

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/347614754>

Hydraulic redistribution buffers climate variability and regulates grass–tree interactions in a semiarid riparian savanna

Article in *Ecohydrology* · December 2020

DOI: 10.1002/eco.2271

CITATIONS

0

READS

57

11 authors, including:



Greg Barron-Gafford

The University of Arizona

154 PUBLICATIONS 4,447 CITATIONS

[SEE PROFILE](#)



John Francis Knowles

United States Department of Agriculture

47 PUBLICATIONS 605 CITATIONS

[SEE PROFILE](#)



Enrique P. Sánchez-Cañete

University of Granada

63 PUBLICATIONS 887 CITATIONS

[SEE PROFILE](#)



Rebecca Larkin Minor

The University of Arizona

18 PUBLICATIONS 96 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Towards an integrated GHG balance in national ecosystems with relevant social and economical impact [View project](#)



AGU 2019: Examining Transpiration and Photosynthesis from Ecosystem to Global Scales: Observations, Linkages, and Drivers [View project](#)



RESEARCH ARTICLE

WILEY

Hydraulic redistribution buffers climate variability and regulates grass-tree interactions in a semiarid riparian savanna

Greg A. Barron-Gafford^{1,2} | John F. Knowles^{1,3} |
Enrique P. Sanchez-Cañete^{4,5} | Rebecca L. Minor^{1,2,6} | Esther Lee⁷ |
Leland Sutter^{1,2} | Newton Tran⁸ | Patrick Murphy^{1,9} |
Erik P. Hamerlynck¹⁰ | Praveen Kumar⁷ | Russell L. Scott³

¹School of Geography, Development and Environment, University of Arizona, Tucson, Arizona, USA

²Biosphere 2, University of Arizona, Tucson, Arizona, USA

³Southwest Watershed Research Center, USDA-ARS, Tucson, Arizona, USA

⁴Centro Andaluz de Medio Ambiente, IISTA-CEAMA, Granada, Spain

⁵Department of Applied Physics, University of Granada, Granada, Spain

⁶Department of Earth and Climate Sciences, Bates College, Lewiston, Maine, USA

⁷Department of Civil and Environmental Engineering, University of Illinois at Urbana-Champaign, Urbana, Illinois, USA

⁸Center for Tree Science, The Morton Arboretum, Lisle, Illinois, USA

⁹Department of Geosciences, University of Arizona, Tucson, Arizona, USA

¹⁰Eastern Oregon Agricultural Research Center, USDA-ARS, Burns, Oregon, USA

Correspondence

Greg Barron-Gafford, School of Geography, Development and Environment, University of Arizona, 1064 E. Lowell St, #5513, Tucson, AZ 85721, USA.
Email: gregbg@email.arizona.edu;

Funding information

Division of Earth Sciences, Grant/Award Numbers: 1331408, 1331906, 1417101, 1417444; Marie Curie International Outgoing Fellowship, Grant/Award Number: 625988; National Science Foundation, Grant/Award Numbers: ACI 1261582, EAR 1331906, EAR 1331408, EAR 1417444, EAR 1417101

Abstract

Anticipating the ability of ecosystems to maintain functional integrity across predicted altered precipitation regimes remains a grand ecohydrological challenge. Overstory trees and understory grasses within semiarid savannas vary in their structure and sensitivity to environmental pressures, underscoring the need to examine the ecohydrological implications of this climatic variability. Whereas precipitation has long been recognized as a key driver of landscape ecohydrology, understanding a site's hydraulic redistribution regime (the balance in downward and upward movement of water and the seasonality of these bidirectional flows) may be equally important to understanding moisture availability to vegetation in these dryland ecosystems. As a result, we linked measures of ecosystem-scale carbon exchange, overstory tree sap flux and leaf-level gas exchange to understory whole-plot and leaf-level carbon and water exchange within intact and trenched plots (isolating trees from grasses) in a riparian savanna ecosystem. We maintained measurements across 2 years with distinct precipitation regimes. We found that interannual precipitation variability yielded a categorical shift in the directionality and magnitude of the hydraulic redistribution regime—even within this single site. Additionally, we found that connectivity between overstory trees and understory grasses through hydraulic redistribution created a short period of competition within an average rain year but that facilitation of understory function by overstory trees was much greater and lasted longer during drier years. Together, these findings suggest that hydraulic redistribution can serve as a hydrologic buffer against interannual precipitation variability. Given current climate projections of more variable precipitation within and across years, understanding how hydraulic redistribution regimes vary through time will greatly enhance our capacity to anticipate future ecohydrological function.

KEYWORDS

drylands, hydraulic lift, interannual variability, leaf gas exchange, mesquite (*Prosopis velutina*), photosynthesis, sap flow, woody plant encroachment

1 | INTRODUCTION

Ecohydrologists have long strived to link above- and below-ground processes through the study of water exchange and movement across resource pools that drive abiotic and biotic processes.

Within drylands, where water drives episodic and seasonal pulses of productivity (Huxman et al., 2004; Noy-Meir, 1973), meteorological variability can create extreme 'blooms and busts' in ecosystem function (Luong et al., 2017; Potts, Barron-Gafford, Butterfield, Fay, & Hultine, 2019; Roque-Malo & Kumar, 2017). Understanding how an increasingly variable future climate might influence the biodiversity, function and goods and services provided by drylands is key to developing predictions about ecosystem behaviour across this expansive terrestrial biome (Kulmatiski & Beard, 2013b; Potts et al., 2019). Here, we focus on how the ecohydrological relationships between coexisting grasses and trees—characteristic plant functional types across drylands—are influenced by interannual precipitation variability. Questions of how these contrasting vegetative life forms coexist, how overstory trees may facilitate or hinder understory function, and how dynamic these relationships are in time and space have been driving ecohydrological research for decades (Barron-Gafford et al., 2017; D'Odorico, Caylor, Okin, & Scanlon, 2007; Lee et al., 2018; Maestre & Cortina, 2004; McCluney et al., 2012; Michalet et al., 2006; K. L. Yu & D'Odorico, 2015). In upland environments without access to groundwater, experimental manipulations and numerical modelling studies agree that grasses primarily use shallow soil water whereas deeper rooting trees have access to deeper soil water (Barron-Gafford et al., 2017; Holdo, 2013; Kulmatiski, Beard, Verweij, & February, 2010; Lee et al., 2018; Quijano & Kumar, 2015; Quijano, Kumar, Drewry, Goldstein, & Misson, 2012; Heinrich Walter, 1939; H. Walter, 1971; Ward, Wiegand, & Getzin, 2013). However, in bottomland locations, the potential for deeper-rooted plants to reliably access groundwater resources may alter the competition versus facilitation dynamic between trees and grasses (Barron-Gafford, Scott, Jenerette, Hamerlynck, & Huxman, 2013; Lee et al., *In review*; R.L. Scott et al., 2014). Research in these bottomland areas has shown that overstory trees do move water among soil layers to maintain their own hydraulic function (Hultine, Scott, Cable, Goodrich, & Williams, 2004) but the ecohydrology of grass-tree connections in riparian, groundwater-dependent systems remains understudied.

Movement of water by plants between 'shallow' and 'deep' soil moisture sources can blur predictions of how precipitation inputs translate to ecosystem function. Hydraulic redistribution (HR) is the bidirectional flow of water within plants, wherein roots serve as preferential, low-resistance pathways for water movement between wet and dry soil layers along soil water potential gradients (Kramer, 1932, 1933; Schulze et al., 1998). Depending on the moisture state above-ground and across the soil profile, HR can result in downward (hydraulic descent, HD) or upward (hydraulic lift, HL) water movement through plant roots and into the soil (as recently summarized by Barron-Gafford et al., 2017). Recently, model simulations based on field measurements have shown that water can even move both

downward and upward simultaneously to drier middle layers, if trees have access to groundwater below and moist soil layers near the surface due to rainfall—a concept termed convergent HR (Lee et al., *In review*). The ecohydrological implications of HR have been examined through both field measurements (Barron-Gafford et al., 2017; Kulmatiski & Beard, 2013a; Kulmatiski et al., 2010; Potts, Scott, Bayram, & Carbonara, 2010; I. Prieto, Pugnaire, & Ryel, 2014; I. Prieto & Ryel, 2014; Quijano et al., 2013; Schulze et al., 1998; Scott, Cable, & Hultine, 2008; Verweij, Higgins, Bond, & February, 2011; T. F. Yu et al., 2013) and numerical models (Alton, 2014; Amenu & Kumar, 2008; Fu et al., 2016; Gou & Miller, 2014; Lee et al., 2018; Quijano & Kumar, 2015; Ryel, Caldwell, Yoder, Or, & Leffler, 2002; K. L. Yu & D'Odorico, 2014), and numerous efforts have investigated the overstory-understory implications of HR on spatiotemporal patterns of species coexistence (K. L. Yu & D'Odorico, 2015; K. L. Yu & Foster, 2016; Zhu, Sun, Young, Caldwell, & Pan, 2015) and local biogeochemistry (Armas, Kim, Bleby, & Jackson, 2012; Cardon, Stark, Herron, & Rasmussen, 2013; Ludwig, Dawson, Prins, Berendse, & de Kroon, 2004; Priyadarshini et al., 2016; Quijano et al., 2012, 2013). Nevertheless, experimental studies where the ecohydrological impacts of HR are studied over multiple seasons or years are rare and generally lack physiological measures of plant function.

