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Key Points:

- Piñon mortality in a piñon-juniper woodland did not alter evapotranspiration but had a large effect on evapotranspiration partitioning
- Piñon mortality increased evapotranspiration from sources other than the canopy and decreased root zone water and sap flow of surviving trees
- Mortality in semiarid biomes may trigger feedback mechanisms that leave these biomes drier and potentially more vulnerable to drought

Supporting Information:

- Supporting Information S1
- Data Set S1
- Data Set S2
- Data Set S3
- Data Set S4
- Data Set S5

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Tree Mortality Decreases Water Availability and Ecosystem Resilience to Drought in Piñon-Juniper Woodlands in the Southwestern U.S.

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Abstract Climate-driven tree mortality has increased globally in response to warmer temperature and more severe drought. To examine how tree mortality in semiarid biomes impacts surface water balance, we experimentally manipulated a piñon-juniper (PJ) woodland by girdling all adult piñon trees in a 4 ha area, decreasing piñon basal area by ~65%. Over 3.5 years (2009–2013), we compared water flux measurements from this girdled site with those from a nearby intact PJ woodland. Before and after girdling, the ratio of evapotranspiration (ET) to incoming precipitation was similar between the two sites. Girdling altered the partitioning of ET such that the contribution of canopy transpiration to ET decreased 9–14% over the study period, relative to the intact control, while noncanopy ET increased. We attributed the elevated noncanopy ET in the girdled site each year to winter increases in sublimation and summer increases in both soil evaporation and below-canopy transpiration. Although we expected that mortality of a canopy dominant would increase the availability of water and other resources to surviving vegetation, we observed a decrease in both soil volumetric water content and sap flow rates in the remaining trees at the girdled site, relative to the control. This postgirdling decrease in the performance of the remaining trees occurred during the severe 2011–2012 drought, suggesting that piñon mortality may trigger feedback mechanisms that leave PJ woodlands drier relative to undisturbed sites and potentially more vulnerable to drought.

1. Introduction

Climate-driven (i.e., related to drought, high temperature, etc.) forest mortality has recently increased on every forested continent (Allen et al., 2010; Breshears et al., 2005), a trend that is expected to continue with global increases in precipitation variability and temperature (Dai, 2013; IPCC, 2014). Even in regions with unchanged precipitation, increased temperature alone will drive a near-term increase in drought- and heat-driven tree mortality through a combination of physiological stress (hydraulic failure, carbon limitation, and/or collapse of phloem), pest and pathogen outbreaks, or altered disturbance regime (Adams et al., 2010; Allen et al., 2010; Anderegg et al., 2015; Breshears et al., 2013; Hicke et al., 2012; McDowell et al., 2013, 2016; Williams et al., 2012). Although the frequency of mortality events triggered by such “global-change-type drought” is expected to increase, we still know very little about the actual consequences of large changes in ecosystem structure on water cycling following mortality (Anderegg et al., 2016). Quantifying these responses is crucial for understanding how disturbance alters ecosystem function, water and energy budgets, and resilience in semiarid biomes.

When tree mortality occurs, the prevailing expectation in most biomes is that evapotranspiration (ET) should immediately decrease due to reduced plant transpiration. By this so-called “moisture release” hypothesis, the water no longer consumed by transpiration should proportionally increase some combination of soil moisture, runoff, streamflow, and/or groundwater recharge (Chen et al., 2015; He et al., 2013; Matheny et al., 2014; Simonin et al., 2007; Williams et al., 2014). The expectation is that tree mortality-induced increases in soil moisture, as well as surface radiation, and nutrient availability should facilitate higher photosynthetic rates, rapid recovery of leaf area index (LAI), and vegetation regrowth (Anderegg et al., 2016; Dore et al., 2012;

Edburg et al., 2012; Frank et al., 2014; He et al., 2013; Romme et al., 1986). As transpiration recovers with vegetation and canopy regrowth, ET, and other water fluxes, should recover over time (Anderegg et al., 2016; Villegas et al., 2015). Yet, observations and modeling during two decades of recent tree mortality in western North America reveal a range of responses in ET, soil moisture, and streamflow, suggesting that we do not fully understand the mechanisms governing hydrological responses in semiarid biomes (Adams et al., 2012; Anderegg et al., 2012; Biederman et al., 2015; Guardiola-Claramonte et al., 2011; Simonin et al., 2007).

Forest canopy structure plays an important role in regulating surface energy and water balance through its influence on canopy interception of precipitation, net available energy, and turbulent heat exchange (Novak et al., 2000; Varhola et al., 2010). In southwestern U.S. coniferous forests, changes in canopy structure influence sublimation rates, snowpack volume, and the timing of snowmelt (Atchley & Maxwell, 2011; Biederman, Brooks, et al., 2014; Gustafson et al., 2010; Harpold et al., 2014; Molotch et al., 2009; Musselman et al., 2008; Pugh & Gordon, 2013; Pugh & Small, 2012; Veatch et al., 2009). In these biomes, the combined effects of higher subcanopy radiation and surface turbulence following a decrease in canopy can also enhance both bare soil evaporation and transpiration of the understory (Breshears et al., 1998; D'Odorico et al., 2007; Giambelluca, 2002; Novak et al., 2000; Raz-Yaseef et al., 2010; Royer et al., 2012; Simonin et al., 2007; Stark et al., 2016; Villegas et al., 2010). The extent to which any of these processes are altered, in addition to temporal variability in climate and meteorological conditions, has consequences for the rate of recharge of water in the soil, persistence of soil moisture, and the availability of water for ET or streamflow.

Water and vegetation dynamics are coupled in all biomes, but in semiarid regions, this coupling is particularly important where potential evapotranspiration (PET) often far exceeds precipitation, ET typically dominates the water budget, and water availability is the dominant control over productivity (Ludwig & Tongway, 1995; Newman et al., 2006). We know that the impact of structural changes on hydrological processes is complex, particularly following large-scale tree mortality in an already sparse canopy with high evaporative demand and solar load. Understanding the role of factors like canopy density, species-specific responses, edaphic factors, and climate in regulating these responses will increase our understanding of not only the impact of these mortality events but also the trajectory of recovery in these biomes.

The large range and inconsistent hydrological responses to tree mortality in semiarid biomes highlight the need for long-term, continuous, in situ measurements to capture the complex cascade of changes in hydrological processes that follow mortality in these biomes (Adams et al., 2012; Anderegg et al., 2016; McDowell et al., 2013). We studied a pair of piñon-juniper (PJ) woodland sites in central New Mexico, one site where all adult piñon were girdled to trigger large-scale piñon mortality and a second untreated site as a control. After girdling, we compared (1) the response of total ET and ET partitioning, (2) the timing of these responses, (3) species-specific sap flow response of the tree canopy at each site, and (4) changes in soil water availability.

We hypothesized the following:

1. Piñon mortality should not alter total ET because of high evaporative demand and low topographic relief at the sites but should change the partitioning of ET by altering the balance between canopy and noncanopy fluxes.
2. Available soil moisture should increase due to reduced canopy transpiration following mortality, and therefore, sap velocity of the remaining trees (juniper and small, ungirdled piñon) should increase.

These hypotheses allowed us not only to examine the potential modification of hydrological processes after mortality but also to test the validity of the soil moisture release hypothesis which is critical to understanding the trajectory of recovery in semiarid biomes. Mortality of piñon pine (*Pinus edulis*) in piñon-juniper (PJ) woodlands, driven by recent global-change-type droughts in the southwestern U.S., is among the best documented cases of drought-induced forest mortality (Adams et al., 2010; Allen et al., 2015; Breshears et al., 2005; Clifford et al., 2013; Krofcheck et al., 2014; McDowell et al., 2013; Meddens et al., 2015). Given the ubiquitous nature of mortality events in semiarid biomes (Allen et al., 2010), and the predicted increase in such mortality events in the coming decades (Williams et al., 2012), our objectives were to explore the feedbacks between tree mortality, tree physiology, and site hydrology and to improve our ability to predict the potentially large hydrological and climate-forcing consequences of these disturbances.

2. Materials and Methods

2.1. Site Description

Our girdled (PJG) and control (PJC) sites are located less than 3 km apart in piñon-juniper woodland (*Pinus edulis* and *Juniperus monosperma*) on an extended mesa at 2,100 m in central New Mexico (girdled: 34°26′48.54″N, 106°12′48.63″W; control: 34°26′18.42″N, 106°14′15.70″W). Before girdling, the overstory vegetation at both sites was exclusively dominated by *P. edulis* and *J. monosperma*, with an understory of annual forbs and grasses. Mean canopy height was approximately 2.8 m at both sites. The climate is semiarid with a 30 year mean (1981–2010) annual precipitation of 393 mm and 30 year mean annual temperature of $10.4 \pm 0.01^\circ\text{C}$, with mild winters (mean minimum temperature of $2.18 \pm 0.02^\circ\text{C}$) and hot summers (mean maximum temperature of $30.13 \pm 0.58^\circ\text{C}$) (30 year temperature and precipitation data from Parameter-elevation Regressions on Independent Slopes Model (PRISM) Climate Group, Oregon State University, <http://prism.oregonstate.edu>). The precipitation regime is driven by irregular snow-dominated winter events (from December to March), dry springs (April to June), and summer monsoonal events (from July to September), with roughly 50% of the hydrological year precipitation occurring during the monsoon period and the rest primarily during winter. Both sites are relatively flat (<3% of slope) with Turkey Springs stony loam soils and alluvially deposited limestone that generates a shallow, discontinuous petrocalcic horizon or “caliche” layer between 30 and 80 cm depth. United States Forest Service soil pit descriptions at the two sites are almost identical in terms of color, hardness, structure, texture, and surface characteristics, with the exception that the petrocalcic horizon in several soil pits at PJG started as shallow as 30 cm, compared to 40 cm in PJC.

Micrometeorological conditions monitored at both sites were very similar during the study period (supporting information Figure S1). Annual precipitation totals in 2009 and 2010 were only slightly less than the 30 year PRISM annual mean precipitation (12% and 6% lower, respectively for 2009 and 2010), but 2011 and 2012 were considerably drier years (annual precipitation was 30% and 45% lower, respectively, than the long-term annual mean).

