistent with previous results from short-term (i.e. 60 min) post-pulse measurements of the  $\delta^{18}\text{O}$  value of soil  $\text{CO}_2$  effluxes at our site (Powers et al., 2010). ISOLSM was not consistently accurate in simulating  $\delta_R$  depletions within hours of the

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rainfall events, for several reasons. First, comparisons between the available precipitation  $\delta^{18}\text{O}$  measurements at the site for the time periods presented in our study in 2006 indicates that the ISOLSM forcing precipitation isotope composition was, on average, 3.1‰ more enriched than observed (Fig. A7). Therefore, the imposed  $\delta^{18}\text{O}$  value of above-canopy vapor following precipitation would also be too enriched in the simulations (Riley et al., 2002). ISOLSM precipitation and were less dynamic than observations, particularly depletions during pulse events. Second, pulse events often trigger a brief large burst of soil  $\text{CO}_2$  efflux (i.e. the Birch effect, Birch, 1964) in arid and semi-arid ecosystems, which can impact  $\delta_{\text{R}}$  for short periods. Modeling the Birch effect is difficult because it cannot be simply formulated using only soil temperature and moisture, as done in ISOLSM and many terrestrial ecosystem models. Despite these caveats, the model simulations are useful because we focus not on the immediate few hours following rainfall but on the multi-day responses following rainfall. 93 % of our analysis periods (in which data was used in the results) contained zero rainfall because nearly all rain events occurred during the day from convective storms and the data analysis was for periods starting the subsequent nights after a rain event. ISOLSM captured the measured  $\delta_{\text{R}}$  within 7 days of the precipitation ( $r^2 = 0.7$ ; Fig. 6) after we imposed (1) a two-hour turnover time to the leaf water pool considering leaf water may be enriched several hours after transpiration ceases due to slow turnover of the leaf water pool (Cuntz et al., 2003a; Lai et al., 2006) and incorporated (2) one-way flux model proposed by Cernusak et al. (2004).

Comparison of modeled and observed  $\delta_{\text{R}}$  at this site in 2006 demonstrated that nocturnal isotopic equilibration of  $\text{CO}_2$  with leaf water  $\delta^{18}\text{O}$  value and subsequent atmospheric retro-flux may drive large enrichment in  $\delta_{\text{R}}$  (McDowell et al., 2008b). The higher accuracy of the one-way flux model is consistent with large enrichment of chloroplast  $\text{CO}_2$  (Cernusak et al., 2004). This one-way flux model is similar to  $\text{CO}_2$  invasion and retro-flux in soils (Tans, 1998; Riley et al., 2005; Seibt et al., 2006). Stomata are assumed to be closed at night in many isotope land models; however, accumulated evidence has shown that stomata are leaky at night in many species (Barbour et al.,

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2005; Dawson et al., 2007). Limited nocturnal, leaf-level measurements of stomatal conductance ( $g_c$ ) confirmed that junipers do maintain some degree of stomatal conductance after sundown (up to  $0.11 \text{ mol m}^{-2} \text{ s}^{-1}$ ,  $se = 0.003$ , unpublished data). Markedly improved  $\delta_R$  prediction by ISOLSM suggests nocturnal  $g_c$  leads to high  $\text{CO}_2$  retrodiffusion and a faster exchange of leaf water with atmospheric water vapor at night and the  $\delta^{18}\text{O}$  composition of leaf water may not be in equilibrium with xylem water at night (Cernusak et al., 2004; Seibt et al., 2006; Lai et al., 2006; Cuntz et al., 2007).

The  $\delta_R$  values over four years of study showed  $\delta_R$  enrichment following pulse events in 95% of the observations (Fig. 2). Correlations of  $\delta_R$  with VPD and RH over the subsequent days after pulse events and lasting up to 11 days were stronger than for SWC (Table 2). These relationships suggest that declines in atmospheric vapor content following precipitation pulses were a stronger driver of  $\delta_R$  patterns than the availability of soil moisture per se (i.e. water content), consistent with observations from more mesic sites (Bowling et al., 2003a,b; Wingate et al., 2010).

The underlying drivers of the correlations of VPD and RH with  $\delta_R$  are likely driven by both soil evaporation and canopy transpiration. The post-pulse normalized  $\delta_R$  enrichment correlated strongly with  $E_T/E_S$  over the three years from DOY 100 to 273 (Fig. 8a). Post-pulse  $\delta_R$  enrichment was relatively small when  $E_T/E_S < 2$ , due in part to  $E_T$  constraints and a higher contribution of soil  $\text{C}^{18}\text{OO}$  flux to total isoflux (Figs. 1, 5 see in legend). Post-pulse  $\delta_R$  enrichment was significantly larger when  $E_T$  and its relative contribution to ecosystem scale evapotranspiration were large (Figs. 5, 8a) consistent with leaf-level observations in droughted plants. This  $\delta_R$  enrichment was likely a result of the enrichment of foliar water as well as retro-diffusion with atmospheric  $\text{CO}_2$ . With active transpiration, water transpired by foliage is more enriched than soil water (Table 1, Wingate et al., 2010) because evaporation results in more efficient accumulation of heavier water molecules in leaf water than soil water (Table 1, Wang and Yakir, 1995; Barbour et al., 2005; Wingate et al., 2010). In our system, this enrichment resulted in a strong relationship between VPD and foliar water  $\delta^{18}\text{O}$  values, but no relationship between VPD and soil water  $\delta^{18}\text{O}$  values (Fig. 3b). This more enriched foliar water

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is likely to persist several hours at night after transpiration ceases, as suggested by ISOLSM.

The post pulse normalized  $\delta_R$  enrichment correlated well with  $E_T/E_S$  over the three years from DOY 100 to 273 (Fig. 8a). The magnitudes of post-pulse  $E_T$  and  $\delta_R$  enrichment were larger and more frequently observed during pre-monsoon periods than during monsoon periods (Fig. 5). Strong positive responses of  $E_T$  to VPD were more common when more soil water was available (Fig. 3a). Strong responses of  $E_T/E_S$  to pulses corresponded with high  $\Psi_{pd}$  and lower VPD (not shown). All of these factors were most common pre-monsoon when snowmelt had recharged the entire soil water profile (Fig. 1). The source partitioning analysis from ISOLSM provides evidence of higher foliar contribution to total ecosystem isoflux relative to soil and stem components during pre-monsoon periods (Fig. 7). Both  $E_T$  and  $E_S$  responded strongly to spring rains despite their small size, yet  $E_T/E_S$  frequently exceeded 2 because of transient  $E_S$  spikes and more sustained increases in  $E_T$  (Figs 1c in inset, 5 see in legend).