The ecohydrological implications of overstory-understory interactions can be contextualized by the hydraulic redistribution regime (HRR)—a unifying ecosystem metric, which captures the balance in downward and upward movement of water (HL relative to HD) and the seasonality of these bidirectional flows (Barron-Gafford et al., 2017; Lee et al., 2018). Across spatial gradients, overstory-understory interactions occur across a range of HRRs from hydraulic-lift dominated (positive HRR) to hydraulic-descent dominated (negative HRR), and these HRRs largely explain patterns of competition versus facilitation among members of a vegetation community. In places with an overall positive HRR (HL > HD) resulting from root access to deep soil moisture, previous studies have identified facilitative dynamics through water resource sharing (Quijano et al., 2013), leading to improved understory plant germination (Pang et al., 2013; Quijano et al., 2012), as well as plant nutrient and water status (Cardon et al., 2013; Matimati, Verboom, & Cramer, 2014; Quijano et al., 2013; Sun, Meng, Zhang, & Wan, 2014). In contrast, other locations have documented how a negative HRR (HD > HL) can foster competitive interactions where downward water movement by the overstory limits understory seedling establishment, constrains understory growth, or reduces photosynthetic capacity in response to seasonal precipitation (Barron-Gafford et al., 2017; Prieto, Padilla, Armas, & Pugnaire, 2011). Because most HRR studies have been conducted within a single year, understanding the effects of interannual HRR variability on associated plant functioning is limited.

A conceptual model proposed by Dohn et al. (2013) predicts that facilitative mechanisms increase in importance relative to competitive mechanisms with increasing environmental stress, that is, as one moves from a negative HRR towards a positive HRR. Based on this stress-gradient hypothesis, facilitative mechanisms should outweigh competitive interactions as the intensity of an abiotic stressor

increases along a spatial gradient, and this has generally been validated for tropical and temperate savannas (Dohn et al., 2013). Still, Dohn et al. (2013) found significant variation in the pivot point between facilitative and competitive interactions for overstory versus understory vegetation across different regions and within tropical and temperate savannas. To date, no study has quantified the ecophysiological impacts of overstory HR on understory photosynthetic function through time, in order to capture temporal variation in HRR and across spatial (leaf-to-ecosystem) scales within drylands.

Given predictions for increased precipitation variability for many dryland ecosystems (Collins et al., 2014; Melillo, Richmond, & Yohe, 2014; Pendergrass, Knutti, Lehner, Deser, & Sanderson, 2017), the HRR could vary substantially from year to year at a single place. Therefore, we asked two questions: (1) how do patterns of HR influence overstory and understory plant ecophysiological function across multiple years with different HRRs? And (2) how do these patterns vary with respect to metrics of individual overstory and understory plant function and at the whole-ecosystem scale? To address these questions, we experimentally manipulated tree understory plots in a semiarid riparian savanna to physically isolate understory grass patches from hydraulic connectivity with the overstory trees. In this riparian semiarid savanna, (i) the overstory has prolonged access to subsurface water, (ii) interannual and seasonal variation in water and carbon fluxes is attributed to the timing and magnitude of summer precipitation (Scott et al., 2004, 2008; Scott, Cable, Huxman, et al., 2008; Williams, Scott, Huxman, Goodrich, & Lin, 2006), (iii) isotopic studies have shown that understory grasses use water lifted by overstory trees (Yepez, Williams, Scott, & Lin, 2003) and (iv) understory grasses regularly green-up ahead of the onset of summer precipitation. As a result, we hypothesized that dry periods would be characterized by HL and would yield facilitation between the overstory and understory, because shallow-rooted understory grasses would have no other access to soil moisture, whereas the tree roots tap into a stable groundwater source. Further, we hypothesized that periods of HD would be relatively limited in this riparian system but could occur after large precipitation events. However, because this system would be predominantly characterized by upward HRR, we would rarely—if ever—find competition between overstory trees and understory grasses.

2 | MATERIALS AND METHODS

2.1 | Study site, species and experimental manipulation

The site is located on an alluvial terrace of the San Pedro River (31.6636°N, 110.1777°W; elevation: 1,200 m), approximately 12 km southwest of Tombstone, AZ, USA. The alluvial soils are mostly composed of sandy loams interspersed with layers of gravels and clays with a water table depth of around 10 m (Hultine et al., 2004). Velvet mesquite tree (*Prosopis velutina*) cover at this site is approximately 70%, with an understory primarily of sacaton bunchgrass (*Sporobolus*

wrightii) and various annual herbaceous species (Scott et al., 2004). Mesquite trees average 7 m in height, and previous studies have demonstrated that these trees tap into deeper groundwater at ~10 m (Hultine et al., 2004; Scott, Goodrich, et al., 2006; Scott, Shuttleworth, Goodrich, & Maddock, 2000). Bunchgrasses have relatively deep roots (~1.5–3 m), but they have not been found to access groundwater deeper than ~3 m (Scott et al., 2000; Scott, Huxman, et al., 2006) and therefore likely do not have groundwater access at this site. Mean annual precipitation (1971–2000) in the San Pedro valley ranges from 313 to 386 mm, with about 60% falling between late June through September during the North American Monsoon (Adams & Comrie, 1997; Barron-Gafford, Scott, Jenerette, Hamerlynck, & Huxman, 2012; R.L. Scott et al., 2014). The growing season generally lasts from mid-April through November and is principally regulated by freezing temperatures.

On May 11, 2016, we identified eight mesquite trees of average height and eight 2.0 × 2.0 m² grass plots on the south side of them, inserting rebar posts at the corners of each grass plot to ensure that repeat measurements through time were located at the same position; four of these trees and associated grass plots served as controls. For the four remaining plots, we established a 0.5 m buffer around each plot, creating a 4 m² treatment area. We prevented all potential HR into the plot by trenching to 1 m depth around the perimeter of the treatment area, thereby severing all shallow mesquite lateral roots that would have entered into the plot area, following the techniques used by Verweij et al. (2011) and Barron-Gafford et al. (2017). We then lined this trench with ground cover fabric (DeWitt Sunbelt weed fabric, Sikeston, MO, USA), which allowed water and air to pass through it but prevented regrowth of roots into the treatment plot.

2.2 | Ecosystem-scale micrometeorology and carbon dioxide exchange

We utilized the eddy covariance technique to monitor surface-atmosphere carbon dioxide (CO₂), water vapour and energy fluxes at the ecosystem (~1 km) scale. Briefly, we used a three-dimensional sonic anemometer (Model CSAT3, Campbell Scientific, Inc., Logan UT) and an open path infrared gas analyser (IRGA; Model LI-7500, LI-COR, Inc., Lincoln, NE) mounted at a height of 14 m above ground level at the top of a scaffolding tower to quantify 30-min averages of the net ecosystem exchange of CO₂ (NEE). We also measured air temperature, vapour pressure deficit (VPD), photosynthetically active radiation (PAR) and precipitation, and we monitored profiles of vadose zone soil moisture at multiple soil depths (5–30, 30–50 and 50–100 cm) and depth to groundwater using a colocated piezometer. In December 2016, we added an additional soil moisture profile associated with the control and treatment plots. We installed three soil moisture sensors (Model CS616, Campbell Scientific, Inc., Logan UT) at a slight angle to integrate across the 25–45 cm depth range, which is the rooting zone of the understory bunchgrass. At this same time, we had installed six Decagon MPS2 sensors (METER Group, Pullman, WA). Unfortunately, we had 100% failure in these instruments, and

the sensor array did not yield any usable data. As such, we illustrate the impacts of our trench treatment on soil water at the rooting depth of the grasses, but we cannot speak to the impacts in terms of water potential. We partitioned whole ecosystem NEE into its component processes of ecosystem photosynthesis, or gross ecosystem production (GEP) and ecosystem respiration (R_{eco}); detailed descriptions of the data collection and processing procedures at this site are available in Scott et al. (2014).

2.3 | Determination of HRR through sap flux measurements

We used the heat-ratio method (HRM), in which temperature probes are placed at equal distances upstream and downstream from a pulsed heat source to allow for measures of high, low and reverse flow rates within the xylem (Burgess et al., 2001; Burgess, Adams, Turner, White, & Ong, 2001; Hultine, Cable, Burgess, & Williams, 2003; Hultine et al., 2004; Scott, Cable, & Hultine, 2008). Following the protocol developed for an upland savanna site in the region (Barron-Gafford et al., 2017), we installed sap flow metres (SFM1, ICT International, Australia) in the taproot, two lateral roots and the stem of each of the four trees associated with the control plots to measure the heat transmitted upstream and downstream along each plant organ, in order to estimate the magnitude of sap flux (sap flow per unit time). The operation of the SFM1 sap flow sensors is described in detail by Barron-Gafford et al. (2017); briefly, each sensor consists of three 35 mm stainless steel probes, each spaced 5 mm apart. A filament in the centre produces heat, and the resultant heat flux is measured by two thermistors in the outer two probes. Sap flux was measured every 10 min. At the end of the experiment, we imposed zero flow conditions by drilling 35 mm deep by 13 mm wide holes upstream and downstream from the sap flux sensors and filling the holes with silicone caulk. This procedure allowed for measurement calibration to account for any thermal or physical asymmetry in the installation (Becker, 1998). These measurements within a single taproot and two lateral roots are representative of the magnitude and directionality of water movement through time but do not capture the entirety of water movement among and through the complete root system. As such, we use these data to understand shorter- and longer-term water movement but do not characterize a comprehensive water budget.

In this measurement framework, positive values indicate hydrological movement towards the stem and canopy of the tree, positive values in the taproot coupled with negative values in the lateral roots indicate HL of deep water to shallower soils and negative values in the taproot sap flux indicate HD (Barron-Gafford et al., 2017). In order to distinguish positive sap flux, which also supports transpiration, from that which signifies HL, we analysed nighttime data independent of the full diel data set, as nocturnal expression of water via lateral roots is the hallmark of HL (Caldwell & Richards, 1989). Across an annual cycle, a hydraulic-lift dominated year would be characterized by a positive HRR, whereas a hydraulic-descent dominated year would be characterized by a negative HRR. To examine patterns of HL or HD

within seasonal periods, we binned the data into dry premonsoon (2016: day of year [DOY] 140–182; 2017: DOY 152–185), wet monsoon (2016: DOY 183–300; 2017: DOY 186–304), postmonsoon/winter (2016:2017 DOY 300–60) and spring (2017: DOY 61–151) data (Table 1).