2.2. Girdling to Change Forest Structure

We girdled all piñon >7 cm diameter breast height in a 1 week period in September 2009 in a 4 ha plot in PJG (~1,630 trees) (Krofcheck et al., 2014). Our decision to girdle only large piñon was based on observations during the 1999–2002 mortality events that piñon mortality was 6.5-fold higher than juniper and large piñon suffered twofold to sixfold greater mortality than small piñon (Mueller et al., 2005). We mechanically girdled the trees by removing a strip of bark (including both the phloem and cambium) around the entire circumference of the piñon at breast height (1.4 m) to completely decouple the transport of photoassimilate from leaves to roots. We left the girdled trees in place and injected a 5% glyphosphate solution directly into the girdled area to ensure rapid tree mortality and change in canopy structure without soil disturbance (Krofcheck et al., 2014). In our study, girdling resulted in complete needle loss in less than 1 year, similar to observations following *Piñon ips* attack in 1999–2002 (Breshears et al., 2005; Clifford et al., 2008). This progression is much shorter than reported following mountain pine beetle attacks (Edburg et al., 2012; Klutsch et al., 2009; Pugh & Small, 2012; Trahan et al., 2015). PJC did not receive any experimental manipulation of stem or canopy cover (Figure 1). The mortality rate in the control site from 2009 to 2012 was <3%.

2.3. Vegetation Sampling

We nondestructively surveyed biomass once per year during summer or fall (June–October) in four permanent 10 m radius circle plots located within the eddy covariance (EC) tower footprint at each site. We recorded status (dead or alive), height, and diameter at breast height (DBH, measured at 1.4 m height) for all trees located in the plots. If trees were shorter than 1.4 m or had substantial branching below 1.4 m (very common in juniper), we measured the root collar diameter (RCD) (Grier et al., 1992; Krofcheck et al., 2016). If branching occurred below ground (also common in juniper), we measured the equivalent stem diameter (ESD) (Grier et al., 1992; Krofcheck et al., 2016). We calculated the basal area of each species in all circle plots using our DBH, RCD, or ESD data and used the average of each year's species-specific basal area in the four circle plots to represent the entire site. We estimated the sapwood area of all trees in each circle plot each year using annual measurements of DBH, RCD, or ESD and stem diameter-sapwood area allometric equations developed in a nearby PJ woodland in New Mexico (Pangle et al., 2015). We calculated the ratio of sapwood

Figure 1. Images of the (top) control (PJC) and (bottom) girdled (PJG) sites taken from the top of the towers at each site. Images taken in July 2010.

(A_S) to square meters of ground area (A_G) of each species as A_{Si}/A_G , where $i = P$ or J for piñon or juniper, respectively, in each circle plot and used the average of the four circle plots to estimate site level A_{Si}/A_G every year and scale sap flow estimates to the ecosystem scale at both sites (described below). For 2009, at PJG only, we only estimated A_{Si}/A_G values representative for pregirdling conditions.

2.4. Hydrological Measurements

2.4.1. Eddy Covariance and Micrometeorological Measurements

We continuously measured ecosystem-atmosphere exchange of carbon, water, and energy fluxes above both sites using open-path eddy covariance (EC). EC measurements were installed in the control site in 2008 and in the girdled site in February 2009. EC instrumentation was identical at both sites (CSAT-3 sonic anemometer, Campbell Scientific, Logan, UT, USA; and LI-7500 open-path infrared gas analyzer (LI-COR, Lincoln, NE, USA), mounted at 9 m and 7 m height at PJC and PJG, respectively (the instrument height was lower at PJG to insure that the girdled area dominated the contribution of fluxes measured by the EC tower instruments). To assure that the signal measured at the PJG tower was dominated by the region which we experimentally manipulated, we determined the tower flux footprints using the flux source area model derived by Hsieh et al. (2000) and subsequently expanded to two dimensions by Detto et al. (2006), as described in Krofcheck et al. (2014).

We recorded EC data at both sites using Campbell Scientific CR5000 data loggers. Thirty minute evapotranspiration fluxes (ET) were calculated from 10 Hz sampled data and corrected for air density fluctuations due to temperature (Webb et al., 1980) and frequency response (Massman, 2000). Data were filtered for low turbulence conditions ($u^* < 0.16$ m/s), rain events, instrument malfunction, and for wind direction conditions $\pm 30^\circ$ behind the tower. These gaps in the ET flux data were filled following the methodologies of Falge et al. (2001) and Reichstein et al. (2005) (see more details in Anderson-Teixeira et al., 2011). Gap-filling uncertainty in our annual ET fluxes resulting from random measurement errors, gap filling, and flux partitioning were estimated at half-hourly time scales and propagated to daily and annual time scales using a Monte Carlo approach (Barr et al., 2013; Richardson & Winn, 2012). We used daily fluxes from January 2009 to September 2012 for both sites. Mean energy closure of our EC measurements at the daily time scale were 73% and 74% for PJC and PJG sites, respectively. Due to the similar energy closure at both sites, and presumed equivalent sources of flux measurement error due to identical instrumentation and flux processing, energy closure was not forced. While not forcing energy closure can impact absolute ET values, it also prevents the introduction of additional uncertainty and potential bias associated with energy closure methods in our site-site comparison.

Additional micrometeorological measurements made at both sites include net radiation, short- and long-wave radiation components (CNR1 Kipp & Zonen, Bohemia, NY, USA), air temperature and relative humidity (HMP45C Vaisala, Helsinki, Finland) from which vapor pressure deficit was estimated, photosynthetically active radiation (LI-190SB, Licor Bioscience), soil heat flux (HFP01SC, Hukseflux), and precipitation (TE525MM-L50 tipping bucket rain gauge, Texas Electronic and TR-525 Series Rainfall Sensor at PJC and PJG, respectively). We calculated 30 min averages of these sensors and used daily averages or totals of these parameters for our analyses. When daily precipitation records were lost because of instrumental failure, daily PRISM data for the coordinates of each site were used to gap-fill missing records. Due to incomplete records for PJG in 2009, PRISM precipitation data were used the entire year. In all years, we used volumetric water content (VWC) measurements at 5 cm from open areas to check the reliability of this precipitation gap-filling method. Only PRISM precipitation events larger than 2 mm that coincided with an increase in VWC were used for gap filling. Of all 30 min precipitation data during 2010–2012, we gap filled $< 1\%$ at the control sites and 11% at the girdled site.

2.4.2. Transpiration Measurements

We measured whole-tree sap flux at both study sites using 10 mm Granier heat dissipation sap flow sensors (Granier, 1985, 1987). At both sites, we installed the sensors in the trunks of 10 trees, 5 juniper and 5 piñon (at PJG, these piñon were the trees < 7 cm DBH that were not girdled). Two sensors were installed per tree at a height > 1 m above ground level, randomized with respect to tree circumference. The sensors, constructed at the University of New Mexico (Plaut et al., 2012), used the standard design with heated and unheated reference probes (Granier, 1987), with an additional pair of probes located 5 cm apart horizontally to correct for the axial temperature gradients in the stem (Goulden & Field, 1994). This design is critical to reduce measurement noise under open-canopy and high irradiance conditions typical of PJ woodlands (Pangle et al., 2012; Plaut et al., 2012). We inserted the sensors radially into the outermost sapwood (xylem tissue), covered them with reflective insulation for protection, and recorded 30 min averages of the temperature gradient outputs using a CR23X data logger (Campbell Scientific). We estimated sap flux density J_s ($\text{g m}^{-2} \text{s}^{-1}$) from the recorded heated-unheated probe temperature differences following the empirical equation of Granier (1987) assuming no nocturnal canopy transpiration loss and zero flow in the xylem nocturnally after stem capacitance storage was recharged (see Pangle et al., 2015) (Table S1). We determined tree J_s by averaging the individual J_s measurements from the two sensors installed in each tree when both flow rates were available. To scale J_s rates to the whole tree, we used J_s rates measured in the outer sapwood (0–10 mm) to represent the entire xylem profile, as previous work in a nearby PJ woodland did not observe a significant decline in J_s rates with sapwood depth for either of these species (Pangle et al., 2015). We installed sap flow probes in June 2009 at both sites, but because of instrumental errors at PJG, probes measuring in small piñon trees at PJG did not start recording data until 22 August. We replaced all sap flow probes at both sites in August 2011 to eliminate/minimize errors due to a potential decline in sensitivity over time. We filtered out erroneous measurements caused by low temperatures (all days with minimum temperature $< -2^\circ\text{C}$ were removed) and equipment failure.

We estimated site level 30 min transpiration from each species (T_i , where $i = P$ or J , for piñon or juniper, respectively) at both sites from annual and site-specific sapwood to ground area ratios (A_{Si}/A_G) and 30 min J_{Si} data as

$$T_i = J_{Si} \times A_{Si}/A_G \quad (1)$$

Daily values of T_i were calculated and reported as the sum of T_i over 24 h. We estimated total canopy site transpiration (T_c) as the sum of both species T_i at each site. Because our 30 min J_{Si} measurement record was not complete for either species during the entire study period, we developed site-, year-, and species-specific multivariate linear models to predict daily T_i from meteorological variables when estimates of T_i were missing (more details on T_i gap filling are provided in supporting information section S2). J_s values presented in Figure 3 represent the mean daytime sap flow (incoming shortwave radiation >0) for each species.

2.4.3. Partitioning of ET

We partitioned ET using the component-based assumption of ET according to the following equation:

$$ET = ET_o + T_c \quad (2)$$

where T_c is total tree canopy transpiration, estimated by scaling up sap flow observations in piñon and juniper trees at both sites and ET_o is the evapotranspiration flux from all noncanopy sources including evaporation/sublimation of intercepted rain/snow, snowpack sublimation, understory transpiration, and bare soil evaporation. We estimated daily values of ET_o by subtracting daily totals of canopy transpiration (T_c) from daily ET measured with tower-based eddy covariance at each site.

2.4.4. Soil Water Availability Analyses

At both sites, volumetric soil water content (CS610 probes, Campbell Scientific) and soil temperature probes (T107, Campbell Scientific) were installed horizontally at depths of 5 cm, 10 cm, and 30 cm under the three main cover types: piñon, juniper, and open areas ($n = 3$ for each cover type and depth). Due to the slightly shallower petrocalcic horizon at PJG, only three probes, one for each cover type, were installed at 30 cm depth (overall $n = 27$ WVC and temperature probes in the control site, and $n = 21$ in the girdled site). We averaged the WVC measurements from the three replicates by cover type and depth for each site.