Soil isoflux contributed relatively more than leaf isoflux to the ecosystem signal during the monsoon periods (Fig. 7). The monsoon periods typically had more negative  $\Psi_{pd}$ , lower soil water content deep in the soil profile (Fig. 1), and higher temperatures, thus only particularly large rain events or many rainy days in a row triggered significant  $\delta_R$  responses.  $E_T$  increased within a few days after monsoon rains, but the  $E_T$  amplitudes were small and post-pulse  $E_T/E_S$  usually remained below 1.5 (particularly for the dry 2007 and 2008 monsoon seasons, Figs. 1c, 5). The least  $\delta_R$  enrichment after rain events was observed during seasons when the post-rainfall  $E_T$  response was small and the drought index  $P - E_P$  was highly negative (Fig. 8b). While  $\delta_R$  was strongly related to atmospheric vapor pressure deficit (VPD), the degree of enrichment appears constrained by the trees' capacity to increase  $E_T$  (Figs. 1, 5e, A1, Ferrio et al., 2009).

Coupling of  $\delta_R$  with VPD, RH, and  $E_T$  occurred more rapidly, and more frequently, than observed for the  $\delta^{13}\text{C}$  value of ecosystem respiration ( $\delta^{13}\text{C}_R$ ) at this ecosystem for the same years (Table 2, Fig. A2, Shim et al., 2011). This more rapid coupling is likely due to the immediate exchange of oxygen atoms between respiring  $\text{CO}_2$  and

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water pools leading to fast incorporation of the water isotopic signature into ecosystem respiration (Wingate et al., 2010). In contrast,  $\delta^{13}\text{C}_R$  is derived from the relatively slower transport of carbon from foliage to the mean location of respiration (foliage, stems, roots, and heterotrophic biomass), including additional lags due to autotrophic and heterotrophic storage (Bowling et al., 2008). These storage effects, in particular, make deciphering the information derived from  $\delta^{13}\text{C}_R$  measurements more difficult because  $\delta^{13}\text{C}_R$  is frequently un-coupled from climate, at least in this semi-arid woodland (Shim et al., 2011). Thus, the relative value of  $\delta_R$  is enhanced not only by its unique representation of terrestrial hydrology, but also because its dependence on climate and physiology is more easily detected.

## 5 Conclusions

In our system, the  $\delta^{18}\text{O}$  value of ecosystem respiration ( $\delta_R$ ) was highly variable (Fig. 2); this variability was reduced as drought increased ( $P - E_P$ , Fig. A3). Evaporative demand plays a significant role in the  $\delta_R$  enrichment following rain events, and this response was strongly influenced by  $E_T$  and  $E_T/E_S$  (Figs. 5, 8) due in part to strong leaf water enrichment (Fig. 3) and subsequent foliar respiration and retro-diffusion (Figs. 5, A4). Conditions that limit  $E_T$  subsequently limit the  $\delta_R$  enrichment post-rain events (Figs. 1, 2, 5, 6), resulting in reduced enrichment when  $P - E_P$  is more negative (Fig. 8b). Thus, deciphering the drought signal associated with  $\delta_R$  requires consideration of episodic dynamics of precipitation pulses, their impacts on the  $\delta^{18}\text{O}$  value of source water pools, and the magnitude of  $E_T$  responses.

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**Table 1.**  $\delta^{18}\text{O}$  values of leaf water, stem water and soil water in 2005 and 2006. Alphabetic superscripts (<sup>a</sup>, <sup>b</sup> and <sup>c</sup>) within columns indicate differences among the three groups using Tukey test ( $F = 225.1$ ,  $p < 0.001$ ). Different soil depths denote as; <sup>d</sup>: 2 cm, <sup>e</sup>: 5 cm, <sup>f</sup>: 7 cm, <sup>g</sup>: 10 cm, <sup>h</sup>: 15 cm.

DOY/Year	Day(s) after rain	$\delta^{18}\text{O}$ (SMOW, ‰)		
		juniper foliage <sup>a</sup>	juniper stem <sup>b</sup>	Soils <sup>c</sup>
111/2005	6	21.3	-11.4	-10.5 <sup>d</sup>
137/2005	2	18.2	-12.2	-8.9 <sup>f</sup>
152/2005	18	15.2	-12.8	-3.2 <sup>d</sup> , -11.3 <sup>f</sup>
180/2005	3	25.3	-10.7	-1.1 <sup>g</sup>
184/2005	7	20.8	-10.1	
207/2005	8	16.4	-8.1	-5.6 <sup>g</sup>
208/2005	0	9.6	-9.2	1.4 <sup>g</sup>
223/2005	5	16.9	-6.7	
151/2006	9			-1.5 <sup>d</sup> , 3.7 <sup>e</sup> , 2.6 <sup>f</sup> , 2.5 <sup>g</sup> , 0.6 <sup>h</sup>
167/2006	7	23.2	-6.9	
181/2006	1	17.6	-6.6	-1.8 <sup>g</sup>
195/2006	4	26.7	-4	-1.4 <sup>g</sup>
214/2006	1	13.9	-7.2	-2.2 <sup>g</sup>
223/2006	1	14.6	-7.5	-8.4 <sup>g</sup>
240/2006	2	16.5	-7.6	
271/2006	6	15.1	-8.4	-4.3 <sup>g</sup>
292/2006	4	10.5	-10.2	-2.4 <sup>g</sup>
Mean $\pm$ SE	4.9 $\pm$ 1.1	17.6 $\pm$ 1.2	-8.7 $\pm$ 0.6	-2.2 $\pm$ 1.0

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**Table 2.** Correlation coefficients ( $r^2$ ) of  $\delta_R$  with VPD, SWC, RH, and  $E_T$  for each pulse event. The number of days lagged is presented along with the sign of relationship in parenthesis.