2.4 | Leaf-level physiological measurements of carbon dioxide and water exchange

We conducted measurements of leaf-level net photosynthesis (A_{net}) using a portable photosynthesis system (LI-6400, LI-COR, Lincoln, NE, USA). We used a red-blue light source (LI-6400-02b) attached to the leaf cuvette to provide a constant irradiance of $1,500 \mu\text{mol m}^{-2} \text{s}^{-1}$ and held the cuvette reference CO_2 constant at 400 ppm across all measurement dates. We set cuvette air temperature to match ambient conditions on each measurement date by first measuring air temperature with the cuvette's fine wire leaf thermocouple under open, shaded conditions prior to enclosing leaf samples. We conducted all measurements between 09:00 and 12:00 MST on fully unfurled south facing leaves of similar age. For each of the eight plots, we measured the overstory mesquite and two individuals of the bunchgrasses. We harvested all leaves within the $2 \times 3 \text{ cm}$ cuvette for gas exchange measurements and stored them in paper envelopes in a chilled cooler for transport to the lab so that we could correct our measurements on a per unit leaf area basis. After we obtained wet leaf mass, sample leaf area was determined using an LI-3100C area metre (LI-COR, Lincoln, NE, USA). Samples were then air-dried to obtain dry leaf mass (Barron-Gafford et al., 2012, 2013). We repeated these protocols on 11 measurement dates to capture environmental conditions across the spring, premonsoon, monsoon and postmonsoon seasons within 2016 and 2017.

2.5 | Understory carbon dioxide exchange

Following techniques similar to Hamerlynck et al. (2012, 2011) and others (Barron-Gafford et al., 2017; Huxman et al., 2004; Potts, Huxman, Scott, Williams, & Goodrich, 2006), we covered each plot with a $1.0 \times 1.0 \times 1.0 \text{ m}^3$ chamber of tightly sewn polyethylene held taut by a PVC pipe tent frame (Shelter Systems, Santa Cruz, CA, USA). We placed a small fan over the plot to ensure atmospheric mixing within the chamber, positioned the translucent chamber on the plot and then sealed the chamber base with a chain. This polyethylene material allowed $\sim 90\%$ of PAR to pass through onto the plots (Barron-Gafford et al., 2017; E.P. Hamerlynck et al., 2012). We allowed air to mix within the chamber for 30 s and then logged CO_2 , atmospheric pressure and air temperature (T) data every second for a minimum of 90 s using an open-path infrared gas analyser (LI-7500; LI-COR, Lincoln, NE, USA). We then removed the chamber, aerated it for $\sim 1 \text{ min}$, replaced and resealed the chamber over the same plot and shaded it with a blanket to repeat the same measurements in the dark, in order to estimate understory ecosystem respiration (R_{Under}).

TABLE 1 Directionality of sap flux movement, implications for plant and soil water and the percentage of nights characterized by hydraulic redistribution regime (average nighttime hydraulic lift [HL] vs. hydraulic descent [HD]) of the overstory mesquite vegetation

Taproot sap flux sign	Lateral root sap flux sign	Direction of net water movement	Ecohydrologic outcome	2016			2017		
				Premonsoon	Monsoon	Postmonsoon and winter	Spring	Premonsoon	Monsoon
+	+	Upward and inward	Plant soil-water extraction: water being pulled from deep and shallow soil layers	19	12	10	0	16	95
–	+	Downward and inward	HD: Water being pulled in laterally and moved down vertically	62	88	45	0	0	0
+	–	Upward and outward	HL: Water being moved up vertically and expressed out laterally	0	0	1	83	46	5
–	–	Downward and outward	Soil plant-water extraction: water being pulled from plant into soil	19	0	44	17	38	0

Note. Data are summarized for distinct seasonal periods of the dry premonsoon (2016: day of year [DOY] 140–182; 2017: DOY 152–185), wet monsoon (2016: DOY 183–300; 2017: DOY 186–304), postmonsoon/winter (2016:2017 DOY 300–60), and spring (2017: DOY 61–151).

As with the leaf-level measurements, we conducted all understory ecosystem measurements between 09:00 and 12:00 MST and measured the understory ecosystem CO₂ flux at all eight measurement plots each time we made the leaf-level measures described above. We estimated understory gross ecosystem productivity (GEP_{Under} ; in units of $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ ground area s}^{-1}$) from these measurements, where $GEP_{Under} = -1 * (NEE_{Under} - R_{Under})$ (E.P. Hamerlynck et al., 2012; Huxman et al., 2004; Potts, Huxman, Cable, et al., 2006).

2.6 | Measurements of soil carbon dioxide efflux

Within each of the eight plots described above, we permanently installed two soil gas flux measurement collars. Each 10.2 cm-diameter collar was inserted 5 cm into the soil to prevent sample contamination by ambient air. At each collar, we measured soil moisture integrated over 12 cm depth using a handheld water content sensor (HydroSense system, Campbell Scientific Inc., Logan, UT, USA), and soil temperature integrated over 10 cm depth using a temperature probe (Temp-100, OAKTON Instruments, Illinois, USA), as described by Barron-Gafford et al. (2014, 2017) and Barron-Gafford, Scott, Jenerette, and Huxman (2011). We measured rates of soil CO₂ efflux to the atmosphere (F_{soil} ; in units of $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ ground area s}^{-1}$) using a LI-8100 automated soil gas flux system outfitted with the 10-cm survey chamber (8,100–102; LI-COR, Lincoln, NE, USA). We repeated these measurements of F_{soil} on all of the measurement dates as the leaf-level measures of A_{net} and NEE_{Under} .

2.7 | Statistical analysis

We used an analysis of variance (ANOVA; Statistix v. 8.0, Analytical Software, Tallahassee, FL) to test for differences between control and treatment plots in terms of leaf-level net photosynthesis (A_{net}) within the individual trees and bunchgrasses, GEP_{Under} and F_{soil} for each of the measurement day. We denote any detected differences between treatments within each measurement date with an asterisk within the corresponding figure. On each of these 11 measurement days, we repeated A_{net} measurements on four mesquite and eight bunchgrasses per treatment, and we repeated GEP_{Under} and F_{soil} measurements on four plots per treatment. We used an α of 0.05.

3 | RESULTS

Cumulative precipitation in 2016 and 2017 was 243 and 313 mm, respectively, and the 2 years differed significantly in the timing and magnitude of precipitation events (Figure 1a). The year 2016 received precipitation more regularly throughout the growing season, whereas 78% of the annual precipitation was received during a 31-day period (DOY 185–215) in 2017, which was an otherwise drier year. The cumulative gross ecosystem productivity (GEP) was $1,176 \text{ g C m}^{-2}$ in 2016 and $1,374 \text{ g C m}^{-2}$ in 2017 (Figure 1b). During the more consistently rainy year of 2016, soil moisture within the upper 5–30 and 30–50 cm profiles illustrated the characteristic response to repeated wetting from warm-season rains (Figure 2a). Throughout the

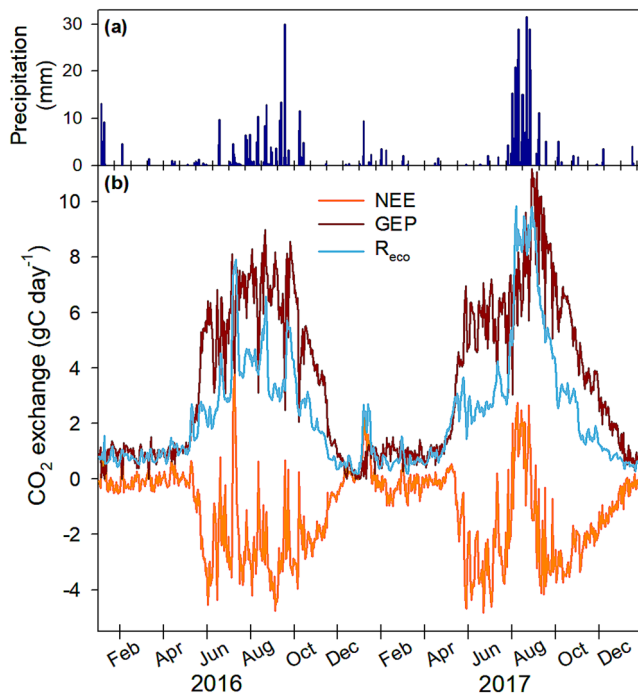


FIGURE 1 (a) Daily total precipitation at the study site in 2016 and 2017. (b) Daily average rates of the net ecosystem exchange of carbon dioxide (NEE), gross ecosystem productivity (GEP) and ecosystem respiration (R_{eco}). Negative NEE values correspond to ecosystem carbon gains

premonsoon and monsoon seasons, the average nighttime taproot sap flux was generally negative, indicating downward water movement (Figure 2c). At the same time, trunk sap flux was positive (indicating nocturnal water replenishment and/or transpiration), and

lateral root sap flux was positive, indicating sap movement towards the trunk. As a result, 2016 was predominantly characterized by HD (62% and 88% of the time during the premonsoon and monsoon seasons, respectively; Table 1), with little evidence of HL during the growing season. The same pattern of HD continued throughout the postmonsoon and wet winter into 2017. During the drier spring and premonsoon periods of 2017, the average daily lateral root sap flux was always negative, whereas the taproot sap flux was consistently positive (Figure 2), which is indicative of HL (83% and 46% of the time during the spring and premonsoon seasons, respectively; Table 1). This pattern was corroborated by soil moisture data that remained similar between control and trenched treatment plots until 20 March 2017 when soil moisture began to increase at the control plot (Figure 2b). Once summer monsoon rains arrived in mid-July 2017, soil moisture returned to comparable levels at the control and trenched treatment plots (Figure 2b), and sap flux movement corresponded to water extraction from both surface and deep layers 95% of the time (Table 1).