We estimated depth-averaged volumetric soil water content of the top 30 cm (VWC_{0-30}) for each cover type following Miller et al. (2007). This method divides the rooting zone into portions represented by each depth measurement. Using soil pit analysis data from the United States Department of Agriculture, we assumed that the readings from 5 cm (VWC_{5cm}) were representative of the soil between 0 and 7.5 cm; the readings from measurements at 10 cm (VWC_{10cm}) were representative of the water content between 7.5 and 15 cm; and measurements at 30 cm (VWC_{30cm}) represented the content between 15 and 30 cm:

$$VWC_{0-30} = \frac{7.5 \times VWC_{5cm} + 7.5 \times VWC_{10cm} + 15 \times VWC_{30cm}}{30} \quad (3)$$

2.5. Statistical Analyses

To examine differences in soil water content between the two sites, we compared averaged daily observations of soil water content within each season and year. We used repeated measures linear mixed effects models to account for the temporal nonindependence of observations within a set of sensors (nlme package Pinheiro et al., 2017, R Core Team, 2017). Models included the random effect of sensor set and fixed factors of girdling treatment, sensor depth, season, and year as well as their two-way interactions with the treatment, which tested the degree to which treatment effects varied temporally and with soil depth. To determine the structure of the variance-covariance matrix that best accounted for temporal autocorrelation in soil water content observations, we selected among three candidate models (autoregressive 1, autoregressive 2, and no autocorrelation) using the second-order Akaike information criterion (AICc). An autoregressive 2 structure, in which the previous two time points influence the current observation of soil water content, outranked the other models by $\Delta AICc = 9$. When the effect of treatment depended on other factors, as indicated by statistically significant interaction effects, we decomposed the pairwise difference between treatment and control using post hoc Tukey honestly significant difference (HSD) tests.

We used similar repeated measures linear mixed models to compare differences between the two sites in ET, its components, T_c and ET_o , T_c/ET and ET_o/ET ratios, and canopy-scale transpiration rates from piñon (T_p) and juniper (T_j). These models included the fixed factors of girdling treatment, season, and year as well as their

Table 1
Biomass Indicators of Tree Canopy Species From Vegetation Sampling at Both Sites

	2009 (pregirdling)		2010		2011		2012	
	PJC	PJG	PJC	PJG	PJC	PJG	PJC	PJG
Total basal area (m ² /ha)	31.3	29.3	31.3	26.2	31.1	25.3	31.0	25.3
Piñon basal area (m ² /ha)	8.8	4.6	8.8	1.5	8.6	0.6	8.5	0.6
Juniper basal area (m ² /ha)	22.5	24.7	22.5	24.7	22.5	24.7	22.5	24.7
Total sapwood area (m ² /ha)	7.7	5.6	7.7	4.2	7.6	3.9	7.6	3.9
Piñon sapwood area (m ² /ha)	4.1	2.1	4.1	0.7	4.0	0.4	4.0	0.4
Juniper sapwood area (m ² /ha)	3.6	3.5	3.6	3.5	3.6	3.5	3.6	3.5

two-way interactions with the treatment. For each of these variables, the best model (using AICc) did not include a signature of temporal autocorrelation or nonsignificant interactions. The results from these best fit models are shown in Table S3. We also looked for treatment effects in each year separately using a special case of general linear models, the likelihood ratio test, because year was always a strong effect, though with no interactions (results in Table S3).

3. Results

3.1. Effects of Girdling Treatment on Site Biomass, Leaf Area Index, and Litter

Juniper basal and sapwood areas were similar at both sites before and after the girdling (Table 1). Therefore, sapwood and basal area differences between PJC and PJG after girdling were due primarily to the mortality of piñon. Girdling immediately reduced the piñon sapwood area and basal area per ground area of PJG by 68%. Compared to PJC, after girdling, piñon sapwood area and basal area per ground area at PJG were 83% lower than at PJC (Table 1). Following the initial decrease due to girdling, piñon basal and sapwood areas at the

Table 2
Hydrological Year Precipitation, ET, and Components of ET in the Control (PJC) and Girdled (PJG) Sites

	Units	Site	2009	2010	2011	2012
Precipitation	(mm)	PJC	251	376	208	249
		PJG	243	389	197	228
ET	(mm)	PJC	238 ± 9	432 ± 12	263 ± 11	317 ± 9
		PJG	248 ± 9	414 ± 12	237 ± 11	289 ± 9
T_c	(mm)	PJC		125	88	53
		PJG		81	45	20
ET_o	(mm)	PJC		307	175	264
		PJG		333	192	269
ET/P	(%)	PJC	0.95	1.15	1.26	1.27
		PJG	1.02	1.06	1.20	1.27
T_c/ET	(%)	PJC		0.29	0.33	0.17
		PJG		0.20	0.19	0.07
ET_o/ET	(%)	PJC		0.71	0.67	0.83
		PJG		0.80	0.81	0.93
T_p	(mm)	PJC		59	39	19
		PJG		11	3	2
T_j	(mm)	PJC		67	49	35
		PJG		70	42	17
T_p/T_c	(%)	PJC		0.47	0.44	0.36
		PJG		0.14	0.07	0.10
T_j/T_c	(%)	PJC		0.53	0.56	0.67
		PJG		0.86	0.93	0.90

Note. The 2009 values are all from pregirdling period (January–September 2009). ET refers to total ET ± random uncertainty as explained in the text; T_c is canopy transpiration; ET_o is evapotranspiration contributed from noncanopy sources; ET/P is ET expressed as a fraction of incoming precipitation; T_c/ET and ET_o/ET are the contribution of T_c and ET_o to total ET, respectively; T_p and T_j are total scaled-up transpiration from piñon and juniper, respectively; and T_p/T_c and T_j/T_c are the contribution of piñon and juniper to total canopy transpiration, respectively.

Figure 2. Weekly means of daily (a–d) evapotranspiration (ET), (e–h) canopy transpiration (T_c), and (i–l) noncanopy evapotranspiration (ET_o) for hydrological year 2009–2012 in both PJC (black) and PJG (gray). The gray bar area represents the girdling period in 2009. Daily ET in the girdled site was statistically higher in 2009 (Figure 2a), lower in 2011 (Figure 2c), and similar to the control site in 2010 (Figure 2b) and 2012 (Figure 2d). Daily T_c was significantly lower in the girdled site in all years postgirdling (Figures 2f–2h). Daily ET_o did not differ between sites postgirdling (Figures 2j–2l), but the daily ET_o/ET ratio was significantly higher in the girdling site ($p < 0.0001$) in both 2010 and 2012 (Table S3). Asterisks indicate significant differences in daily values between sites in each year using post hoc general linear model where $*p < 0.05$, $**p < 0.01$, and $***p < 0.001$. Statistical results are shown in Table S3.

girdled site decreased even more, from $1.5 \text{ m}^2 \text{ ha}^{-1}$ in 2010 to $0.6 \text{ m}^2 \text{ ha}^{-1}$ in 2011 and 2012, as mortality of the small piñon we did not girdle (e.g., $< 7 \text{ cm DBH}$) occurred during the 2011–2012 drought (Table 1).

The needles on the girdled trees were almost all chlorotic by November 2009, 2 months after girdling (Eitel et al., 2011). Overall, field allometric measurements suggested that girdling decreased leaf area at the girdled site by 33% and contributed $216 \text{ g of litter/m}^2$ to the site by August 2010 (Krofcheck et al., 2014).

3.2. Effects of Tree Mortality on Hydrological Year Fluxes

3.2.1. P , ET, and ET Partitioning

Hydrological year (1 October to 30 September) precipitation and rainfall distribution patterns were very similar between the two sites during the study period, differing only by 3–8% on a year-to-year basis (Table 2 and supporting information Figure S1). Total ET flux in the two sites was also very similar in January–September 2009 prior to the girdling treatment (Table 2), but we observed a slight decrease in ET at PJG, relative to PJC, following the girdling treatment (Table 2). However, when we compare ET expressed as a fraction of incoming P , ET/P , the differences between the two sites, both before and after girdling, are more negligible, suggesting at least part of the decrease in ET at the girdled site was due to less precipitation received at this site in 2011 and 2012 (Table 2).

Although piñon mortality did not alter ET/P , it did trigger a large decrease in canopy transpiration (T_c) in all years postgirdling (Figure 2 and Tables 2 and S3). Daily T_c was similar between the control and girdled

Figure 3. Comparisons between daytime mean sap flow velocity (J_s) for (a–d) juniper, (e–h) piñon, and (i–l) 24 h totals of canopy transpiration (T_c) at both sites (PJG on y axis and PJC on x axis) for each hydrological year during the study period. The gray dashed line is the 1:1 fit line, and the black solid line represents the linear fit for each regression. We only used measured (not gap filled) J_s and T_c for these analyses. R^2 is included only when correlation is significant (p value < 0.05).

sites prior to the girdling (although only 10 days of data prior to the girdling were available) (Figure 2) but decreased in PJG relative to PJC following the girdling in late 2009 and remained lower through 2012 (Figures 2 and 3 and Tables 2 and S3). In 2010 and 2011, T_c accounted for roughly one third of the total ET fluxes in the control site, compared to only ~20% of the total ET fluxes in the girdled site (Table 2). In 2012, the second year of the severe drought, T_c significantly decreased in both sites, to 17% of total ET in the control site but accounted for only 7% of total ET in the girdled site (Table 2).