Day of Year	VPD	SWC.2cm	RH	$E_T$	Pulse size (mm)
Pre-monsoon					
125–132(2005)	<b>0.33 (0,+)<sup>a</sup></b>	<b>0.81 (0,-)<sup>b</sup></b>	<b>0.87 (0,-)<sup>b</sup></b>		2.1
135–143(2005)	<b>0.71 (0,+)<sup>b</sup></b>	<b>0.53 (0,-)<sup>a</sup></b>	<b>0.79 (0,-)<sup>b</sup></b>		2.1
Monsoon					
198–206(2005)	0.36 (0,+)	0.5 (0,-)	0.67 (0,-)		3.5
207–213(2005)	<b>0.5 (0,+)<sup>a</sup></b>	0.43 (0,-)	<b>0.45 (0,-)<sup>a</sup></b>		2
234–244(2005)	0.27 (0,+)	<b>0.71 (0,-)<sup>b</sup></b>	<b>0.51 (0,-)<sup>a</sup></b>		21.9
Post-Monsoon					
245–253(2005)	<b>0.83 (1,+)<sup>b</sup></b>	<b>0.81 (0,-)<sup>b</sup></b>	<b>0.9 (1,-)<sup>b</sup></b>		9.4
271–278(2005)	~ 0 (0,+)	<b>0.78 (0,-)<sup>b</sup></b>	0.05 (0,+)	0.63 (0,-)	61.7
282–287(2005)	<b>0.94 (0,+)<sup>b</sup></b>	0.02 (0,-)	<b>0.94 (0,-)<sup>b</sup></b>	0.36 (0,+)	9.9
Pre-monsoon					
118–123(2006)	<b>0.86(1,+)<sup>b</sup></b>	<b>0.52(1,+)<sup>a</sup></b>	<b>0.83(1,-)<sup>b</sup></b>	<b>0.69(1,+)<sup>b</sup></b>	6
125–131(2006)	<b>0.69(2,+)<sup>a</sup></b>	<b>0.93(0,-)<sup>b</sup></b>	0.43(2,-)	0.53(0,+)	2.3
135–141(2006)	<b>0.86(2,+)<sup>a</sup></b>	<b>0.98(4,-)<sup>a</sup></b>	<b>0.89(3,-)<sup>a</sup></b>	<b>0.95(4,+)<sup>a</sup></b>	1.6
160–167(2006)	0.39(3,-)		<b>0.76(2,+)<sup>a</sup></b>	<b>0.73(1,+)<sup>a</sup></b>	2.2
173–178(2006)	0.06(0,+)	0.53(0,+)	0.14(1,+)	0.44(0,+)	16.4
Monsoon					
184–191(2006)	<b>0.34(0,+)<sup>a</sup></b>	~ 0(0,+)	<b>0.38(0,-)<sup>a</sup></b>	<b>0.34(0,+)<sup>a</sup></b>	29.1
217–222(2006)	<b>0.74(0,+)<sup>b</sup></b>	<b>0.72(0,+)<sup>b</sup></b>	<b>0.73(0,-)<sup>b</sup></b>	0.42(0,+)	31
225–230(2006)	0.07(0,+)	<b>0.75(0,+)<sup>a</sup></b>	0.07(0,-)	~(0,-)	28.3
231–235(2006)	<b>0.82(0,+)<sup>a</sup></b>	0.1(0,+)	<b>0.76(0,-)<sup>a</sup></b>	0.03(0,+)	16.8
236–241(2006)	<b>0.98(0,+)<sup>b</sup></b>	0(0,+)	<b>0.98(0,-)<sup>b</sup></b>	0.27(0,+)	29.1
243–248(2006)	0.23(0,+)	0.06(0,+)	0.22(0,-)	0.01(0,+)	10.6
Post-Monsoon					
249–255(2006)	<b>0.88(1,+)<sup>a</sup></b>	<b>0.86(3,-)<sup>b</sup></b>	<b>0.99(1,-)<sup>b</sup></b>	<b>0.69(4,+)<sup>a</sup></b>	13.4
254–259(2006)	<b>0.73(0,+)<sup>b</sup></b>	<b>0.83(0,-)<sup>b</sup></b>	<b>0.92(0,-)<sup>b</sup></b>	0.41(0,+)	1
282–286(2006)	<b>0.95(0,+)<sup>b</sup></b>	<b>0.83(0,+)<sup>a</sup></b>	<b>0.96(0,-)<sup>b</sup></b>	<b>0.87(0,+)<sup>a</sup></b>	9



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Table 2. Continued.

Day of Year	VDP	SWC.2 cm	RH	$E_T$	Pulse size (mm)
Pre-monsoon					
103–106(2007)	<b>0.94(0,+)</b> <sup>b</sup>	0.57(0,+)	<b>0.93(0,-)</b> <sup>b</sup>	<b>0.97(0,+)</b> <sup>b</sup>	4.3
128–133(2007)	<b>0.82(0,+)</b> <sup>b</sup>	<b>0.62(0,+)</b> <sup>a</sup>	<b>0.75(0,-)</b> <sup>b</sup>	0.22(0,-)	16.3
134–140(2007)	<b>0.54(0,+)</b> <sup>a</sup>	<b>0.74(3,-)</b> <sup>b</sup>	<b>0.54(0,-)</b> <sup>a</sup>	0.19(0,-)	9.6
140–150(2007)	0.17(3,-)	<b>0.24(1,+)</b> <sup>a</sup>	0.67(3,+)	0.16(3,-)	8.6
162–166(2007)	0.4(0,+)	<b>0.89(0,+)</b> <sup>a</sup>	0.34(0,-)	0.17(0,+)	11.2
Monsoon					
200–206(2007)	0.19(0,+)	0.62(0,+)	0.26(0,-)	0.5(0,+)	6
211–216(2007)	<b>0.87(0,+)</b> <sup>b</sup>	0.25(0,+)	<b>0.71(0,-)</b> <sup>a</sup>	<b>0.6(0,+)</b> <sup>a</sup>	20.6
218–223(2007)	<b>0.73(0,+)</b> <sup>b</sup>	<b>0.67(0,+)</b> <sup>a</sup>	<b>0.75(0,-)</b> <sup>b</sup>	<b>0.47(0,+)</b> <sup>a</sup>	11.2
224–229(2007)	<b>0.85(0,+)</b> <sup>b</sup>	~ 0(0,+)	<b>0.92(0,-)</b> <sup>b</sup>	0.22(0,-)	8.9
230–234(2007)	<b>0.79(0,+)</b> <sup>b</sup>	0.28(0,-)	<b>0.78(0,-)</b> <sup>a</sup>	0.08(0,+)	4.8
236–240(2007)	0.07(0,+)	0.05(0,-)	0.08(0,-)		9.6
241–246(2007)	0.4(0,+)	0.41(2,-)	0.41(2,+)		22.1
Post-Monsoon					
247–254(2007)	<b>0.8(2,-)</b> <sup>b</sup>	0.55(3,+)	<b>0.6(2,+)</b> <sup>a</sup>		8.6
260–266(2007)	0.36(2,-)	<b>0.88(4,+)</b> <sup>a</sup>	0.3(0,-)		40.1
271–276(2007)	<b>0.84(1,-)</b> <sup>a</sup>	<b>0.8(0,-)</b> <sup>a</sup>	0.61(1,+)		10.9
Pre-monsoon					
107–114(2008)	<b>0.66(0,+)</b> <sup>b</sup>	<b>0.6(0,-)</b> <sup>b</sup>	0.4(0,+)	<b>0.94(0,+)</b> <sup>b</sup>	3.5
134–140(2008)	<b>0.64(2,+)</b> <sup>a</sup>	<b>0.76(0,-)</b> <sup>a</sup>	0.29(1,-)	<b>0.66(3,+)</b> <sup>d</sup>	4.8
142–147(2008)	0.1(0,+)	<b>0.86(0,-)</b> <sup>b</sup>	0.13(0,+)	<b>0.7(0,+)</b> <sup>a</sup>	2.8
148–155(2008)	~ 0(0,+)	0.09(0,-)	0.03(0,+)	<b>0.64(0,+)</b> <sup>d</sup>	3.3
Monsoon					
197–206(2008)	0.46(0,+)	0.69(0,+)	0.04(0,+)	<b>0.93(0,-)</b> <sup>b</sup>	21.8
207–215(2008)	0.46(0,+)	<b>0.85(0,-)</b> <sup>a</sup>	0.42(0,+)	0.13(0,+)	4.8
216–225(2008)	0.03(0,-)	<b>0.70(0,-)</b> <sup>a</sup>	0.02(0,+)	0.46(0,-)	50.5
222–229(2008)	<b>0.48(5,-)</b> <sup>a</sup>	0.27(4,-)	<b>0.42(3,-)</b> <sup>a</sup>	<b>0.62(0,+)</b> <sup>a</sup>	38.4
228–234(2008)	0.03(0,-)	<b>0.87(0,-)</b> <sup>b</sup>	<b>0.62(0,+)</b> <sup>a</sup>	<b>0.61(0,+)</b> <sup>a</sup>	12.5
235–241(2008)	0.06(1,+)	<b>0.75(1,+)</b> <sup>a</sup>	<b>0.59(1,-)</b> <sup>a</sup>	0.20(0,-)	28.2
Post-Monsoon					
243–251(2008)	<b>0.46(4,+)</b> <sup>a</sup>	0.22(2,-)	0.18(4,-)	<b>0.74(0,+)</b> <sup>a</sup>	22
263–268(2008)	0.01(0,-)	0.32(0,-)	0.07(0,+)	0.01(0,+)	3.6
269–274(2008)	0.13(0,-)	0.28(0,-)	0.16(0,+)	0.11(0,-)	3.3
284–293(2008)	<b>0.79(0,+)</b> <sup>a</sup>	<b>0.89(0,+)</b> <sup>a</sup>	<b>0.86(0,-)</b> <sup>a</sup>	0.62(0,+)	28.7