Rates of net leaf-level photosynthesis (A_{net}) within the overstory mesquite were similar prior to the onset of our trenching treatment that reduced the potential for HR (Figure 3a). Further, A_{net} did not differ between mesquite in control plots and those in trenched treatment plots, regardless of seasonal measurement period (Figure 3a). Rates of understory plot-level GEP_{Under} were similar prior to the onset of the trenching treatment and during the early 2016 growing season (Figure 3b). However, by August of the 2016 growing season, when HR was predominantly HD due to the availability of near-surface soil moisture from monsoon rains, rates of understory productivity within the trenched treatment plots (where HR was eliminated) were significantly greater than those in the control plots ($F_{4, 32} = 14.55$; $P \leq 0.0001$). There was no difference between control and treatment

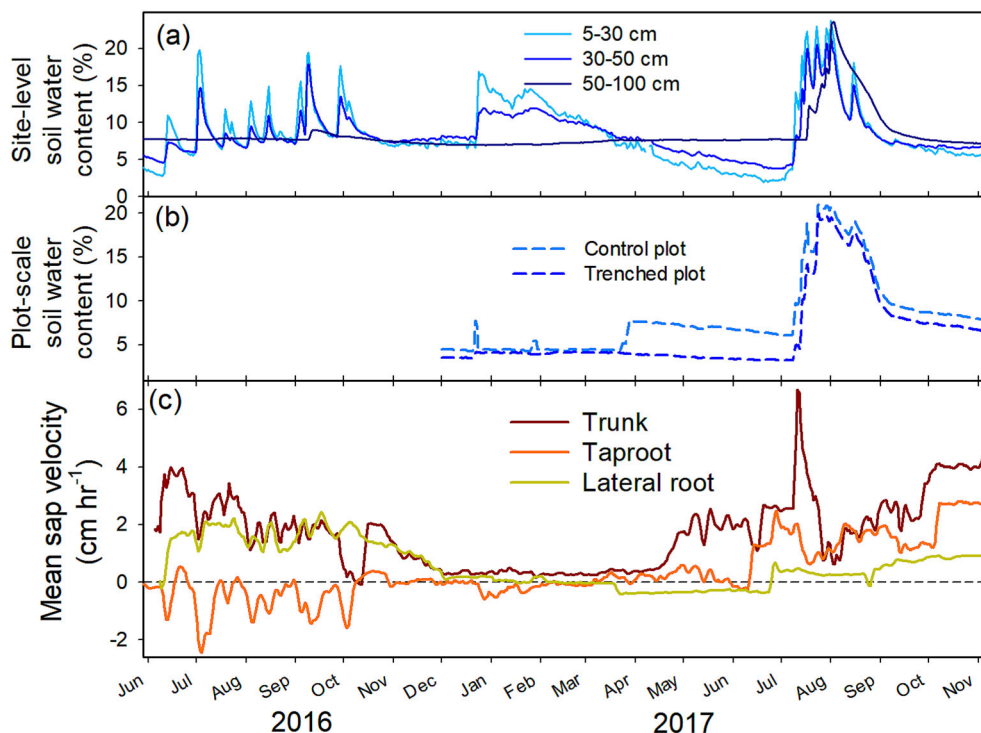
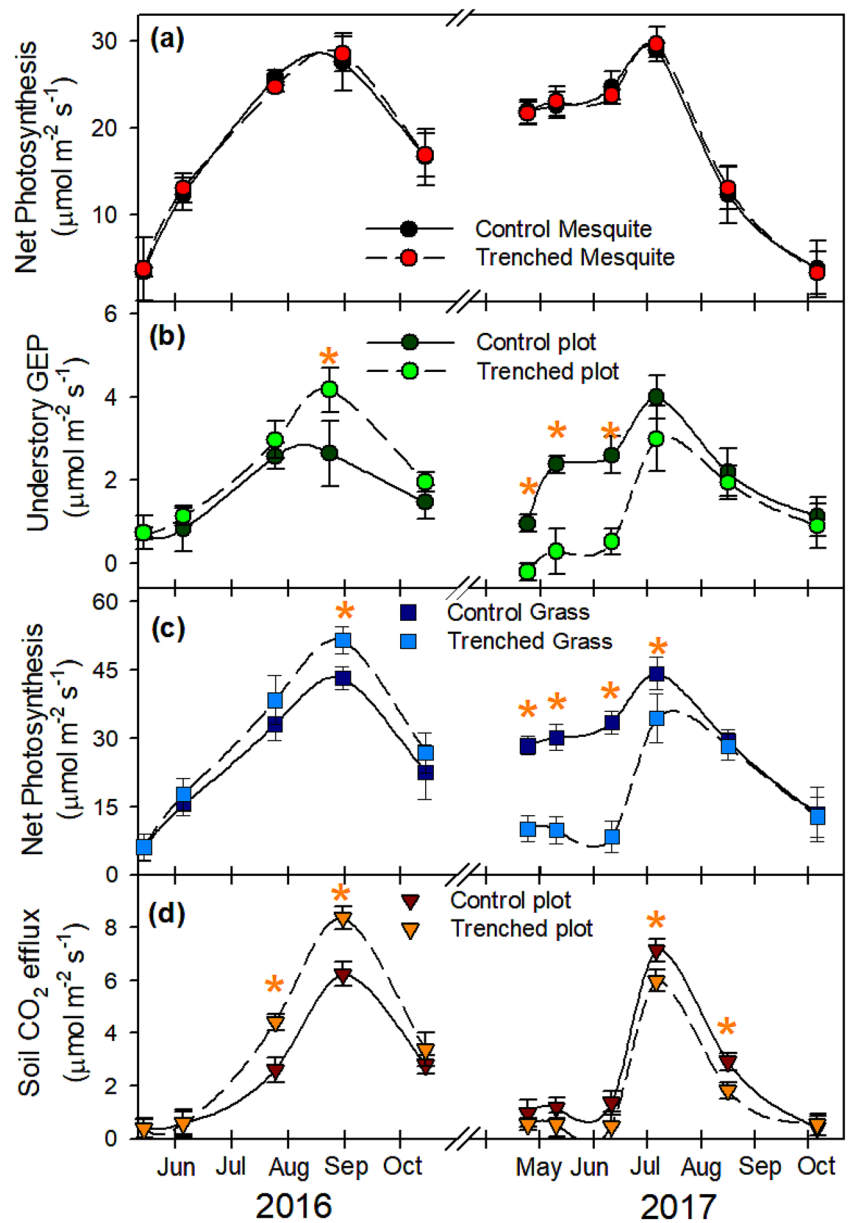


FIGURE 2 (a) Daily average soil water content across three profile depths for the control area. (b) Daily average soil water content within control and trenched treatment plots integrating across 25–45 cm depth. (c) Daily averages of nighttime trunk (red), taproot (orange) and lateral root (green) sap flux velocity in 2016 and 2017. Positive values in the roots indicate flow towards the tree base, and negative sap flux indicates flow away from the tree base. Positive values in the trunk indicate flow towards the canopy

FIGURE 3 Daily average (a) leaf-level net photosynthesis rates in overstory mesquite trees, (b) understory plot gross ecosystem productivity (GEP_{Under}), (c) leaf-level net photosynthesis rates of understory sacaton bunchgrasses and (d) soil CO_2 efflux within control and trenched plots where hydraulic redistribution was eliminated. Measurements were repeated across 11 separate days (five sampling dates in 2015 and six in 2016). Bars represent one standard error around the mean, and asterisks indicate significant differences based on ANOVA results ($P < 0.01$)



GEP_{Under} during the postmonsoon cool period. In contrast, during the drier spring, premonsoon and early-monsoon periods of 2017, when significant HL was occurring, GEP_{Under} was significantly greater in the control plots where connectivity with overstory mesquite allowed plants to take advantage of lifted water (Figure 3b). These differences in whole-understory productivity were consistent with the functional capacity of individual grasses, as we found concomitant differences in leaf-level rates of A_{net} between grasses in the control and trenched plots (Figure 3c).

Rates of soil CO_2 efflux were similarly near zero prior to the onset of trenching (Figure 3d). However, during the more consistently rainy, HD-dominated 2016 growing season, rates of soil CO_2 efflux in trenched plots significantly exceeded the controls. We found no differences between control and treatment plots during the 2016 postmonsoon period when rates of soil CO_2 efflux declined or

throughout the 2017 spring and premonsoon. Conversely, during the drier 2017 growing season when trees were facilitating HL, rates of soil CO_2 efflux were greater in the untrenched controls than in the trenched plots where connectivity had been eliminated.

4 | DISCUSSION

The amount and timing of rainfall drives the net direction (HL vs. HD) and cumulative rates of HR by way of root-zone soil water infiltration (e.g., Yu & D'Odorico, 2014). All of this water exchange between roots and the surrounding soil affects aboveground and belowground eco-hydrological dynamics and exchange of energy and nutrients (Brooks, Meinzer, Coulombe, & Gregg, 2002; Brooks, Meinzer, Warren, Domec, & Coulombe, 2006; Burgess, Adams, Turner,

Beverly, et al., 2001; Burgess, Adams, Turner, & Ong, 1998; Burgess, Adams, Turner, White, & Ong, 2001; Burgess, Pate, Adams, & Dawson, 2000; Caldwell & Richards, 1989; Dawson, 1996; Hultine et al., 2004; Muler, van Etten, Stock, Howard, & Froend, 2018; White & Smith, 2020). Here, we demonstrate that this dynamic movement of water among soil horizons and plants can provide significant hydrologic buffering capacity to both individual plants and whole ecosystems, particularly those that experience episodic precipitation or may be subject to increased interannual precipitation variability because of a changing climate. Although these benefits of HR have been previously demonstrated in terms of the capacity to increase productivity and plant transpiration (Amenu & Kumar, 2008; Barron-Gafford et al., 2017; Quijano et al., 2012; Scott, Cable, & Hultine, 2008), buffer the loss of soil moisture loss dry periods (Bleby, McElrone, & Jackson, 2010; Muler et al., 2018) and extended individual growing seasons (Fu et al., 2016; Scott, Cable, & Hultine, 2008; Ryel et al., 2002; Wu, Fu, Wu, & Zhang, 2020), multiyear studies are rare. We specifically linked measures of water movement within vegetation stems and roots, meteorological data and measurements of leaf- and understory-ecosystem carbon dioxide exchange to determine a riparian savanna's HRR across multiple years of distinct precipitation amounts and timing. In contrast to our initial hypotheses, these differences in precipitation translated to variation in the annual-scale HRR and the resulting impacts on overstory-understory relations. This finding suggests that HR within overstory trees may provide some hydrologic buffering capacity to dryland ecosystems that pivot between having enough surface and subsurface water and being constrained by persistent moisture stress, yielding a novel perspective on the variability of ecosystem functioning.