We interpret the decrease in canopy transpiration at PJG as evidence that girdling also triggered a corresponding increase in ET_o (i.e., noncanopy sources such as evaporation/sublimation of intercepted rain/snow, snowpack sublimation, understory transpiration, and bare soil evaporation) (Table 2). This conclusion is based on our observations that all other components of the water budget were unaffected by the girdling treatment (P , ET, surface runoff, and recharge (given the high annual ET/ P ratios in both sites); Table 2). It also suggests that the largest hydrological shift triggered by piñon mortality was a change in the partitioning of ET. In 2010, 2011, and 2012, ET_o/ET in the girdled site was 80%, 81%, and 93%,

Figure 4. Comparisons between daily VWC_{0-30} at both sites (PJG on y axis and PJC on x axis) in (a–d) open areas, (e–h) under piñon, and (i–l) under juniper for each hydrological year during the study period. In 2009, the gray symbols and equation are prior to the girdling, and the black symbols and equation are days during/after the girdling. The gray dashed line is the 1:1 fit line, and the black solid line represents the linear fit for each regression. We only used measured (not gap filled) VWC for this plot. R^2 is included only when correlation is significant (p value < 0.05).

respectively, and only 71%, 67%, and 83%, respectively, in the control site. This increase in ET_o/ET following girdling was only significant in 2010 and 2012 (Table S3).

3.2.2. Effects of Tree Mortality on Soil Water Availability

Subcanopy root zone available water (VWC_{0-30cm}) was higher in the girdled site than the control site under all cover types prior to girdling (Figure 4). Contrary to expectation, following mortality of half the canopy, VWC decreased relative to the control site over time under all cover types, particularly during the 2011 and 2012 drought years (Table 3 and Figure 4). The decrease in VWC in the girdled site relative to the control site was evident at all depths but particularly in the deeper soil layers (10 cm and 30 cm) (Figure 5 and Table 3).

Although a decline in VWC under all cover types was observed immediately postgirdling under all cover types in 2009 (Figures 4a, 4e, and 4i), this decline should be interpreted with caution. The intersite differences in VWC in the final 7–10 days of the hydrological year immediately following girdling likely reflected the effect of a precipitation event that was larger at the control site (Figure 5m) rather than the girdling treatment itself.

Table 3

Hydrological Year Differences in Daily Site Level Soil Volumetric Water Content (VWC), Expressed as the Mean $\pm$ SE of Three Cover Types (Open, Piñon, and Juniper) in Shallow (5 cm), Middle (10 cm), and Deep (30 cm) Soil Layers

Year	VWC _{5cm}	VWC _{10cm}	VWC _{30cm}
2009	12.4 $\pm$ 1.7	9.7 $\pm$ 1.6	2.9 $\pm$ 0.5
2010	3.6 $\pm$ 1.0	−17.2 $\pm$ 0.5	−9.8 $\pm$ 0.5
2011	6.0 $\pm$ 0.94	−10.9 $\pm$ 0.6	−10.5 $\pm$ 0.3
2012	−6.8 $\pm$ 2.45	−18.8 $\pm$ 1.8	−7.8 $\pm$ 0.8

Note. Differences are expressed as percent of PJG-PJC. Negative numbers indicate drier soils in the girdled site. The data from 2009 only include the pregirdling period from January to September 2009. Overall treatment $\times$ depth interaction was significant ($p < 0.0001$). From post hoc Tukey HSD test, differences in VWC_{5cm} are not significant ($p = 0.18$) but are significant in VWC_{10cm} ($p = 0.007$) and VWC_{30cm} ($p = 0.0001$).

3.2.3. Effects of Piñon Mortality on Remaining Tree Sap Flow

Sap flow rates in juniper trees were actually higher at the girdled site than the control site in 2009 (Figure 3a). Contrary to what we expected in terms of increased physiological performance in the remaining trees following the girdling, J_s of the remaining juniper at PJG started to decrease compared to the juniper in PJC (Figures 3c and 3d and Table 2) in 2010, and this decrease was clearly evident in 2011, following a very dry spring (only 4 mm of precipitation). This decrease continued and intensified during the drought to the extent that the daily J_s of juniper at PJG was $\sim 40\%$ lower on average than at PJC in 2012. Daily sap flow rates in the remaining small piñon at PJG were higher than the piñon at PJC postgirdling in 2009 and 2010 (Figures 3e and 3f), but, similar to the pattern we observed in juniper, daily J_s in the remaining piñon significantly decreased at PJG in 2011 and even more so in 2012 (Figures 3g and 3h). The decrease in both piñon leaf area and

sap flow rates of the remaining trees in the girdled site relative to the control site explain both the immediate decrease in canopy transpiration in the girdled site relative to the control site and how this decrease intensifies over time (Figures 3i–3l and Tables 2 and S3).

Figure 5. Weekly mean soil volumetric water content in both sites averaged for all cover types (a–d) at 5 cm (shallow), (e–h) at 10 cm (middle soil layer), and (i–l) at 30 cm (deep soil layer). (m–p) Precipitation in both sites, PJC (black) and PJG (gray). The gray shaded area represents the girdling period. In 2009, site-specific differences in VWC in all depths were not significant. In 2010–2012, girdled VWC was significantly lower than VWC at the control site but dependent on depth ($p < 0.0001$). From post hoc Tukey HSD test, shallow VWC was similar between the two sites ($p = 0.18$), but both middle VWC ($p = 0.001$) and deep VWC ($p = 0.007$) were significantly lower at PJG.

4. Discussion

4.1. Hydrological Responses to Piñon Mortality

To understand the consequences of mortality-induced change in the canopy structure of semiarid woodland ecosystems, we used a girdling treatment to simulate piñon mortality in a southwestern U.S. piñon-juniper woodland. Although total ET, after accounting for incoming precipitation, did not change following girdling (Table 2), the decrease in both subcanopy root zone available water (i.e., VWC_{0-30} , Figures 4 and 5) and physiological activity (i.e., J_s , Figure 3) of the surviving trees following piñon mortality reflects an important shift in site level hydrology triggered by the loss of one of the canopy dominants in this semiarid biome. Our findings suggest that one of the most important consequences of large-scale mortality in these biomes is that changes in the rate and timing of evaporation and transpiration may alter both the temporal dynamics and spatial distribution of soil water to the detriment of the surviving plants. This is a somewhat surprising conclusion given that theory and empirical data would suggest that abrupt tree death should “release” soil water and improve the water status of remaining vegetation and new recruits (Bearup et al., 2014; Dore et al., 2012; He et al., 2013). Because the amount of precipitation to support woody growth is already limited in these biomes, mortality-induced decreases in root zone available water can have important consequences for the trajectory of recovery and sensitivity of these biomes to drought.

4.2. Piñon Mortality Altered Evapotranspiration Partitioning More Than Total ET

Despite a decrease in canopy density of about 50%, total ET fluxes in the girdled site were very similar to the control site throughout our study (Figure 2). In general, ET responses to recent canopy loss in semiarid biomes are quite variable (Adams et al., 2012). The range of change in ET following beetle infestation in observations following insect-driven forest disturbance in other sites in western North America is quite large and varies from a 28% decrease to a 5% increase (Biederman, Harpold, et al., 2014; Bright et al., 2013; Chen et al., 2015; Frank et al., 2014; Mikkelsen et al., 2013). A more limited comparison between sites with low precipitation suggests that ET is commonly conserved after disturbance in semiarid forest landscapes, where potential evapotranspiration far exceeds precipitation and annual ET approximates, or even exceeds, annual precipitation (Biederman et al., 2015; Huxman et al., 2005; Simonin et al., 2007).

Given that hydrological year ET was never less than P at both sites (common in semiarid biomes, Schlesinger & Jasechko, 2014), we assume that runoff and infiltration were both negligible at each site throughout the study. Our results therefore suggest total ET was more or less conserved following girdling because the increase in noncanopy ET fluxes following treatment balanced the observed decrease in canopy transpiration (Table 2). A similar shift in the partitioning of ET was observed after thinning in a *Pinus ponderosa* forest in Arizona, particularly during extreme drought (Simonin et al., 2007) and following mortality induced by mountain pine beetle in Colorado (Biederman, Harpold, et al., 2014). Although using sap flux measurements to estimate T_c and calculating ET_o by subtraction from ET has underlying uncertainty (Raz-Yaseef et al., 2009; West et al., 2008), our estimates of ET_o/ET are comparable to values from other studies in PJ woodlands in the SW U. S. For example, West et al. (2008) reported annual values of ET_o/P ($\sim ET_o/ET$ in semiarid sites) ranging from 85% to 93% in a PJ woodland with a basal area of 18.4 m²/ha. In addition, Pangle et al. (2015) reported canopy transpiration (sap flow scaled) to precipitation ratios (T_c/P) similar to this study that ranged from 8 to 11% depending on drought severity in a nearby PJ woodland with a basal area of 18.6 m²/ha. These T_c/P ratios correspond to an approximate ET_o/P ratio of 89% to 92%, assuming no net loss of P to runoff or deep drainage. High values of ET_o/ET , ranging from 81% to 97%, have been also found in other semiarid sparsely vegetated ecosystems (Méndez-Barroso et al., 2014).

4.3. Mechanisms That Link Tree Mortality, Shift in ET Partitioning, and Decrease in Soil Water Availability in Semiarid Biomes

Total canopy cover of woody plants is an important structural attribute in semiarid biomes that strongly influences both microclimate and ecohydrological processes that in turn regulates soil water availability (Breshears et al., 1998; Huxman et al., 2005; Villegas et al., 2015). Relative to the intact control, structural changes following widespread piñon mortality intensified water stress during our study, particularly during the severe drought in 2011 and 2012. These changes not only resulted in decreased performance of the remaining trees but in more rapid senescence of the intercanopy herbaceous vegetation at the girdled site (Krofcheck et al., 2014), which could, in turn, intensify soil moisture stress by removing a protective layer.

Figure 6. Potential mechanisms following piñon mortality that lead to decreased soil water availability in PJ woodlands. Gray arrows indicate an overall decrease in the process triggered by mortality. Black arrows indicate an overall increase in the process following mortality.

Importantly, the response that we observed suggests that sparse tree density and site hydrology may be linked by positive feedbacks in semiarid woodlands, such that the loss of a canopy dominant above a crucial threshold can trigger mechanisms that lead to a decrease in plant-available soil moisture that may be unique to semiarid biomes. Understanding the potential mechanisms is crucial given that the increased aridification observed following tree mortality has important consequences for the recovery of these biomes following mortality events, particularly as drought increases in this region in the coming decades (Williams et al., 2012).