<sup>a</sup> Regression significance:  $P \leq 0.1$ .

<sup>b</sup> Regression significance:  $P \leq 0.05$ .

Blanks: Data not available.

Horizontal lines indicate season shifts between pre-monsoon, monsoon, and post-monsoon.

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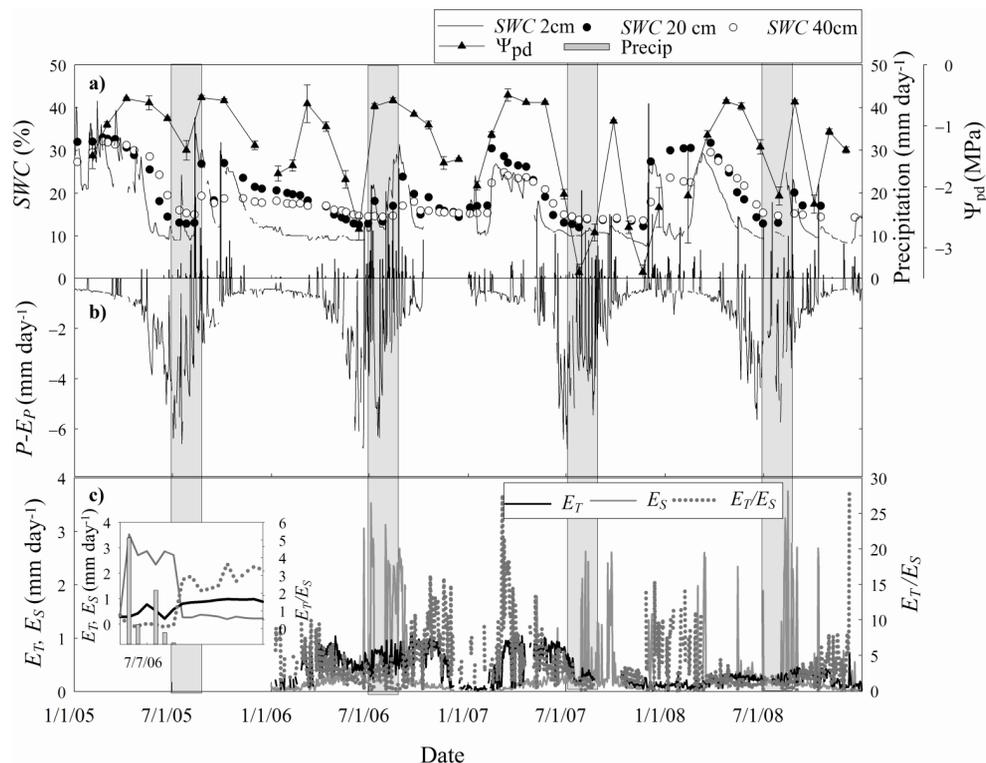


**Table A1.** Seasonal rain pulse sizes and inter-pulse duration shown as the percentage of events and durations, respectively. The numbers within parentheses are the number of rain events. The maximum days column shows the maximum number of days between pulse events.

Year/Season	Pulse sizes (%)				Inter-pulse durations (%)			Maximum clays
	1–5 mm	5–15 mm	15–30 mm	> 30 mm	1 day	2–5 days	> 5 days	
<b>2005</b>								
Pre-monsoon (5)	100	0	0	0	0	22	78	19
Monsoon (21)	85	5	5	5	22	56	22	14
Post-monsoon (11)	82	0	9	9	50	25	25	14
<b>2006</b>								
Pre-monsoon (14)	100	0	0	0	14	50	36	16
Monsoon (31)	61	25	14	0	29	64	7	10
Post-monsoon (8)	78	22	0	0	33	50	17	8
<b>2007</b>								
Pre-monsoon (15)	86	14	0	0	18	55	27	21
Monsoon (23)	76	20	4	0	33	47	20	18
Post-monsoon (12)	75	25	0	0	20	80	0	5
<b>2008</b>								
Pre-monsoon (9)	91	9	0	0	14	29	57	26
Monsoon (31)	69	19	12	0	46	40	14	8
Post-monsoon (5)	100	0	0	0	20	20	60	10
Means ± SE	83.6 ± 3.7	11.6 ± 3.0	3.7 ± 1.5	1.2 ± 0.8	24.9 ± 4.1	44.8 ± 5.3	30.3 ± 6.8	14.1 ± 1.8

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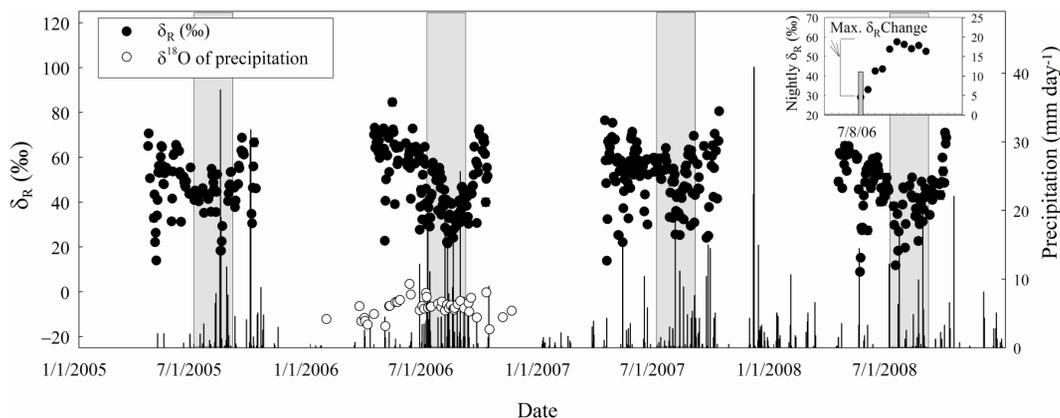
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**Fig. 1.** (a) Time series of precipitation (bars), daily SWC at 2 cm (lines), and biweekly SWC at 20 cm (circles). (b) Time series of the drought index  $P - E_P$  (grayed area) and its percentiles (gray line). (c) Time series of modeled soil evaporation ( $E_S$ ) from ISOLSM (solid line), canopy transpiration ( $E_T$ ) (dashed line), and the  $E_T/E_S$  ratio. We include winter time periods because winter precipitation and soil water content could affect the water cycle during pre-monsoon periods ( $\sim$  April to June). Typical post pulse patterns of  $E_S$ ,  $E_T$ , and  $E_T/E_S$  are displayed as an inset in (c).