4.1 | Interannual variability in HRR and the impacts on plant function

Whereas 2016 was an average year in terms of the timing and cumulative amount of precipitation, 2017 was characterized by a prolonged dry period that stretched across much of the cool season, spring and premonsoon periods before an anomalously late start of the monsoon season (Figure 1). For the 2016 hydrological year, wet conditions beginning in fall 2015 extended through 2016 and created a gradient of decreasing soil moisture with vadose zone depth. As a result, the 2016 HRR of this system was dominated by HD, in which the trees relocated and stored abundant near-surface moisture deeper into the vadose zone (Figure 2; Table 1). This pattern suggests that downward hydrological redistribution effectively stores moisture in the vadose zone, largely below the roots of grasses and the depth of rainfall infiltration, but above the water table in this riparian system, as evidenced by deep vadose zone soil moisture observations of Hultine et al. (2004) and the modelling work of Lee et al. (In review). In fact, Lee et al. (In review) note that although the average directional flow in 2016 was HD, sap flow was likely following what is termed convergent HR, wherein water was simultaneously moving both downward from the surface and upward from the capillary fringe to drier

intermediate soil depths due to the combination of groundwater below and moist soil layers near the surface after rainfall. We found a completely different HRR in 2017, when the foresummer was characterized by drought, and the opposite vertical hydrologic gradient was created with more soil moisture in the deep vadose zone or capillary fringe than in the near surface. As a result, the 2017 HRR was largely opposite to 2016 and was dominated by upward HL, in which the trees relocated abundant vadose zone water to the near-surface and intermediate soil depths to support ecosystem function. This interannual variation contrasts previous work in an upland savanna that experienced predictable patterns of surface wetting and drying after individual rains and associated periods of HD and HL, respectively (Barron-Gafford et al., 2017; Lee et al., 2018). Across the entire year, that water-limited site was characterized as having a HD-dominated HRR, such that there was a predominantly competitive interaction between the overstory and understory. The lack of 'sharing' of lifted water by overstory plants resulted in persistent precipitation dependency whereby upland savanna understory vegetation remained dormant until the summer rains stimulated function and increased leaf area (Hamerlynck, Scott, Moran, Keefer, & Huxman, 2010; Ignace, Huxman, Weltzin, & Williams, 2007; Potts et al., 2019; Potts, Huxman, Scott, et al., 2006; Scott, Cable, & Hultine, 2008). No research to date has documented the type of categorical shift in a single site's HRR through time as shown here.

Treatment impacts varied between the overstory and understory. Removing access to 4 m² of soil surface area (the trenched plot) near the base of each treatment mesquite tree (roughly 20% of the below canopy/1 m deep rooting area) did not change rates of mesquite photosynthesis at any measurement point throughout the 2 years of this study (Figure 3), which underscores a relative insensitivity of these trees to precipitation inputs. This experimental conclusion is supported by prior work based on eddy covariance measurements at this site (Scott et al., 2014; Scott, Huxman, et al., 2006) showing that connectivity to subsurface water decouples tree function from precipitation (as measured by ET and GEP). Additionally, despite the delayed arrival of growing season precipitation in 2017, rates of daytime photosynthetic assimilation in the mesquite overstory were equal to those in 2016 when precipitation was abundant (Figure 3a). That ecosystem function was independent of precipitation in this semiarid riparian setting starkly contrasts the paradigm of upland areas where function is tied to rainfall (Barron-Gafford et al., 2013, 2014; Hamerlynck et al., 2010; Potts, Scott, Cable, Huxman, & Williams, 2008).

Disrupting hydraulic connectivity significantly impacted understory grasses. During the more frequent rains of the 2016 growing season, when the majority of the trees' HR activity was HD, we found greater photosynthetic function for understory grasses in trenched plots at both the individual leaf and whole understory ecosystem scales. However, we observed the opposite pattern in 2017 when the majority of the overstory trees' HR activity was HL. As a result of our treatment, understory grasses within trenched plots did not have access to lifted water, and accordingly, photosynthetic function in these grasses was significantly reduced (Figure 3b,c). The subsequent

convergence in A_{net} between control and trenched trees could have originated from increasing storm frequencies that curtailed moisture limitation (Figures 2 and 3) or an increase in fine root biomass that captured water resources more effectively. By continuing our measurements throughout distinct periods of moisture surplus (2016) and deficit (2017) on the landscape, we learned that a site's HRR can be dynamic through time.

4.2 | Impacts of overstory and understory plant function on ecosystem-scale dynamics

Despite the sensitivity of understory vegetation to the variable HR and precipitation regimes across years, this tree-dominated ecosystem appears to be well buffered against gaps in precipitation inputs. For example, in 2017, the ecosystem received roughly one third the precipitation in the early growing season as it did in 2016, but cumulative gross ecosystem productivity (GEP) during this time period was actually greater in 2017 ($2016 = 351 \text{ g C m}^{-2}$ vs. $2017 = 439 \text{ g C m}^{-2}$; Figure 1). Scott et al. (2014), Scott, Huxman, et al. (2006) had previously noted that connectivity to subsurface water could decouple a tree-dominated ecosystem's function from precipitation—even within a semiarid riparian setting. Due to otherwise high rates of evapotranspiration, deep soil water infiltration from precipitation is generally restricted to cool season and winter periods in the south-western USA (Barron-Gafford et al., 2017; McAfee & Russell, 2008; Scott et al., 2000). Here, we show that mesquite trees in a riparian savanna ecosystem are capable of supplementing deep soil moisture by way of HD that can be utilized in drier years and outside of the typical summer monsoon precipitation season (D'Odorico et al., 2007; Lee et al., In review; Yu & D'Odorico, 2015). As such, this work suggests that interannual carryover of moisture through facultative shifts in HRR may serve as a potential mechanism for this decoupling and buffering against interannual variability in precipitation.

The stress gradient hypothesis suggests that drier landscapes should see more facilitative effects on the understory due to lifted water by overstory trees (Dohn et al., 2013). Consistent with this hypothesis, we did find that *drier years* yielded facilitative interactions between overstory trees and understory grasses, whereas years with greater precipitation created patterns characterized by HD and competition between these same plant functional types. Based on a meta-analysis, Dohn et al. (2013) noted that drier temperate savannas (those that receive less than $\sim 480 \text{ mm}$) typically experience net facilitative interaction (improved water relations) if the trees have access to a deeper water source but also that there is significant variability among individual savanna sites. The interannual variability in HRR documented here may speak to some of the complex interactions that determine net facilitative or competitive interaction among trees and grasses. As a result, we add to the call for multiyear tracking of sap flux in both stems and roots, as well as empirical studies that evaluate understory production, in order to more fully understand and even predict competition–facilitation relationships under projected climate change scenarios.

Simultaneous measurement of component fluxes provided insights into the close relationship between rates of understory leaf-level photosynthesis and soil CO_2 efflux. Overall, our multiyear measurements strongly suggest that grass root respiration makes up a significant proportion of the total soil CO_2 efflux (Figure 3c,d). In 2016, we found elevated rates of soil CO_2 efflux in the trenched plots, paralleling the elevated rates of photosynthetic uptake by the understory grasses at the leaf and ecosystem level. This pattern was reversed in 2017 when the control plots received HL water that stimulated both understory photosynthesis and soil CO_2 efflux in excess of the treatment plots. A tight connectivity between understory uptake and soil CO_2 efflux has been well documented in semiarid systems through measurements and modelling efforts (Barron-Gafford et al., 2011, 2014; Cable et al., 2012, 2013), but this link between overstory HRR, understory plant function and the resulting interannual variability in soil CO_2 efflux has not been previously documented. These findings suggest that a site's annual HRR likely modulates a significant portion of ecosystem respiration. Coupled to recent experimental evidence about the impact of plant functional type, interstorm duration and antecedent soil moisture on diurnal patterns of soil CO_2 efflux (Dusza et al., 2020), the current results support that knowledge about a site's HRR variability may also influence the fidelity of numerical soil CO_2 efflux predictions.

5 | CONCLUSION

The precipitation regime (the timing and magnitude of precipitation) has long been recognized as a key driver of landscape ecohydrology, but we demonstrate that understanding a site's HRR (the balance in downward and upward movement of water and the seasonality of these bidirectional flows) is equally important. We set out to address two questions: (1) how do patterns of HR influence overstory and understory plant ecophysiological function across multiple years with different HRRs? And (2) how do these patterns vary with respect to metrics of individual overstory and understory plant function and at the whole-ecosystem scale? Surprisingly, we found that interannual variability in the precipitation regime yielded a categorical shift in the directionality and magnitude of the HRR—even within a single site. This novel finding supported our first hypotheses that dry periods would be characterized by HL but contrasted our second hypothesis that periods of HD would be relatively limited in this riparian system. Our experimental manipulation further illustrated that connectivity between overstory trees and understory grasses through HR created a short period of competition within an average rain year but that overstory facilitation of understory function was much greater and lasted longer during drier years. Together, these findings suggest that HR can serve as a hydrologic buffer against interannual variation in precipitation. Moving forward, the current study demonstrates that a process-based understanding of hydrological context is imperative to anticipate the HRR of a system, as evidenced by HRR differences between upland and riparian semiarid savanna sites. These findings suggest that riparian savannas

may increasingly shift towards a HL-dominated HRR under projected drier conditions, facilitating understory vegetation. Conversely, under prolonged, multiyear dry periods, which are likely to lower the water table, the increased costs associated with maintaining root structures to access subsurface water resources might result in a shift towards a more competitive HD-dominated regime, as is currently the case for upland savannas.