The largest hydrological shift triggered by the decrease in piñon canopy that we observed was a shift in the partitioning of ET, where noncanopy sources of ET significantly increased relative to the intact PJ woodland. We suggest that it is this shift that contributed to the decrease in available soil moisture in the girdled site following piñon mortality. The specific mechanisms that link the decrease in canopy density to an increase in ET_o vary on a seasonal basis (Figure 6). In winter, reduction of the canopy due to mortality allows greater throughput of incident radiation to the surface and higher turbulence, both of which have been observed to trigger increased rates of sublimation in other disturbed southwestern forests and, thus, ET_o (Biederman, Brooks, et al., 2014; Harpold et al., 2014; Pugh & Small, 2012; Veatch et al., 2009). Increased rates of sublimation could also be enhanced by a decrease in albedo at the surface due to accumulated litter from the dead trees (Pugh & Small, 2012). A reduction in the time the winter snowpack remains on the ground will reduce the status of available moisture during the growing season. During the monsoon, higher ET_o/ET and reduced soil moisture in the girdled site (Figure 5) was likely driven by an increase in soil evaporation, again driven by higher surface solar radiation and turbulence following canopy loss (Royer et al., 2012). In many water-limited biomes, including our PJ woodland, soil evaporation and understory transpiration during the monsoon can significantly reduce water availability for dominant vegetation (Huxman et al., 2005).

Two additional mechanisms could enhance growing season water stress in disturbed woodlands and deserve more detailed study. First, tree mortality may modify the magnitude of hydraulic redistribution (HR), the well-documented movement of soil water between soil compartments at different water potentials via transporting roots (reviewed in Neumann & Cardon, 2012). Although poorly documented in PJ woodlands, the ubiquity of this phenomenon in species with large root systems (e.g., Bleby et al., 2010) spanning vertical and horizontal soil water potential gradients suggests that it is likely to occur there (Kitajima et al., 2013; Kizito et al., 2012; Prieto et al., 2014; Quijano et al., 2012; Yan & Dickinson, 2014). Tree mortality would reduce the

magnitude of HR by reducing the number of living root systems in the system. Moreover, the overall drier soils due to progressive drought and increased ET_o following girdling also may have reduced the magnitude of HR in the girdled site (Huang et al., 2017; Prieto et al., 2012). The possible impacts of decreased HR on the plant responses (i.e., J_s) include decreased volume of transpirable water redistributed in the soil profile, decreased ability to maintain viable absorbing roots during drought, and decreased nutrient uptake due to declining microbial activities in the soil (e.g., Prieto et al., 2012; Ryel et al., 2002, 2008). Moreover, by facilitating water transport between depths, HR may increase the importance of the well-developed petrocalcic horizon present at our site and in many semiarid ecosystems. Petrocalcic horizons are a poorly understood element of water cycling in semiarid ecosystems even though they occur widely (Foxy & Tierney, 1985), have distinct moisture release characteristics that may make them a source of water when surface soils are dry (Hennessy et al., 1983), and are frequently explored by roots of woody species (e.g., Gibbens & Lenz, 2001; Schwinning, 2010).

A second potential mechanism is that the surface accumulation of litter from dead piñon could alter soil moisture availability, by promoting the development of a subcanopy hydrophobic soil layer. This increase in hydrophobicity has enhanced surface runoff in some studies by impeding infiltration in the shallow soil layer and favoring infiltration to the deeper soil profile through preferential flow (Doerr et al., 2000; Lebron et al., 2007; Robinson et al., 2010). Given that we never observed $P > ET$ in either site, it is unlikely that surface runoff played an important role in these sites during the study period, but it could be important in other sites.

4.4. Piñon Mortality May Have Increased Sensitivity of Remaining Trees to Drought

Both the control and girdled sites were influenced by the 2011–2012 drought. In both sites, hydrological year ET decreased and ET/P ratios increased from near 1 in 2009 to greater than 1 (Table 2) during the second year of drought in 2012, suggesting that up to 27% of ET came from stored soil moisture in deeper layers of the profile. During the measurement period, there was only one significant recharge event that penetrated to the deeper soil layers, in winter 2010 (Figure 5). Year-to-year variability in the ET/P ratio and extraction of water deeper in the soil profile in dry years is not uncommon in semiarid biomes (Dodd et al., 1998; Lee & Lauenroth, 1994; Nagler et al., 2007).

Several lines of evidence, however, suggest that piñon mortality may have made the girdled site more sensitive to the 2011–2012 drought. The decreased subcanopy soil water availability that we observed following girdling (Figures 4 and 5) is consistent with some but not all examples in the literature. Several observations, particularly those from the more arid end of forested systems, suggest that our results may be applicable to a broader range of biomes throughout the region. For example, Arizona sites with high piñon mortality had 31% to 16% lower predawn water potentials than low-mortality sites (Swaty et al., 2004). Bark beetle-infested ponderosa and lodgepole forests in Wyoming and Colorado also experienced an overall decrease in soil water compared to intact stands under drier than average conditions (Biederman, Brooks, et al., 2014). Nevertheless, soil moisture increased following bark beetle infestation of a Rocky mountain alpine spruce forest and lodgepole pine forest (Frank et al., 2014; Mikkelsen et al., 2013) and girdling in a northern temperate mixed deciduous forest (He et al., 2013; Matheny et al., 2014).

Although canopy transpiration decreased in both sites in 2011 and 2012 (Figure 2), the steeper decline in transpiration from the remaining trees at the girdled site compared to their counterparts at the control site (Figure 3) suggests that disturbed woodlands may be more vulnerable to drought than intact woodlands. This is also reflected by the decrease in the sapwood area of remaining piñon in the girdled site after the 2 year extended drought period that was not observed in the control site (Table 1). Other studies have also reported the greatest differences in hydrological processes between disturbed and undisturbed woodlands in drier than average years (Kaiser et al., 2012; Simonin et al., 2007; Winkler et al., 2014). This increased sensitivity to drought following mortality is important given that the regions that have already observed increased aridity and drought-induced mortality are likely to see an increase in the frequency and severity of droughts in the near future (Anderegg et al., 2013; Seager & Vecchi, 2010).

4.5. Implications

Our results advance the current understanding of the ecohydrological consequences of drought-induced mortality in semiarid woodlands. Although mortality of piñon in PJ woodlands had very little effect on total ET , it decreased woody canopy cover over a threshold that altered ET partitioning and decreased soil water

content, the function of the remaining trees, and the resilience of PJ woodlands to drought. This is contrary to recent predictions that functional impacts of climate-related tree mortality may be relatively mild and short lived (Anderegg et al., 2016). The impacts that we observed may be somewhat unique to water-limited semi-arid biomes that lack some of the compensating mechanisms that lead to high performance of surviving vegetation after mortality in mesic systems, such as increased light use efficiency, higher resource availability, and fast recovery of LAI (Allen & Breshears, 1998; Anderegg et al., 2016). Our research raises two questions: (1) Was the large response that we observed specifically due to differential mortality of piñon, or would the loss of equivalent leaf area and basal area of juniper or any other coniferous species have led to the same result? (2) Would our conclusions regarding the moisture release hypothesis and decreased performance of remaining trees be different if mortality was not closely followed by severe drought? Answers to both of these questions are required to know how applicable these results are to mortality events across a range of semiarid biomes. Given that projected regional changes in climate include an increase in the frequency of global change type droughts and associated woody mortality events (Williams et al., 2012), assuming our results are applicable to other biomes, continued coniferous mortality in the southwestern U.S. could alter the availability of water and trajectory of forest succession in these landscapes (Grant et al., 2013). These results have implications not only for the resilience of PJ woodlands but for all woody biomes, particularly those in water-limited ecosystems, and suggest interactions between climate change, forest disturbance, and forest management that may have important consequences for the predicted availability of water in these landscapes.

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References

- Adams, H. D., Luce, C. H., Breshears, D. D., Allen, C. D., Weiler, M., Hale, V. C., ... Huxman, T. E. (2012). Ecohydrological consequences of drought- and infestation- triggered tree die-off: Insights and hypotheses. *Ecohydrology*, 5, 145–159. <https://doi.org/10.1002/eco.233>
- Adams, H. D., Macalady, A. K., Breshears, D. D., Allen, C. D., Stephenson, N. L., Saleska, S. R., ... McDowell, N. (2010). Climate-induced tree mortality: Earth system consequences. *Eos, Transactions American Geophysical Union*, 91, 153–154. <https://doi.org/10.1029/2010EO170003>
- Allen, C. D., & Breshears, D. D. (1998). Drought-induced shift of a forest–woodland ecotone: Rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences of the United States of America*, 95(25), 14,839–14,842. <https://doi.org/10.1073/pnas.95.25.14839>
- Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, 6, 129.
- Allen, C. D., Macalady, A. K., Chenchouni, H., Chenchouni, H., Bachelet, D., McDowell, N., ... Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259, 660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>
- Anderegg, L. D. L., Anderegg, W. R. L., & Berry, J. A. (2013). Not all droughts are created equal: Translating meteorological drought into woody plant mortality. *Tree Physiology*, 33(7), 672–683. <https://doi.org/10.1093/treephys/tpt044>
- Anderegg, W. R. L., Hicke, J. A., Fisher, R. A., Allen, C. D., Aukema, J., Bentz, B., ... Zeppel, M. (2015). Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytologist*, 208(3), 674–683. <https://doi.org/10.1111/nph.13477>
- Anderegg, W. R. L., Kane, J. M., & Anderegg, L. D. L. (2012). Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change*, 3, 30–36. <https://doi.org/10.1038/nclimate1635>
- Anderegg, W. R. L., Martinez-Vilalta, J., Cailleret, M., Camarero, J. J., Ewers, B. E., Galbraith, D., ... Trotsiuk, V. (2016). When a tree dies in the forest: Scaling climate-driven tree mortality to ecosystem water and carbon fluxes. *Ecosystems*, 19(6), 1133–1147. <https://doi.org/10.1007/s10021-016-9982-1>
- Anderson-Teixeira, K. J., Delong, J. P., Fox, A. M., Brese, D. A., & Litvak, M. E. (2011). Differential responses of production and respiration to temperature and moisture drive the carbon balance across a climatic gradient in New Mexico: Carbon balance across NM elevational gradient. *Global Change Biology*, 17, 410–424. <https://doi.org/10.1111/j.1365-2486.2010.02269.x>
- Atchley, A. L., & Maxwell, R. M. (2011). Influences of subsurface heterogeneity and vegetation cover on soil moisture, surface temperature and evapotranspiration at hillslope scales. *Hydrogeology Journal*, 19, 289–305. <https://doi.org/10.1007/s10040-010-0690-1>
- Barr, A. G., Richardson, A. D., Hollinger, D. Y., Papale, D., Arain, M. A., Black, T. A., ... Schaeffer, K. (2013). Use of change-point detection for friction–velocity threshold evaluation in eddy-covariance studies. *Agricultural and Forest Meteorology*, 171–172, 31–45.
- Bearup, L. A., Maxwell, R. M., Clow, D. W., & McCray, J. E. (2014). Hydrological effects of forest transpiration loss in bark beetle-impacted watersheds. *Nature Climate Change*, 4(6), 481–486. <https://doi.org/10.1038/nclimate2198>
- Biederman, J. A., Brooks, P. D., Harpold, A. A., Gochis, D. J., Gutmann, E., Reed, D. E., ... Ewers, B. E. (2014). Multiscale observations of snow accumulation and peak snowpack following widespread, insect-induced lodgepole pine mortality: Snowpack following insect-induced pine mortality. *Ecohydrology*, 7(1), 150–162. <https://doi.org/10.1002/eco.1342>
- Biederman, J. A., Harpold, A. A., Gochis, D. J., Ewers, B. E., Reed, D. E., Papuga, S. A., & Brooks, P. D. (2014). Increased evaporation following widespread tree mortality limits streamflow response. *Water Resources Research*, 50(7), 5395–5409. <https://doi.org/10.1002/2013WR014994>
- Biederman, J. A., Somor, A. J., Harpold, A. A., Guttman, E. D., Breshears, D. D., Troch, P. A., ... Brooks, P. D. (2015). Tree die-off has little effect on streamflow in contrast to expected increases from historical studies. *Water Resources Research*, 51(12), 9775–9789. <https://doi.org/10.1002/2015WR017401>
- Bleby, T. M., Mcelrone, A. J., & Jackson, R. B. (2010). Water uptake and hydraulic redistribution across large woody root systems to 20 m depth. *Plant, Cell, and Environment*, 33(12), 2132–2148. <https://doi.org/10.1111/j.1365-3040.2010.02212.x>