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**Fig. 2.** Annual and seasonal variation in  $\delta_R$  over four years. Precipitation is also shown to facilitate visualization.  $\delta^{18}\text{O}$  of precipitation (open circle) for year 2006 included. Filled boxes represent monsoon periods. An approach to calculate maximum  $\delta_R$  change is visualized as an inset.

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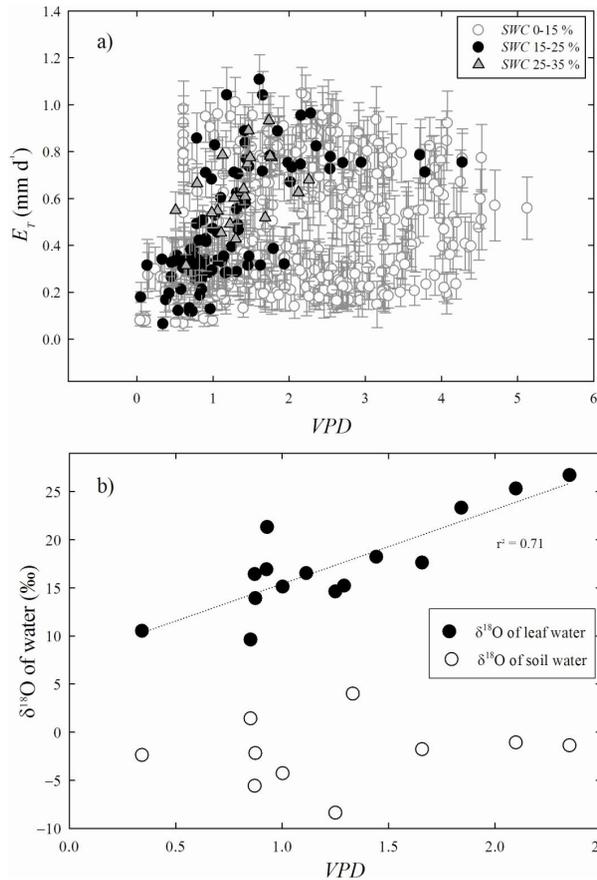
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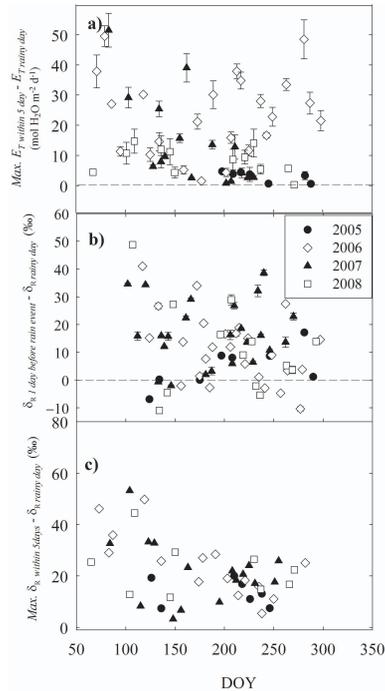
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**Fig. 3. (a)** The inter-annual and seasonal  $E_T$ -VPD relationships for three sets of SWC, 0–15%, 15–25%, and 25–35%. **(b)** Correlations of foliar and soil water  $\delta^{18}\text{O}$  values at 10 cm depth with VPD for year 2005 and 2006. The foliar regression equation is  $\delta^{18}\text{O} = 7.7 + 7.7 \text{ VPD}$ ,  $r^2 = 0.7$ . Soil water  $\delta^{18}\text{O}$  value was not significantly correlated with VPD.



**Fig. 4.** (a) The differences in  $E_T$  between the day of a rain event and the maximum value over the subsequent five days. Positive values indicate  $E_T$  was higher after the rain event than before. All rain events were included from DOY 60 to 300. (b) The difference in  $\delta_R$  between 1 day before a rain event and  $\delta_R$  on the rainy day, shown for 2005–2008. Positive values indicate  $\delta_R$  values become more depleted by the rain event. (c) The difference in normalized  $\delta_R$  between the night of a rain event and the maximum value over the subsequent five nights.  $\delta_R$  values were normalized by the day zero  $\delta_R$  after a rain event to make all starting values zero over the four years, thereby allowing examination of the response to the rain event. The maximum normalized  $\delta_R$  values within 5 days after pulse events typically captured the maximum enrichment (Fig. 5a–c).

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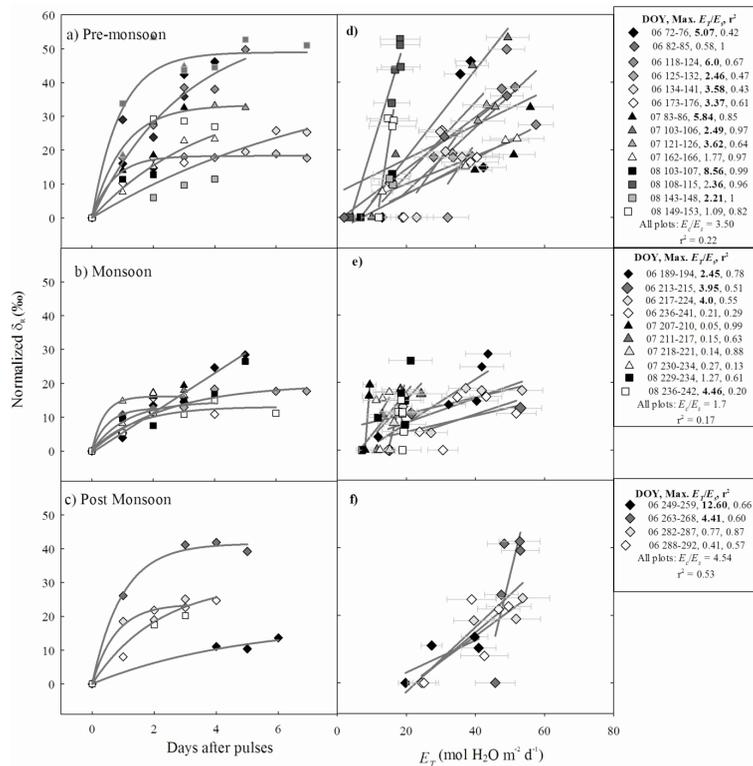
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**Fig. 5. (a–c)** Seasonal patterns of normalized  $\delta_R$  enrichment after rain pulses (the pulses are on day zero).  $\delta_R$  values were normalized by  $\delta_R$  on the day of the rain event to make all starting values zero over the four years. **(d–f)** The seasonal relationships between post rain pulse normalized  $\delta_R$  and  $E_T$ . Maximum  $E_T/E_S$  values and  $r^2$  values for the same period are added in each legend. Maximum  $E_T/E_S > 2$  is expressed as bold.