ACKNOWLEDGEMENTS

This project and data collection were supported by NSF Awards EAR 1417101, EAR 1417444, EAR 1331408, EAR 1331906 and ACI 1261582, as well as by a Marie Curie International Outgoing Fellowship within the 7th European Community Framework Programme, DIESEL project (No. 625988). Additional funding support was provided by the Water, Environmental, and Energy Solutions (WEES) initiative at the University of Arizona Institute of the Environment, the University of Arizona Office of the Vice President of Research and the Phileology Foundation of Ft. Worth, Texas. Funding for the continued operation of the AmeriFlux site is provided by Department of Energy's Office of Science and Department of Agriculture. All data used in this study are freely available by contacting the corresponding author. The authors wish to thank R. Bryant (USDA-ARS) for his careful operation and maintenance of the field measurement devices. EPSC was supported by the Marie Curie International Outgoing Fellowship within the 7th European Community Framework Programme, Division of Earth Sciences.

CONFLICT OF INTEREST

The authors declare no conflicts of interest in this study.

AUTHOR CONTRIBUTIONS

G. B.-G., E. P. H., P. K. and R. L. S. planned and designed the research. G. B.-G., R. L. S., E. P. S. C., R. L. M., E. L., L. S., E. P. S. C. and P. M. performed experiments and conducted fieldwork, and G. B.-G., R. L. M., P. M. and N. T. analysed data. G. B.-G. wrote the manuscript with thoughtful input and revisions from all coauthors.

DATA AVAILABILITY STATEMENT

All data are available upon request.

ORCID

Greg A. Barron-Gafford  <https://orcid.org/0000-0003-1333-3843>

John F. Knowles  <https://orcid.org/0000-0002-3697-9439>

Enrique P. Sanchez-Cañete  <https://orcid.org/0000-0003-0482-6726>

Rebecca L. Minor  <https://orcid.org/0000-0003-1253-6219>

Esther Lee  <https://orcid.org/0000-0002-5659-4800>

Newton Tran  <https://orcid.org/0000-0003-3856-5480>

Patrick Murphy  <https://orcid.org/0000-0002-4918-3376>

Erik P. Hamerlynck  <https://orcid.org/0000-0001-6482-7101>

Praveen Kumar  <https://orcid.org/0000-0002-4787-0308>

Russell L. Scott  <https://orcid.org/0000-0003-2987-5380>

REFERENCES

- Adams, D. K., & Comrie, A. C. (1997). The North American monsoon. *Bulletin of the American Meteorological Society*, 78, 2197–2213. [https://doi.org/10.1175/1520-0477\(1997\)078%3C2197:TNAM%3E2.0.CO;2](https://doi.org/10.1175/1520-0477(1997)078%3C2197:TNAM%3E2.0.CO;2)
- Alton, P. B. (2014). Reconciling simulations of seasonal carbon flux and soil water with observations using tap roots and hydraulic redistribution: A multi-biome FLUXNET study. *Agricultural and Forest Meteorology*, 198, 309–319. <https://doi.org/10.1016/j.agrformet.2014.08.019>
- Amenu, G. G., & Kumar, P. (2008). A model for hydraulic redistribution incorporating coupled soil-root moisture transport. *Hydrology and Earth System Sciences*, 12, 55–74. <https://doi.org/10.5194/hess-12-55-2008>
- Armas, C., Kim, J. H., Bleby, T. M., & Jackson, R. B. (2012). The effect of hydraulic lift on organic matter decomposition, soil nitrogen cycling, and nitrogen acquisition by a grass species. *Oecologia*, 168(1), 11–22. <https://doi.org/10.1007/s00442-011-2065-2>
- Barron-Gafford, G. A., Cable, J. M., Bentley, L. P., Scott, R. L., Huxman, T. E., Jenerette, G. D., & Ogle, K. (2014). Quantifying the timescales over which exogenous and endogenous conditions affect soil respiration. *New Phytologist*, 202(2), 442–454. <https://doi.org/10.1111/nph.12675>
- Barron-Gafford, G. A., Sanchez-Canete, E. P., Minor, R. L., Hendryx, S. M., Lee, E., Sutter, L. F., ... Scott, R. L. (2017). Impacts of hydraulic redistribution on grass-tree competition vs facilitation in a semi-arid savanna. *New Phytologist*, 215(4), 1451–1461. <https://doi.org/10.1111/nph.14693>
- Barron-Gafford, G. A., Scott, R. L., Jenerette, G. D., Hamerlynck, E. P., & Huxman, T. E. (2012). Temperature and precipitation controls over leaf- and ecosystem-level CO₂ flux along a woody plant encroachment gradient. *Global Change Biology*, 18, 1389–1400. <https://doi.org/10.1111/j.1365-2486.2011.02599.x>
- Barron-Gafford, G. A., Scott, R. L., Jenerette, G. D., Hamerlynck, E. P., & Huxman, T. E. (2013). Landscape and environmental controls over leaf and ecosystem carbon dioxide fluxes under woody plant expansion. *Journal of Ecology*, 101(6), 1471–1483. <https://doi.org/10.1111/1365-2745.12161>
- Barron-Gafford, G. A., Scott, R. L., Jenerette, G. D., & Huxman, T. E. (2011). The relative controls of temperature, soil moisture, and plant functional group on soil CO₂ efflux at diel, seasonal, and annual scales. *Journal of Geophysical Research - Biogeosciences*, 116, G01023. <https://doi.org/10.1029/2010JG001442>
- Becker, P. (1998). Limitations of a compensation heat pulse velocity system at low sap flow: Implications for measurements at night and in shaded trees. *Tree Physiology*, 18(3), 177–184. <https://doi.org/10.1093/treephys/18.3.177>
- 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 & Environment*, 33(12), 2132–2148. <https://doi.org/10.1111/j.1365-3040.2010.02212.x>
- Brooks, R., Meinzer, F. C., Coulombe, R., & Gregg, J. (2002). Hydraulic redistribution of soil water during summer drought in two contrasting Pacific northwest coniferous forests. *Tree Physiology*, 22, 1107–1117. <https://doi.org/10.1093/treephys/22.15-16.1107>
- Brooks, R., Meinzer, F. C., Warren, J. M., Domec, J. C., & Coulombe, R. (2006). Hydraulic redistribution in a Douglas-fir forest: Lessons from system manipulations. *Plant, Cell and Environment*, 29(1), 138–150. <https://doi.org/10.1111/j.1365-3040.2005.01409.x>
- Burgess, S. S., Adams, M. A., Turner, N. C., & Ong, C. K. (1998). The redistribution of soil water by tree root systems. *Oecologia*, 115(3), 306–311. <https://doi.org/10.1007/s004420050521>
- Burgess, S. S., Pate, J. S., Adams, M. A., & Dawson, T. E. (2000). Seasonal water acquisition and redistribution in the Australian woody phreatophyte, *Banksia prionotes*. *Annals of Botany*, 85(2), 215–224. <https://doi.org/10.1006/anbo.1999.1019>