- Breshears, D. D., Breshears, D. D., Adams, H. D., McDowell, N. G., Law, D. J., Will, R. E., ... Zou, C. B. (2013). The critical amplifying role of increasing atmospheric moisture demand on tree mortality and associated regional die-off. *Frontiers in Plant Science*, 4, 266. <https://doi.org/10.3389/fpls.2013.00266>
- Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Balice, R. G., ... Meyer, C. W. (2005). Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 15,144–15,148. <https://doi.org/10.1073/pnas.0505734102>
- Breshears, D. D., Nyhan, J. W., Heil, C. E., & Wilcox, B. P. (1998). Effects of woody plants on microclimate in a semiarid woodland: Soil temperature and evaporation in canopy and intercanopy patches. *International Journal of Plant Sciences*, 159(6), 1010–1017. <https://doi.org/10.1086/314083>
- Bright, B. C., Hicke, J. A., & Meddens, A. J. H. (2013). Effects of bark beetle-caused tree mortality on biogeochemical and biogeophysical MODIS products. *Journal of Geophysical Research: Biogeosciences*, 118, 974–982. <https://doi.org/10.1002/jgrg.20078>
- Chen, F., Zhang, G., Barlage, M., Zhang, Y., Hicke, J. A., Meddens, A., ... Frank, J. (2015). An observational and modeling study of impacts of bark beetle-caused tree mortality on surface energy and hydrological cycles. *Journal of Hydrometeorology*, 16(2), 744–761. <https://doi.org/10.1175/JHM-D-14-0059.1>
- Clifford, M. J., Rocca, M. E., Delph, R., Ford, P. L., & Cobb, N. S. (2008). Drought induced tree mortality and ensuing bark beetle outbreaks in southwestern pinyon-juniper woodlands. In A. Gottfried, et al. (Eds.), *Ecology, management, and restoration of pinon-juniper and ponderosa pine ecosystems: Combined Proceedings of the 2005 St. George, Utah and 2006 Albuquerque, New Mexico Workshops* (pp. 39–51). Fort Collins, CO: Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Clifford, M. J., Royer, P. D., Cobb, N. S., Breshears, D. D., & Ford, P. L. (2013). Precipitation thresholds and drought-induced tree die-off: Insights from patterns of *Pinus edulis* mortality along an environmental stress gradient. *New Phytologist*, 200(2), 413–421. <https://doi.org/10.1111/nph.12362>
- D'Odorico, P., Caylor, K., Okin, G. S., & Scanlon, T. M. (2007). On soil moisture–vegetation feedbacks and their possible effects on the dynamics of dryland ecosystems. *Journal of Geophysical Research*, 112, G04010. <https://doi.org/10.1029/2006JG000379>
- Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature Climate Change*, 3, 52–58.
- Detto, M., Montaldo, N., Albertson, J. D., Mancini, M., & Katul, G. (2006). Soil moisture and vegetation controls on evapotranspiration in a heterogeneous Mediterranean ecosystem on Sardinia, Italy. *Water Resources Research*, 42, W08419. <https://doi.org/10.1029/2005WR004693>
- Dodd, M., Lauenroth, W., & Welker, J. (1998). Differential water resource use by herbaceous and woody plant life-forms in a shortgrass steppe community. *Oecologia*, 117(4), 504–512. <https://doi.org/10.1007/s004420050686>
- Doerr, S. H., Shakesby, R. A., & Walsh, R. P. D. (2000). Soil water repellency: Its causes, characteristics and hydro-geomorphological significance. *Earth-Science Reviews*, 51(1–4), 33–65. [https://doi.org/10.1016/S0012-8252\(00\)00011-8](https://doi.org/10.1016/S0012-8252(00)00011-8)
- Dore, S., Montes-Helu, M., Hart, S. C., Hungate, B. A., Koch, G. W., Moon, J. B., ... Kolb, T. E. (2012). Recovery of ponderosa pine ecosystem carbon and water fluxes from thinning and stand-replacing fire. *Global Change Biology*, 18, 3171–3185. <https://doi.org/10.1111/j.1365-2486.2012.02775.x>
- Edburg, S. L., Hicke, J. A., Brooks, P. D., Pendall, E. G., Ewers, B. E., Norton, U., ... Meddens, A. J. (2012). Cascading impacts of bark beetle-caused tree mortality on coupled biogeophysical and biogeochemical processes. *Frontiers in Ecology and the Environment*, 10, 416–424. <https://doi.org/10.1890/110173>
- Eitel, J. U. H., Vierling, L. A., Litvak, M. E., Vierling, L. A., Litvak, M. E., Long, D. S., ... Stoscheck, L. (2011). Broadband, red-edge information from satellites improves early stress detection in a New Mexico conifer woodland. *Remote Sensing of Environment*, 115, 3640–3646. <https://doi.org/10.1016/j.rse.2011.09.002>
- Falge, E., Baldocchi, D., Olson, R., Anthoni, P., Aubinet, M., Bernhofer, C., ... Wofsy, S. (2001). Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agricultural and Forest Meteorology*, 107(1), 43–69. [https://doi.org/10.1016/S0168-1923\(00\)00225-2](https://doi.org/10.1016/S0168-1923(00)00225-2)
- Foxx, T. S., & Tierney, G. D. (1985). *Rooting patterns in the pinyon-juniper woodland*. Reno, NV: Los Alamos National Laboratory.
- Frank, J. M., Massman, W. J., Ewers, B. E., Huckaby, L. S., & Negrón, J. F. (2014). Ecosystem CO₂/H₂O fluxes are explained by hydraulically limited gas exchange during tree mortality from spruce bark beetles. *Journal of Geophysical Research: Biogeosciences*, 119, 1195–1215. <https://doi.org/10.1002/2013JG002597>
- Giambelluca, T. W. (2002). Hydrology of altered tropical forest. *Hydrological Processes*, 16(8), 1665–1669. <https://doi.org/10.1002/hyp.5021>
- Gibbens, R. P., & Lenz, J. M. (2001). Root systems of some Chihuahuan Desert plants. *Journal of Arid Environments*, 49(2), 221–263. <https://doi.org/10.1006/jare.2000.0784>
- Goulden, M. L., & Field, C. B. (1994). Three methods for monitoring the gas exchange of individual tree canopies: Ventilated-chamber, sap-flow and penman-Monteith measurements on Evergreen oaks. *Functional Ecology*, 8(1), 125. <https://doi.org/10.2307/2390121>
- Granier, A. (1985). Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. *Annales des Sciences Forestières*, 42(2), 193–200. <https://doi.org/10.1051/forest:19850204>
- Granier, A. (1987). Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiology*, 3(4), 309–320. <https://doi.org/10.1093/treephys/3.4.309>
- Grant, G. E., Tague, C. L., & Allen, C. D. (2013). Watering the forest for the trees: An emerging priority for managing water in forest landscapes. *Frontiers in Ecology and the Environment*, 11(6), 314–321. <https://doi.org/10.1890/120209>
- Grier, C. C., Elliott, K. J., & McCullough, D. G. (1992). Biomass distribution and productivity of *Pinus edulis*-*Juniperus monosperma* woodlands of north-central Arizona. *Forest Ecology and Management*, 50(3–4), 331–350. [https://doi.org/10.1016/0378-1127\(92\)90346-B](https://doi.org/10.1016/0378-1127(92)90346-B)
- Guardiola-Claramonte, M., Troch, P. A., Breshears, D. D., Huxman, T. E., Switaneck, M. B., Durcik, M., & Cobb, N. S. (2011). Decreased streamflow in semi-arid basins following drought-induced tree die-off: A counter-intuitive and indirect climate impact on hydrology. *Journal of Hydrology*, 406, 225–233. <https://doi.org/10.1016/j.jhydrol.2011.06.017>
- Gustafson, J. R., Brooks, P. D., Molotch, N. P., & Veatch, W. (2010). Quantifying snow sublimation using natural tracer concentrations and isotopic fractionation in a forested catchment. *Water Resources Research*, 46, W12511. <https://doi.org/10.1029/2009WR009060>
- Harpold, A. A., Biederman, J. A., Condon, K., Merino, M., Korgaonkar, Y., Nan, T., ... Brooks, P. D. (2014). Changes in snow accumulation and ablation following the Las Conchas Forest fire, New Mexico, USA. *Ecohydrology*, 7(2), 440–452. <https://doi.org/10.1002/eco.1363>
- He, L., Ivanov, V. Y., Bohrer, G., Thomsen, J. E., Vogel, C. S., & Moghaddam, M. (2013). Temporal dynamics of soil moisture in a northern temperate mixed successional forest after a prescribed intermediate disturbance. *Agricultural and Forest Meteorology*, 180, 22–33. <https://doi.org/10.1016/j.agrformet.2013.04.014>
- Hennessy, J. T., Gibbens, R. P., Tromble, J. M., & Cardenas, M. (1983). Water properties of caliche. *Journal of Range Management*, 36(6), 723–726. <https://doi.org/10.2307/3898195>