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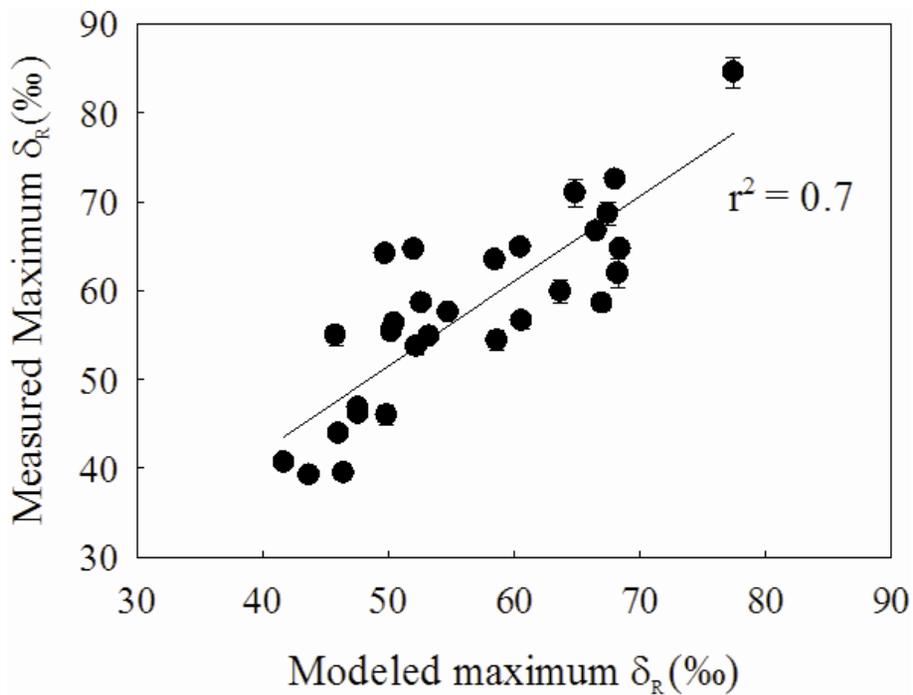
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**Fig. 6.** Comparison between measured and modeled maximum  $\delta_R$  changes within 7 days of precipitation.

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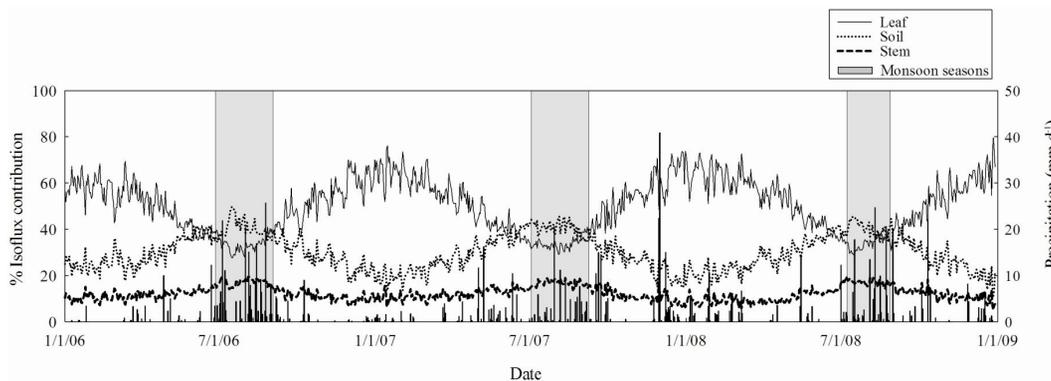
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**Fig. 7.** Time series of foliar, soil, and stem contributions to total ecosystem isoflux derived from ISOLSM. Filled boxes represent monsoon periods.

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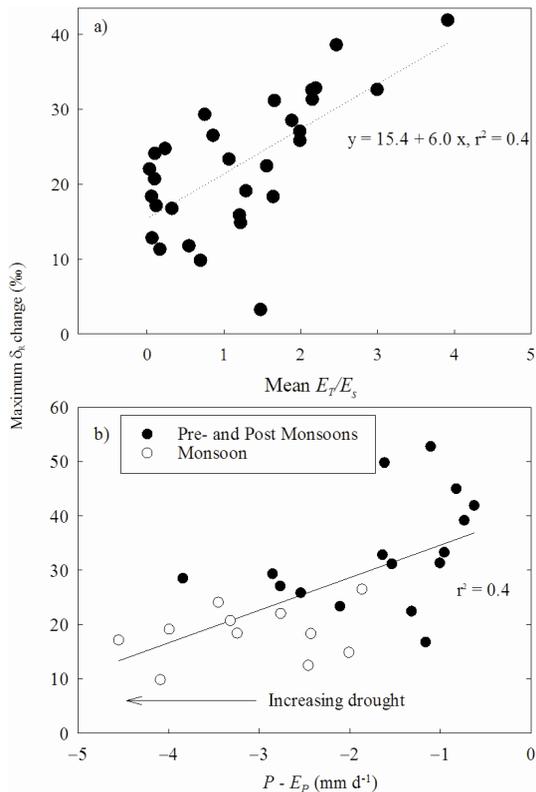
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**Fig. 8. (a)** The relationship between maximum  $\delta_R$  change within 7–11 days after each pulse and mean  $E_T/E_S$  change for the same periods. The regression equation is:  $\delta_R = 15.4 + 6.0 E_T/E_S$ ,  $r^2 = 0.4$ . **(b)** Relationships between maximum  $\delta_R$  change and the drought index  $P - E_p$ . Each data point represents the combination of maximum  $\delta_R$  change and mean  $P - E_p$  over the same period, with each subset starting on the day of the rain pulse and extending to the day before the next rain pulse.