- Burgess, S. S. O., Adams, M. A., Turner, N. C., Beverly, C. R., Ong, C. K., Khan, A. A. H., & Bleby, T. M. (2001). An improved heat pulse method to measure low and reverse rates of sap flow in woody plants. *Tree Physiology*, 21(9), 589–598. <https://doi.org/10.1093/treephys/21.9.589>
- Burgess, S. S. O., Adams, M. A., Turner, N. C., White, D. A., & Ong, C. K. (2001). Tree roots: Conduits for deep recharge of soil water. *Oecologia*, 126(2), 158–165. <https://doi.org/10.1007/s004420000501>
- Cable, J. M., Barron-Gafford, G. A., Ogle, K., Pavao-Zuckerman, M. A., Scott, R. L., Williams, D. G., & Huxman, T. E. (2012). Shrub encroachment alters sensitivity of soil respiration to temperature and moisture. *Journal of Geophysical Research-Biogeosciences*, 117(11). <https://doi.org/10.1029/2011jg001757>
- Cable, J. M., Ogle, K., Barron-Gafford, G. A., Bentley, L. P., Cable, W. L., Scott, R. L., ... Huxman, T. E. (2013). Antecedent conditions influence soil respiration differences in shrub and grass patches. *Ecosystems*, 16(7), 1230–1247. <https://doi.org/10.1007/s10021-013-9679-7>
- Caldwell, M. M., & Richards, J. H. (1989). Hydraulic lift: Water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia*, 79(1), 1–5. <https://doi.org/10.1007/bf00378231>
- Cardon, Z. G., Stark, J. M., Herron, P. M., & Rasmussen, J. A. (2013). Sagebrush carrying out hydraulic lift enhances surface soil nitrogen cycling and nitrogen uptake into inflorescences. *Proceedings of the National Academy of Sciences of the United States of America*, 110(47), 18988–18993. <https://doi.org/10.1073/pnas.1311314110>
- Collins, M., Knutti, R., Arblaster, J., Dufresne, J.-L., Fichet, T., Friedlingstein, P., ... Zickfeld, K. (2014). Long-term climate change: Projections, Commitments and Irreversibility.
- Dawson, T. E. (1996). Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: The roles of tree size and hydraulic lift. *Tree Physiology*, 16(527 1-2), 263–272. <https://doi.org/10.1093/treephys/16.1-2.263>
- 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-Biogeosciences*, 112(G4). <https://doi.org/10.1029/2006jg000379>
- Dohn, J., Dembele, F., Karembe, M., Moustakas, A., Amevor, K. A., & Hanan, N. P. (2013). Tree effects on grass growth in savannas: Competition, facilitation and the stress-gradient hypothesis. *Journal of Ecology*, 101(1), 202–209. <https://doi.org/10.1111/1365-2745.12010>
- Dusza, Y., Sánchez-Cañete, E. P., Le Galliard, J.-F., Ferriere, R., Chollet, S., Massol, F., ... Barron-Gafford, G. A. (2020). Biotic soil-plant interaction processes explain most of hysteretic soil CO₂ efflux response to temperature in cross-factorial mesocosm experiment. *Nature Scientific Reports*, 10, 11(905, 1). <https://doi.org/10.1038/s41598-019-55390-6>
- Fu, C. S., Wang, G. L., Goulden, M. L., Scott, R. L., Bible, K., & Cardon, Z. G. (2016). Combined measurement and modeling of the hydrological impact of hydraulic redistribution using CLM4.5 at eight AmeriFlux sites. *Hydrology and Earth System Sciences*, 20(5), 2001–2018. <https://doi.org/10.5194/hess-20-2001-2016>
- Gou, S., & Miller, G. (2014). A ground-water-soil-plant-atmosphere continuum approach for modelling water stress, uptake, and hydraulic redistribution in phreatophytic vegetation. *Ecohydrology*, 7(3), 1029–1041. <https://doi.org/10.1002/eco.1427>
- Hamerlynck, E. P., Scott, R. L., Barron-Gafford, G. A., Cavanaugh, M. L., Moran, S. M., & Huxman, T. E. (2012). Cool-season whole-plant gas exchange of exotic and native semiarid bunchgrasses. *Plant Ecology*, 213(8), 1229–1239. <https://doi.org/10.1007/s11258-012-0081-x>
- Hamerlynck, E. P., Scott, R. L., Moran, M. S., Keefer, T. O., & Huxman, T. E. (2010). Growing season ecosystem and leaf-level gas exchange of an exotic and native semiarid bunchgrass. *Oecologia*, 163(3), 561–570. <https://doi.org/10.1007/s00442-009-1560-1>
- Hamerlynck, E. P., Scott, R. L., Moran, M. S., Schwander, A. M., Connor, E., & Huxman, T. E. (2011). Inter- and under-canopy soil water, leaf-level and whole-plant gas exchange dynamics of a semi-arid perennial C-4 grass. *Oecologia*, 165(1), 17–29. <https://doi.org/10.1007/s00442-010-1757-3>
- Holdo, R. M. (2013). Revisiting the two-layer hypothesis: Coexistence of alternative functional rooting strategies in savannas. *Plos One*, 8(8). <https://doi.org/10.1371/journal.pone.0069625>
- Hultine, K. R., Cable, W. L., Burgess, S. S. O., & Williams, D. G. (2003). Hydraulic redistribution by deep roots of a Chihuahuan Desert phreatophyte. *Tree Physiology*, 23(5), 353–360. <https://doi.org/10.1093/treephys/23.5.353>
- Hultine, K. R., Scott, R. L., Cable, W. L., Goodrich, D. C., & Williams, D. G. (2004). Hydraulic redistribution by a dominant, warm-desert phreatophyte: Seasonal patterns and response to precipitation pulses. *Functional Ecology*, 18(4), 530–538. <https://doi.org/10.1111/j.0269-8463.2004.00867.x>
- Huxman, T. E., Snyder, K. A., Tissue, D., Leffler, A. J., Ogle, K., Pockman, W. T., ... Schwinning, S. (2004). Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia*, 141(2), 254–268. <https://doi.org/10.1007/s00442-004-1682-4>
- Ignace, D. D., Huxman, T. E., Weltzin, J. F., & Williams, D. G. (2007). Leaf gas exchange and water status responses of a native and non-native grass to precipitation across contrasting soil surfaces in the Sonoran Desert. *Oecologia*, 152(3), 401–413. <https://doi.org/10.1007/s00442-007-0670-x>
- Kramer, P. J. (1932). The absorption of water by root systems of plants. *American Journal of Botany*, 19(2), 148–164. <https://doi.org/10.2307/2436318>
- Kramer, P. J. (1933). The intake of water through dead root systems and its relation to the problem of absorption by transpiring plants. *American Journal of Botany*, 20(7), 481–492. <https://doi.org/10.2307/2436237>
- Kulmatiski, A., & Beard, K. H. (2013a). Root niche partitioning among grasses, saplings, and trees measured using a tracer technique. *Oecologia*, 171(1), 25–37. <https://doi.org/10.1007/s00442-012-2390-0>
- Kulmatiski, A., & Beard, K. H. (2013b). Woody plant encroachment facilitated by increased precipitation intensity. *Nature Climate Change*, 3(9), 833–837. <https://doi.org/10.1038/nclimate1904>
- Kulmatiski, A., Beard, K. H., Verweij, R. J. T., & February, E. C. (2010). A depth-controlled tracer technique measures vertical, horizontal and temporal patterns of water use by trees and grasses in a subtropical savanna. *New Phytologist*, 188(1), 199–209. <https://doi.org/10.1111/j.1469-8137.2010.03338.x>
- Lee, E., Kumar, P., Barron-Gafford, G. A., Hendryx, S. M., Sanchez-Cañete, E. P., Minor, R. L., ... Scott, R. L. (2018). Impact of hydraulic redistribution on multispecies vegetation water use in a semiarid savanna ecosystem: An experimental and modeling synthesis. *Water Resources Research*, 54(6), 4009–4027. <https://doi.org/10.1029/2017wr021006>
- Lee, E., Kumar, P., Knowles, J. F., Minor, R. L., Tran, N., Barron-Gafford, G. A., & Scott, R. L. (In review). Convergent hydraulic redistribution and groundwater access supported facilitative dependency between trees and grasses in a semi-arid environment. *Water Resources Research*.
- Ludwig, F., Dawson, T. E., Prins, H. H. T., Berendse, F., & de Kroon, H. (2004). Below-ground competition between trees and grasses may overwhelm the facilitative effects of hydraulic lift. *Ecology Letters*, 7(8), 623–631. <https://doi.org/10.1111/j.1461-0248.2004.00615.x>
- Luong, T. M., Castro, C. L., Chang, H. I., Lahmers, T., Adams, D. K., & Ochoa-Moya, C. A. (2017). The more extreme nature of north American monsoon precipitation in the southwestern United States as revealed by a historical climatology of simulated severe weather events. *Journal of Applied Meteorology and Climatology*, 56(9), 2509–2529. <https://doi.org/10.1175/jamc-d-16-0358.1>
- Maestre, F. T., & Cortina, J. (2004). Do positive interactions increase with abiotic stress? - a test from a semi-arid steppe. *Proceedings of the Royal*