- Hicke, J. A., Allen, C. D., Desai, A. R., Dietze, M. C., Hall, R. J., Hogg, E. H., ... Vogelmann, J. (2012). Effects of biotic disturbances on forest carbon cycling in the United States and Canada. *Global Change Biology*, 18, 7–34. <https://doi.org/10.1111/j.1365-2486.2011.02543.x>
- Hsieh, C.-I., Katul, G., & Chi, T. (2000). An approximate analytical model for footprint estimation of scalar fluxes in thermally stratified atmospheric flows. *Advances in Water Resources*, 23(7), 765–772. [https://doi.org/10.1016/S0309-1708\(99\)00042-1](https://doi.org/10.1016/S0309-1708(99)00042-1)
- Huang, C.-W., Domec, J.-C., Ward, E. J., Duman, T., Manoli, G., Parolari, A. J., & Katul, G. G. (2017). The effect of plant water storage on water fluxes within the coupled soil–plant system. *New Phytologist*, 213(3), 1093–1106. <https://doi.org/10.1111/nph.14273>
- Huxman, T. E., Wilcox, B. P., Breshears, D. D., Scott, R. L., Snyder, K. A., Small, E. E., ... Jackson, R. B. (2005). Ecohydrological implications of woody plant encroachment. *Ecology*, 86, 308–319. <https://doi.org/10.1890/03-0583>
- IPCC (2014). In Core Writing Team, R. K. Pachauri, & L. A. Meyer (Eds.), *Climate change 2014: Synthesis report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (p. 151). Geneva, Switzerland: IPCC.
- Kaiser, M., Ellerbrock, R. H., Wulf, M., Dultz, S., Hierath, C., & Sommer, M. (2012). The influence of mineral characteristics on organic matter content, composition, and stability of topsoils under long-term arable and forest land use. *Journal of Geophysical Research*, 117, G02018. <https://doi.org/10.1029/2011JG001712>
- Kitajima, K., Allen, M. F., & Goulden, M. L. (2013). Contribution of hydraulically lifted deep moisture to the water budget in a Southern California mixed forest. *Journal of Geophysical Research: Biogeosciences*, 118, 1561–1572. <https://doi.org/10.1002/2012JG002255>
- Kizito, F., Dragila, M. I., Sené, M., Brooks, J. R., Meinzer, F. C., Diedhiou, I., ... Cuenca, R. (2012). Hydraulic redistribution by two semi-arid shrub species: Implications for Sahelian agro-ecosystems. *Journal of Arid Environments*, 83, 69–77. <https://doi.org/10.1016/j.jaridenv.2012.03.010>
- Klutsch, J. G., Negrón, J. F., Costello, S. L., Rhoades, C. C., West, D. R., Popp, J., & Caissie, R. (2009). Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. *Forest Ecology and Management*, 258, 641–649. <https://doi.org/10.1016/j.foreco.2009.04.034>
- Krofcheck, D., Litvak, M., Lippitt, C., & Neuenschwander, A. (2016). Woody biomass estimation in a southwestern U.S. juniper savanna using lidar-derived clumped tree segmentation and existing allometries. *Remote Sensing*, 8(6), 453. <https://doi.org/10.3390/rs8060453>
- Krofcheck, D. J., Eitel, J. U. H., Vierling, L. A., Schulthess, U., Hilton, T. M., Dettweiler-Robinson, E., ... Litvak, M. E. (2014). Detecting mortality induced structural and functional changes in a piñon-juniper woodland using Landsat and RapidEye time series. *Remote Sensing of Environment*, 151, 102–113. <https://doi.org/10.1016/j.rse.2013.11.009>
- Lebron, I., Madsen, M. D., Chandler, D. G., Robinson, D. A., Wendroth, O., & Belnap, J. (2007). Ecohydrological controls on soil moisture and hydraulic conductivity within a pinyon-juniper woodland. *Water Resources Research*, 43, W08422. <https://doi.org/10.1029/2006WR005398>
- Lee, C., & Lauenroth, W. (1994). Spatial distribution of grass and shrub root systems in the shortgrass steppe. *American Midland Naturalist*, 137, 117–123.
- Ludwig, J. A., & Tongway, D. J. (1995). Spatial organisation of landscapes and its function in semi-arid woodlands, Australia. *Landscape Ecology*, 10(1), 51–63. <https://doi.org/10.1007/BF00158553>
- Massman, W. J. (2000). A simple method for estimating frequency corrections for eddy covariance systems. *Agricultural and Forest Meteorology*, 104(3), 185–198. [https://doi.org/10.1016/S0168-1923\(00\)00164-7](https://doi.org/10.1016/S0168-1923(00)00164-7)
- Matheny, A. M., Bohrer, G., Vogel, C. S., Morin, T. H., He, L., Frasson, R. P. M., ... Curtis, P. S. (2014). Species-specific transpiration responses to intermediate disturbance in a northern hardwood forest: Transpiration response to disturbance. *Journal of Geophysical Research: Biogeosciences*, 119, 2292–2311. <https://doi.org/10.1002/2014JG002804>
- McDowell, N. G., Fisher, R. A., Xu, C., Domec, J. C., Hölttä, T., Mackay, D. S., ... Pockman, W. T. (2013). Evaluating theories of drought-induced vegetation mortality using a multimodel–experiment framework. *New Phytologist*, 200(2), 304–321. <https://doi.org/10.1111/nph.12465>
- McDowell, N. G., Williams, A. P., Xu, C., Pockman, W. T., Dickman, L. T., Sevanto, S., ... Koven, C. (2016). Multi-scale predictions of massive conifer mortality due to chronic temperature rise. *Nature Climate Change*, 6, 295–300.
- Meddens, A. J. H., Hicke, J. A., Macalady, A. K., Buotte, P. C., Cowles, T. R., & Allen, C. D. (2015). Patterns and causes of observed piñon pine mortality in the southwestern United States. *New Phytologist*, 206(1), 91–97. <https://doi.org/10.1111/nph.13193>
- Méndez-Barroso, L. A., Vivoni, E. R., Robles-Morua, A., Mascaro, G., Yépez, E. A., Rodríguez, J. C., ... Saiz-Hernández, J. A. (2014). A modeling approach reveals differences in evapotranspiration and its partitioning in two semiarid ecosystems in Northwest Mexico. *Water Resources Research*, 50(4), 3229–3252. <https://doi.org/10.1002/2013WR014838>
- Mikkelsen, K. M., Maxwell, R. M., Ferguson, I., Stednick, J. D., McCray, J. E., & Sharp, J. O. (2013). Mountain pine beetle infestation impacts: Modeling water and energy budgets at the hill-slope scale. *Ecohydrology*, 6(1), 64–72. <https://doi.org/10.1002/eco.278>
- Miller, G. R., Baldocchi, D. D., Law, B. E., & Meyers, T. (2007). An analysis of soil moisture dynamics using multi-year data from a network of micrometeorological observation sites. *Advances in Water Resources*, 30, 1065–1081. <https://doi.org/10.1016/j.advwatres.2006.10.002>
- Molotch, N. P., Brooks, P. D., Burns, S. P., Litvak, M., Monson, R. K., McConnell, J. R., & Musselman, K. (2009). Ecohydrological controls on snowmelt partitioning in mixed-conifer sub-alpine forests. *Ecohydrology*, 2, 129–142. <https://doi.org/10.1002/eco.48>
- Mueller, R. C., Scudder, C. M., Porter, M. E., Talbot, T. R., Gehring, C. A., & Whitham, T. G. (2005). Differential tree mortality in response to severe drought: Evidence for long-term vegetation shifts: Drought-induced differential tree mortality. *Journal of Ecology*, 93(6), 1085–1093. <https://doi.org/10.1111/j.1365-2745.2005.01042.x>
- Musselman, K., Molotch, N. P., & Brooks, P. D. (2008). Quantifying the effects of forest vegetation on snow accumulation, ablation and potential meltwater inputs, Valles Caldera National Preserve, NM, USA. *Hydrological Processes*, 22, 2767–2776. <https://doi.org/10.1002/hyp.70501085%E2%80%93931093>
- Nagler, P. L., Glenn, E. P., Kim, H., Emmerich, W., Scott, R. L., Huxman, T. E., & Huete, A. R. (2007). Relationship between evapotranspiration and precipitation pulses in a semiarid rangeland estimated by moisture flux towers and MODIS vegetation indices. *Journal of Arid Environments*, 70, 443–462. <https://doi.org/10.1016/j.jaridenv.2006.12.026>
- Neumann, R. B., & Cardon, Z. G. (2012). The magnitude of hydraulic redistribution by plant roots: A review and synthesis of empirical and modeling studies: Tansley review. *New Phytologist*, 194, 337–352. <https://doi.org/10.1111/j.1469-8137.2012.04088.x>
- Newman, B. D., Wilcox, B. P., Archer, S. R., Breshears, D. D., Dahm, C. N., Duffy, C. J., ... Vivoni, E. R. (2006). Ecohydrology of water-limited environments: A scientific vision. *Water Resources Research*, 42, W06302. <https://doi.org/10.1029/2005WR004141>
- Novak, M. D., Warland, J. S., Orchansky, A. L., Ketter, R., & Green, S. (2000). Wind tunnel and field measurements of turbulent flow in forests. Part I: Uniformly thinned stands. *Boundary-Layer Meteorology*, 95(3), 457–495. <https://doi.org/10.1023/A:1002693625637>
- Pangle, R. E., Hill, J. P., Plaut, J. A., Yépez, E. A., Elliot, J. R., Gehres, N., ... Pockman, W. T. (2012). Methodology and performance of a rainfall manipulation experiment in a piñon-juniper woodland. *Ecosphere*, 3, 1–20.
- Pangle, R. E., Limousin, J.-M., Plaut, J. A., Yépez, E. A., Hudson, P. J., Boutz, A. L., ... McDowell, N. G. (2015). Prolonged experimental drought reduces plant hydraulic conductance and transpiration and increases mortality in a piñon-juniper woodland. *Ecology and Evolution*, 5(8), 1618–1638. <https://doi.org/10.1002/ece3.1422>

- Pinhoiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team (2017). nlme: Linear and nonlinear mixed effects models. R package version 3.1–131. Retrieved from <https://cran.r-project.org/package=nlme>
- Plaut, J. A., Yezzer, E. A., Hill, J., Pangle, R., Sperry, J. S., Pockman, W. T., & McDowell, N. G. (2012). Hydraulic limits preceding mortality in a piñon–juniper woodland under experimental drought. *Plant, Cell & Environment*, 35, 1601–1617. <https://doi.org/10.1111/j.1365-3040.2012.02512.x>
- Prieto, I., Armas, C., & Pugnaire, F. I. (2012). Water release through plant roots: New insights into its consequences at the plant and ecosystem level. *New Phytologist*, 193, 830–841. <https://doi.org/10.1111/j.1469-8137.2011.04039.x>
- Prieto, I., Pugnaire, F. I., & Ryel, R. J. (2014). Water uptake and redistribution during drought in a semiarid shrub species. *Functional Plant Biology*, 41(8), 812–819. <https://doi.org/10.1071/FP13300>
- Pugh, E., & Gordon, E. (2013). A conceptual model of water yield effects from beetle-induced tree death in snow-dominated lodgepole pine forests. *Hydrological Processes*, 27(14), 2048–2060. <https://doi.org/10.1002/hyp.9312>
- Pugh, E., & Small, E. (2012). The impact of pine beetle infestation on snow accumulation and melt in the headwaters of the Colorado River. *Ecohydrology*, 5, 467–477. <https://doi.org/10.1002/eco.239>
- Quijano, J. C., Kumar, P., Drewry, D. T., Goldstein, A., & Misson, L. (2012). Competitive and mutualistic dependencies in multispecies vegetation dynamics enabled by hydraulic redistribution. *Water Resources Research*, 48, W05518. <https://doi.org/10.1029/2011WR011416>
- R Core Team (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Raz-Yaseef, N., Rotenberg, E., & Yakir, D. (2010). Effects of spatial variations in soil evaporation caused by tree shading on water flux partitioning in a semi-arid pine forest. *Agricultural and Forest Meteorology*, 150, 454–462. <https://doi.org/10.1016/j.agrformet.2010.01.010>
- Raz-Yaseef, N., Yakir, D., Rotenberg, E., Schiller, G., & Cohen, S. (2009). Ecohydrology of a semi-arid forest: Partitioning among water balance components and its implications for predicted precipitation changes. *Ecohydrology*, 3, 143–154.
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., ... Valentini, R. (2005). On the separation of net ecosystem exchange into assimilation and ecosystem respiration: Review and improved algorithm. *Global Change Biology*, 11, 1424–1439. <https://doi.org/10.1111/j.1365-2486.2005.001002.x>
- Richardson, P., & Winn, D. (2012). Investigation of Monte Carlo uncertainties on Higgs boson searches using jet substructure. *The European Physical Journal C*, 72, 2178. <https://doi.org/10.1140/epjc/s10052-012-2178-8>
- Robinson, D. A., Lebron, I., Ryel, R. J., & Jones, S. B. (2010). Soil water repellency: A method of soil moisture sequestration in piñon–juniper woodland. *Soil Science Society of America Journal*, 74, 624. <https://doi.org/10.2136/sssaj2009.0208>
- Romme, W. H., Knight, D. H., & Yavitt, J. B. (1986). Mountain pine beetle outbreaks in the Rocky Mountains: Regulators of primary productivity? *The American Naturalist*, 127(4), 484–494. <https://doi.org/10.1086/284497>
- Royer, P. D., Breshears, D. D., Zou, C. B., Villegas, J. C., Cobb, N. S., & Kurc, S. A. (2012). Density-dependent ecohydrological effects of piñon–juniper woody canopy cover on soil microclimate and potential soil evaporation. *Rangeland Ecology & Management*, 65, 11–20. <https://doi.org/10.2111/REM-D-11-00007.1>
- Ryel, R., Caldwell, M., Yoder, C., Or, D., & Leffler, A. (2002). Hydraulic redistribution in a stand of *Artemisia tridentata*: Evaluation of benefits to transpiration assessed with a simulation model. *Oecologia*, 130(2), 173–184. <https://doi.org/10.1007/s004420100794>
- Ryel, R. J., Ivans, C. Y., Peek, M. S., & Leffler, A. J. (2008). Functional differences in soil water pools: A new perspective on plant water use in water-limited ecosystems. In U. Lüttge, W. Beyschlag, & J. Murata (Eds.), *Progress in botany* (pp. 397–422). Berlin Heidelberg: Springer. https://doi.org/10.1007/978-3-540-72954-9_16
- Schlesinger, W. H., & Jasechko, S. (2014). Transpiration in the global water cycle. *Agricultural and Forest Meteorology*, 189–190, 115–117.
- Schwinning, S. (2010). The ecohydrology of roots in rocks. *Ecohydrology*, 3, 238–245.
- Seager, R., & Vecchi, G. A. (2010). Greenhouse warming and the 21st century hydroclimate of southwestern North America. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 21,277–21,282. <https://doi.org/10.1073/pnas.0910856107>
- Simonin, K., Kolb, T. E., Montes-Helu, M., & Koch, G. W. (2007). The influence of thinning on components of stand water balance in a ponderosa pine forest stand during and after extreme drought. *Agricultural and Forest Meteorology*, 143, 266–276. <https://doi.org/10.1016/j.agrformet.2007.01.003>
- Stark, S. C., Breshears, D. D., García, E. S., Law, D. J., Minor, D. M., Saleska, S. R., & Swann, A. L. S. (2016). Toward accounting for ecoclimate teleconnections: Intra- and inter-continental consequences of altered energy balance after vegetation change. *Landscape Ecology*, 31(1), 181–194. <https://doi.org/10.1007/s10980-015-0282-5>
- Swaty, R. L., Deckert, R. J., Whitham, T. G., & Gehring, C. A. (2004). Ectomycorrhizal abundance and community composition shifts with drought: Predictions from tree rings. *Ecology*, 85, 1072–1084. <https://doi.org/10.1890/03-0224>
- Trahan, N. A., Dynes, E. L., Pugh, E., Moore, D. J. P., & Monson, R. K. (2015). Changes in soil biogeochemistry following disturbance by girdling and mountain pine beetles in subalpine forests. *Oecologia*, 177(4), 981–995. <https://doi.org/10.1007/s00442-015-3227-4>
- Varhola, A., Coops, N. C., Weiler, M., & Moore, R. D. (2010). Forest canopy effects on snow accumulation and ablation: An integrative review of empirical results. *Journal of Hydrology*, 319, 219–233.
- Veatch, W., Brooks, P. D., Gustafson, J. R., & Molotch, N. P. (2009). Quantifying the effects of forest canopy cover on net snow accumulation at a continental, mid-latitude site. *Ecohydrology*, 2, 115–128. <https://doi.org/10.1002/eco.45>
- Villegas, J. C., Breshears, D. D., Zou, C. B., & Law, D. J. (2010). Ecohydrological controls of soil evaporation in deciduous drylands: How the hierarchical effects of litter, patch and vegetation mosaic cover interact with phenology and season. *Journal of Arid Environments*, 74, 595–602. <https://doi.org/10.1016/j.jaridenv.2009.09.028>
- Villegas, J. C., Dominguez, F., Barron-Gafford, G. A., Adams, H. D., Guardiola-Claramonte, M., Sommer, E. D., ... Huxman, T. E. (2015). Sensitivity of regional evapotranspiration partitioning to variation in woody plant cover: Insights from experimental dryland tree mosaics. *Global Ecology and Biogeography*, 24(9), 1040–1048. <https://doi.org/10.1111/geb.12349>
- Webb, E. K., Pearman, G. I., & Leuning, R. (1980). Correction of flux measurements for density effects due to heat and water vapour transfer. *Quarterly Journal of the Royal Meteorological Society*, 106(447), 85–100. <https://doi.org/10.1002/qj.49710644707>
- West, A. G., Hultine, K. R., Sperry, J. S., Bush, S. E., & Ehleringer, J. R. (2008). Transpiration and hydraulic strategies in a piñon–juniper woodland. *Ecological Applications*, 18, 911–927. <https://doi.org/10.1890/06-2094.1>
- Williams, A. P., Allen, C. D., Macalady, A. K., Griffin, D., Woodhouse, C. A., Meko, D. M., ... McDowell, N. G. (2012). Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*, 3, 292–297. <https://doi.org/10.1038/nclimate1693>
- Williams, C. A., Vanderhoof, M. K., Khomik, M., & Ghimire, B. (2014). Post-clearcut dynamics of carbon, water and energy exchanges in a midlatitude temperate, deciduous broadleaf forest environment. *Global Change Biology*, 20(3), 992–1007. <https://doi.org/10.1111/gcb.12388>

- Winkler, R., Boon, S., Zimonick, B., & Spittlehouse, D. (2014). Snow accumulation and ablation response to changes in forest structure and snow surface albedo after attack by mountain pine beetle. *Hydrological Processes*, 28(2), 197–209. <https://doi.org/10.1002/hyp.9574>
- Yan, B., & Dickinson, R. E. (2014). Modeling hydraulic redistribution and ecosystem response to droughts over the Amazon basin using Community Land Model 4.0 (CLM4). *Journal of Geophysical Research: Biogeosciences*, 119(11), 2130–2143. <https://doi.org/10.1002/2014JG002694>