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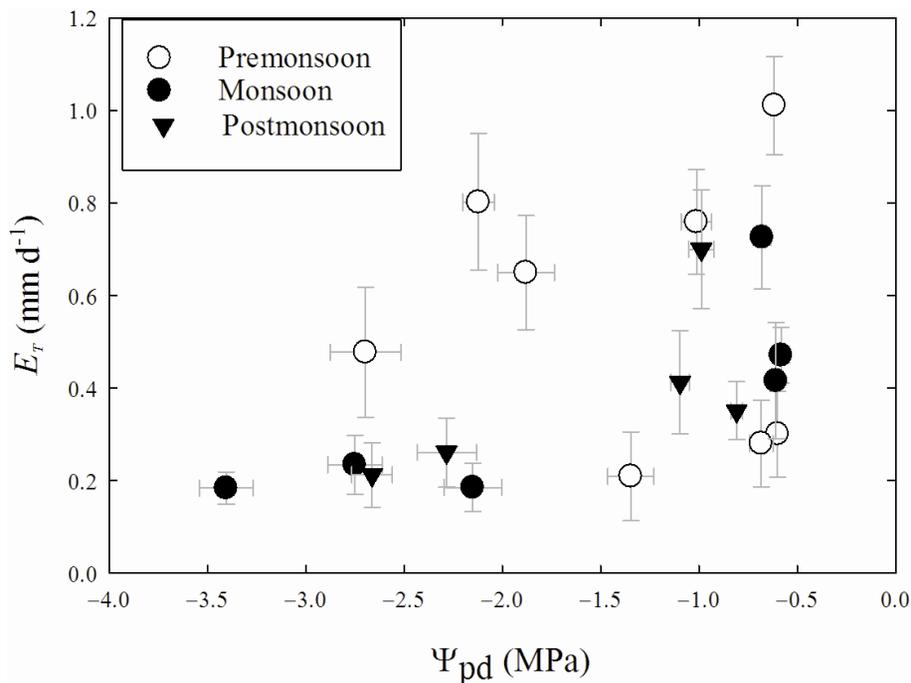
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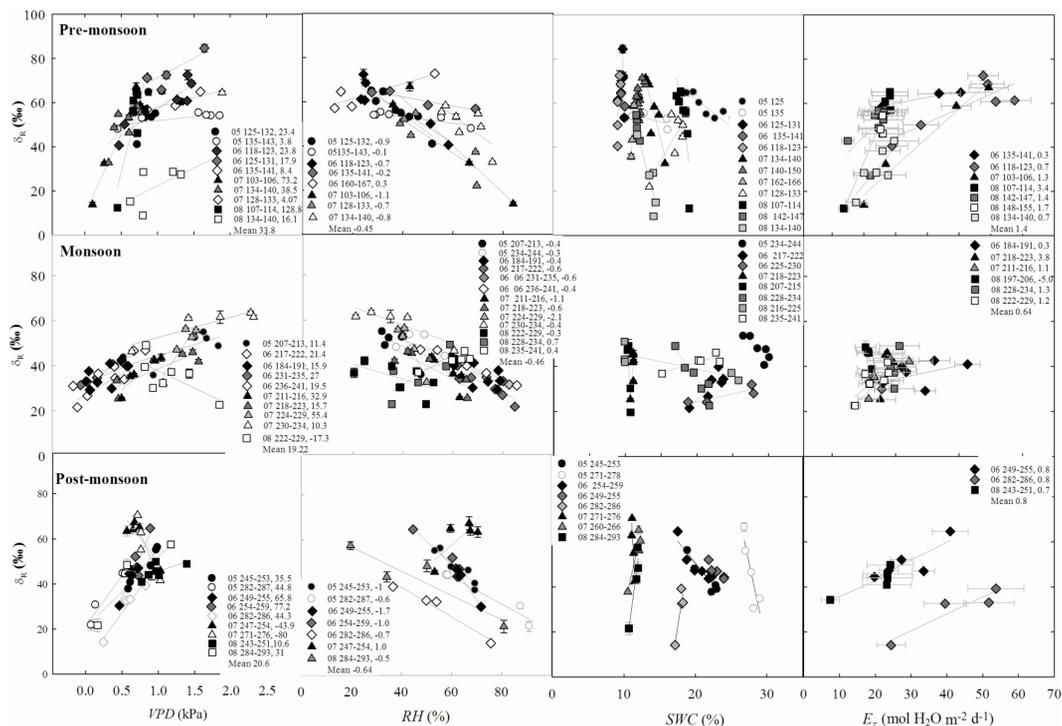
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**Fig. A1.** The relationship between monthly juniper pre-dawn leaf water potential ( $\Psi_{pd}$ ) and  $E_T$  by seasons. The number of data points is limited because not all monthly  $\Psi_{pd}$  observations had corresponding  $E_T$  data.

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**Fig. A2.** Correlations of  $\delta_R$  with VPD, RH, SWC, and  $E_T$ . Correlations were displayed individually for each rain event from day zero to day  $N$  just before the next rain event. We present only significant best fit of regressions from lag analysis. Numbers after DOY in the figure legends represent slopes for each subset.

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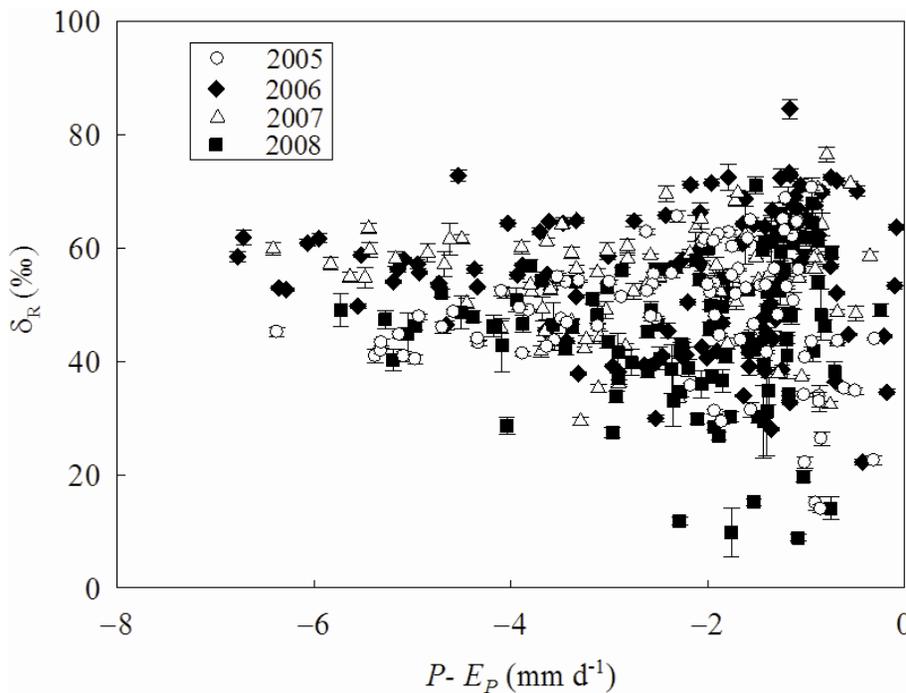
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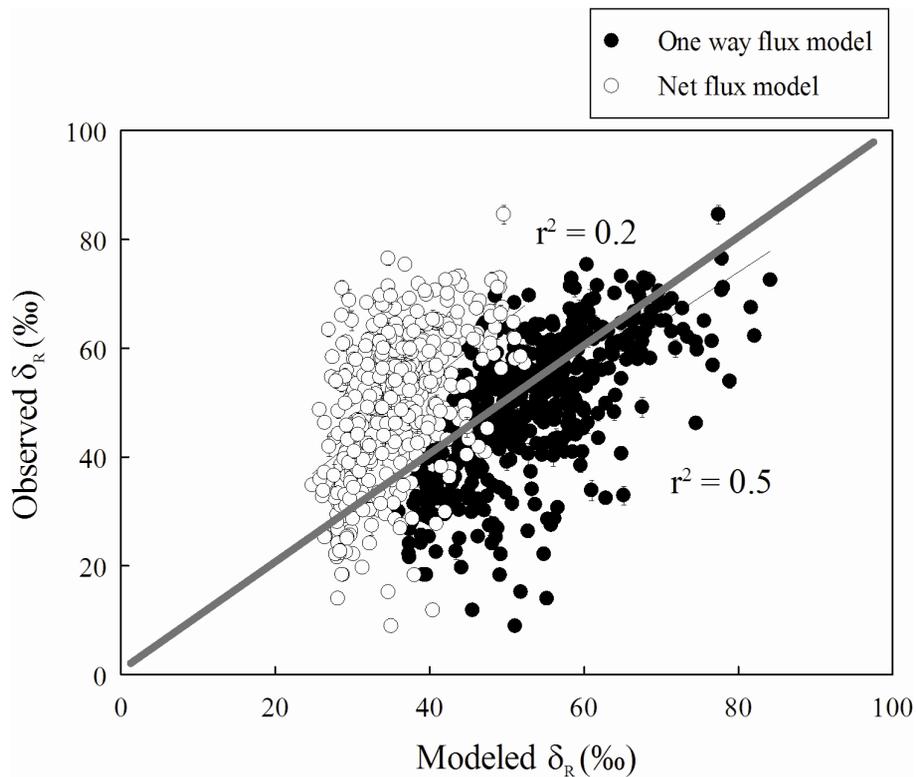
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**Fig. A3.** Relationships between  $\delta_R$  and  $P - E_p$ . All nocturnal Keeling plot intercepts that passed QC criteria from DOY 100–273 were included.