- Society B-Biological Sciences*, 271, S331–S333. <https://doi.org/10.1098/rsbl.2004.0181>
- Matimati, I., Verboom, G. A., & Cramer, M. D. (2014). Do hydraulic redistribution and nocturnal transpiration facilitate nutrient acquisition in *Aspalathus linearis*? *Oecologia*, 175(4), 1129–1142. <https://doi.org/10.1007/s00442-014-2987-6>
- McAfee, S. A., & Russell, J. L. (2008). Northern Annular Mode impact on spring climate in the western United States. *Geophysical Research Letters*, 35, L17701. <https://doi.org/10.1029/2008GL034828>
- McCluney, K. E., Belnap, J., Collins, S. L., Gonzalez, A. L., Hagen, E. M., Holland, J. N., ... Wolf, B. O. (2012). Shifting species interactions in terrestrial dryland ecosystems under altered water availability and climate change. *Biological Reviews*, 87(3), 563–582. <https://doi.org/10.1111/j.1469-185X.2011.00209.x>
- Melillo, J. M., Richmond, T. C., & Yohe, G. W. (2014). (Eds) *Climate change impacts in the United States: The third National Climate Assessment*. U.S. Global Change Research Program, 841 pp. <https://doi.org/10.7930/J0Z31WJ2>
- Michalet, R., Brooker, R. W., Cavieres, L. A., Kikvidze, Z., Lortie, C. J., Pugnaire, F. I., ... Callaway, R. M. (2006). Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters*, 9(7), 767–773. <https://doi.org/10.1111/j.1461-0248.2006.00935.x>
- Muler, A. L., van Etten, E. J. B., Stock, W. D., Howard, K., & Froend, R. H. (2018). Can hydraulically redistributed water assist surrounding seedlings during summer drought? *Oecologia*, 187(3), 625–641. <https://doi.org/10.1007/s00442-018-4158-7>
- Noy-Meir, I. (1973). Desert ecosystems: Environment and producers. *Annual Review of Ecology and Systematics*, 4, 25–51. <https://doi.org/10.1146/annurev.es.04.110173.000325>
- Pang, J. Y., Wang, Y. M., Lambers, H., Tibbett, M., Siddique, K. H. M., & Ryan, M. H. (2013). Commensalism in an agroecosystem: Hydraulic redistribution by deep-rooted legumes improves survival of a droughted shallow-rooted legume companion. *Physiologia Plantarum*, 149(1), 79–90. <https://doi.org/10.1111/ppl.12020>
- Pendergrass, A. G., Knutti, R., Lehner, F., Deser, C., & Sanderson, B. M. (2017). Precipitation variability increases in a warmer climate. *Scientific Reports*, 7, 17966. <https://doi.org/10.1038/s41598-017-17966-y>
- Potts, D. L., Barron-Gafford, G. A., Butterfield, B. J., Fay, P. A., & Hultine, K. R. (2019). Bloom and bust: Ecological consequences of precipitation variability in aridlands. *Plant Ecology*, 220(2), 135–139. <https://doi.org/10.1007/s11258-019-00915-2>
- Potts, D. L., Huxman, T. E., Cable, J. M., English, N. B., Ignace, D. D., Eilts, J. A., ... Williams, D. G. (2006). Antecedent moisture and seasonal precipitation influence the response of canopy-scale carbon and water exchange to rainfall pulses in a semi-arid grassland. *New Phytologist*, 170(4), 849–860. <https://doi.org/10.1111/j.1469-8137.2006.01732.x>
- Potts, D. L., Huxman, T. E., Enquist, B. J., Weltzin, J. F., & Williams, D. G. (2006). Resilience and resistance of ecosystem functional response to a precipitation pulse in a semi-arid grassland. *Journal of Ecology*, 94(1), 23–30. <https://doi.org/10.1111/j.1365-2745.2005.01060.x>
- Potts, D. L., Huxman, T. E., Scott, R. L., Williams, D. G., & Goodrich, D. C. (2006). The sensitivity of ecosystem carbon exchange to seasonal precipitation and woody plant encroachment. *Oecologia*, 150(3), 453–463. <https://doi.org/10.1007/s00442-006-0532-y>
- Potts, D. L., Scott, R. L., Bayram, S., & Carbonara, J. (2010). Woody plants modulate the temporal dynamics of soil moisture in a semi-arid mesquite savanna. *Ecohydrology*, 3(1), 20–27. <https://doi.org/10.1002/eco.91>
- Potts, D. L., Scott, R. L., Cable, J. M., Huxman, T. E., & Williams, D. G. (2008). Sensitivity of mesquite shrubland CO₂ exchange to precipitation in contrasting landscape settings. *Ecology*, 89(10), 2900–2910. <https://doi.org/10.1890/07-1177.1>
- Prieto, I., Padilla, F. M., Armas, C., & Pugnaire, F. I. (2011). The role of hydraulic lift on seedling establishment under a nurse plant species in a semi-arid environment. *Perspectives in Plant Ecology Evolution and Systematics*, 13(3), 181–187. <https://doi.org/10.1016/j.ppees.2011.05.002>
- 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>
- Prieto, I., & Ryel, R. J. (2014). Internal hydraulic redistribution prevents the loss of root conductivity during drought. *Tree Physiology*, 34(1), 39–48. <https://doi.org/10.1093/treephys/tpt115>
- Priyadarshini, K. V. R., Prins, H. H. T., de Bie, S., Heitkonig, I. M. A., Woodborne, S., Gort, G., ... de Kroon, H. (2016). Seasonality of hydraulic redistribution by trees to grasses and changes in their water-source use that change tree-grass interactions. *Ecohydrology*, 9(2), 218–228. <https://doi.org/10.1002/eco.1624>
- Quijano, J. C., & Kumar, P. (2015). Numerical simulations of hydraulic redistribution across climates: The role of the root hydraulic conductivities. *Water Resources Research*, 51(10), 8529–8550. <https://doi.org/10.1002/2014wr016509>
- Quijano, J. C., Kumar, P., & Drewry, D. T. (2013). Passive regulation of soil biogeochemical cycling by root water transport. *Water Resources Research*, 49(6), 3729–3746. <https://doi.org/10.1002/wrcr.20310>
- 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>
- Roque-Malo, S., & Kumar, P. (2017). Patterns of change in high frequency precipitation variability over North America. *Scientific Reports*, 7, 10853. <https://doi.org/10.1038/s41598-017-10827-8>
- Ryel, R. J., Caldwell, M. M., Yoder, C. K., Or, D., & Leffler, A. J. (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>
- Schulze, E. D., Caldwell, M. M., Canadell, J., Mooney, H. A., Jackson, R. B., Parson, D., ... Trimbom, P. (1998). Downward flux of water through roots (ie inverse hydraulic lift) in dry Kalahari sands. *Oecologia*, 115(4), 460–462. <https://doi.org/10.1007/s004420050541>
- Scott, R. L., Cable, W. L., & Hultine, K. R. (2008). The ecohydrologic significance of hydraulic redistribution in a semiarid savanna. *Water Resources Research*, 44(2), W02440. <https://doi.org/10.1029/2007wr006149>
- Scott, R. L., Cable, W. L., Huxman, T. E., Nagler, P. L., Hernandez, M., & Goodrich, D. C. (2008). Multiyear riparian evapotranspiration and groundwater use for a semiarid watershed. *Journal of Arid Environments*, 72(7), 1232–1246. <https://doi.org/10.1016/j.jaridenv.2008.01.001>
- Scott, R. L., Edwards, E. A., Shuttleworth, W. J., Huxman, T. E., Watts, C., & Goodrich, D. C. (2004). Interannual and seasonal variation in fluxes of water and carbon dioxide from a riparian woodland ecosystem. *Agricultural and Forest Meteorology*, 122(1–2), 65–84. <https://doi.org/10.1016/j.agrformet.2003.09.001>
- Scott, R. L., Goodrich, D., Levick, L., McGuire, R., Cable, W. L., Williams, D., ... Huxman, T. E. (2006). Determining the riparian groundwater use within the San Pedro Riparian National Conservation Area and the Sierra Vista Sub-Basin, Arizona. In J. M. Leenhouts, J. C. Stromberg & R. L. Scott (Eds.), *Hydrologic Requirements of and Consumptive Ground-Water Use by Riparian Vegetation along the San Pedro River, Arizona, U.S.* Geological Survey, Scientific Investigations Report 2005–5163 (142 pp).
- Scott, R. L., Huxman, T. E., Barron-Gafford, G. A., Jenerette, G. D., Young, J. M., & Hamerlynck, E. P. (2014). When vegetation change alters ecosystem water availability. *Global Change Biology*, 20(7), 2198–2210. <https://doi.org/10.1111/gcb.12511>
- Scott, R. L., Huxman, T. E., Williams, D. G., & Goodrich, D. C. (2006). Ecohydrological impacts of woody-plant encroachment: Seasonal patterns

- of water and carbon dioxide exchange within a semiarid riparian environment. *Global Change Biology*, 12(2), 311–324. <https://doi.org/10.1111/j.1365-2486.2005.01093.x>
- Scott, R. L., Shuttleworth, W. J., Goodrich, D. C., & Maddock, T. (2000). The water use of two dominant vegetation communities in a semiarid riparian ecosystem. *Agricultural and Forest Meteorology*, 105(1–3), 241–256. [https://doi.org/10.1016/S0168-1923\(00\)00181-7](https://doi.org/10.1016/S0168-1923(00)00181-7)
- Sun, S. J., Meng, P., Zhang, J. S., & Wan, X. C. (2014). Hydraulic lift by *Juglans regia* relates to nutrient status in the intercropped shallow-root crop plant. *Plant and Soil*, 374(1–2), 629–641. <https://doi.org/10.1007/s11104-013-1888-5>
- Verweij, R. J. T., Higgins, S. I., Bond, W. J., & February, E. C. (2011). Water sourcing by trees in a mesic savanna: Responses to severing deep and shallow roots. *Environmental and Experimental Botany*, 74, 229–236. <https://doi.org/10.1016/j.envexpbot.2011.06.004>
- Walter, H. (1939). Grasland, Savanne und Busch der arideren Teile Afrikas in ihrer ökologischen Bedingtheit. *Jahrbucher für Wissenschaftliche Botanik*, 87(5), 750–860.
- Walter, H. (1971). *Ecology of tropical and subtropical vegetation*. Edinburgh, UK: Oliver & Boyd.
- Ward, D., Wiegand, K., & Getzin, S. (2013). Walter's two-layer hypothesis revisited: Back to the roots! *Oecologia*, 172(3), 617–630. <https://doi.org/10.1007/s00442-012-2538-y>
- White, J. C., & Smith, W. K. (2020). Water source utilization under differing surface flow regimes in the riparian species Liquidambar styraciflua, in the southern Appalachian foothills, USA. *Plant Ecology*, 221(11), 1069–1082. <https://doi.org/10.1007/s11258-020-01062-9>
- Williams, D. G., Scott, R. L., Huxman, T. E., Goodrich, D. C., & Lin, G. (2006). Sensitivity of riparian ecosystems in and and semiarid environments to moisture pulses. *Hydrological Processes*, 20(15), 3191–3205. <https://doi.org/10.1002/hyp.6327>
- Wu, H., Fu, C., Wu, H., & Zhang, L. L. (2020). Influence of the dry event induced hydraulic redistribution on water and carbon cycles at five AsiaFlux forest sites: A site study combining measurements and modeling. *Journal of Hydrology*, 587, 124979.
- Yepez, E. A., Williams, D. G., Scott, R. L., & Lin, G. H. (2003). Partitioning overstory and understory evapotranspiration in a semiarid savanna woodland from the isotopic composition of water vapor. *Agricultural and Forest Meteorology*, 119(1–2), 53–68. [https://doi.org/10.1016/S0168-1923\(03\)00116-3](https://doi.org/10.1016/S0168-1923(03)00116-3)
- Yu, K. L., & D'Odorico, P. (2014). Climate, vegetation, and soil controls on hydraulic redistribution in shallow tree roots. *Advances in Water Resources*, 66, 70–80. <https://doi.org/10.1016/j.advwatres.2014.02.003>
- Yu, K. L., & D'Odorico, P. (2015). Hydraulic lift as a determinant of tree-grass coexistence on savannas. *New Phytologist*, 207(4), 1038–1051. <https://doi.org/10.1111/nph.13431>
- Yu, K. L., & Foster, A. (2016). Modeled hydraulic redistribution in tree-grass, CAM-grass, and tree-CAM associations: The implications of crassulacean acid metabolism (CAM). *Oecologia*, 180(4), 1113–1125. <https://doi.org/10.1007/s00442-015-3518-9>
- Yu, T. F., Feng, Q., Si, J. H., Xi, H. Y., Li, Z. X., & Chen, A. F. (2013). Hydraulic redistribution of soil water by roots of two desert riparian phreatophytes in northwest China's extremely arid region. *Plant and Soil*, 372(1–2), 297–308. <https://doi.org/10.1007/s11104-013-1727-8>
- Zhu, J. T., Sun, D. M., Young, M. H., Caldwell, T. G., & Pan, F. (2015). Shrub spatial organization and partitioning of evaporation and transpiration in arid environments. *Ecohydrology*, 8(7), 1218–1228. <https://doi.org/10.1002/eco.1576>

How to cite this article: Barron-Gafford GA, Knowles JF, Sanchez-Cañete EP, et al. Hydraulic redistribution buffers climate variability and regulates grass-tree interactions in a semiarid riparian savanna. *Ecohydrology*. 2021:e2271. <https://doi.org/10.1002/eco.2271>