**Fig. A4.** The relationships between modeled  $\delta_R$  and observed  $\delta_R$ . Dark and open circles represent model output after, and before, the one way flux model (Cernusak et al., 2004) was incorporated, respectively. Data are included DOY 100–273.

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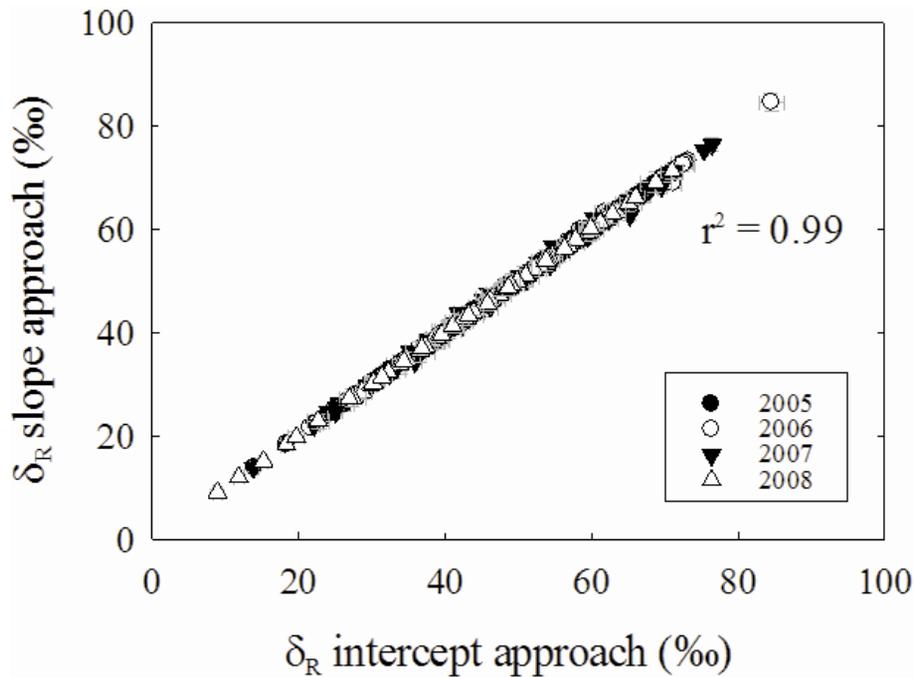
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**Fig. A5.** 1 : 1 Relationships of  $\delta_R$  calculations from the Keeling plots (intercept approach) and Miller/Tans formulation (slope approach).

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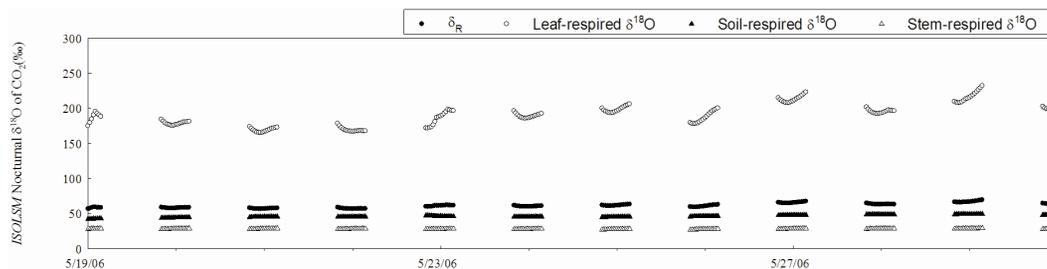
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**Fig. A6.** ISOLSM simulation for nocturnal  $\delta_R$  (filled circle),  $\delta^{18}\text{O}$  of foliar-respired  $\text{CO}_2$  (open circle),  $\delta^{18}\text{O}$  of soil respired  $\text{CO}_2$  (filled triangle) and  $\delta^{18}\text{O}$  of stem-respired  $\text{CO}_2$  (open triangle).

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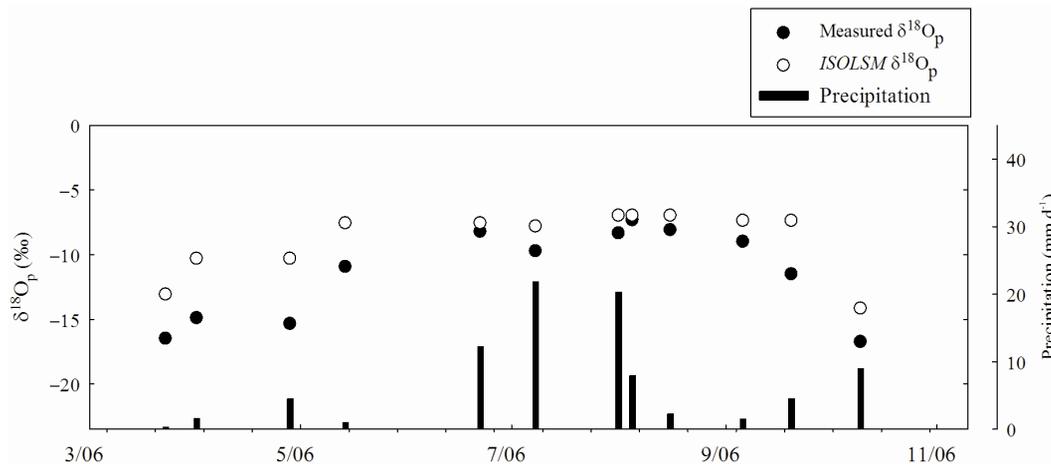
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**Fig. A7.** Pulse precipitation events and associated with  $\delta^{18}\text{O}$  of precipitation in 2006 for the time periods presented in this manuscript.