Impacts of hydraulic redistribution on grass–tree competition vs facilitation in a semi-arid savanna

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Summary

- A long-standing ambition in ecosystem science has been to understand the relationship between ecosystem community composition, structure and function. Differential water use and hydraulic redistribution have been proposed as one mechanism that might allow for the coexistence of overstory woody plants and understory grasses.
- Here, we investigated how patterns of hydraulic redistribution influence overstory and understory ecophysiological function and how patterns vary across timescales of an individual precipitation event to an entire growing season. To this end, we linked measures of sap flux within lateral and tap roots, leaf-level photosynthesis, ecosystem-level carbon exchange and soil carbon dioxide efflux with local meteorology data.
- The hydraulic redistribution regime was characterized predominantly by hydraulic descent relative to hydraulic lift. We found only a competitive interaction between the overstory and understory, regardless of temporal time scale. Overstory trees used nearly all water lifted by the taproot to meet their own transpirational needs.
- Our work suggests that alleviating water stress is not the reason we find grasses growing in the understory of woody plants; rather, other stresses, such as excessive light and temperature, are being ameliorated. As such, both the two-layer model and stress gradient hypothesis need to be refined to account for this coexistence in drylands.

Introduction

A key challenge in ecohydrology is broadening our understanding and ability to predict interactions between above- and below-ground processes. Water exchange and movement within a plant is one primary means by which above-ground ecosystem structure and function are linked to below-ground resource pools that drive abiotic and biotic processes. Within drylands, one pervasive example of this link centers on questions regarding how grasses and trees can coexist, how overstory trees might facilitate or hinder understory function, and how dynamic these relationships are in time and space (Maestre & Cortina, 2004; Michalet *et al.*, 2006; D'Odorico *et al.*, 2007; McCluney *et al.*, 2012; Yu & D'Odorico, 2015; E. Lee *et al.*, unpublished). Multiple mechanisms have been proposed to explain the coexistence of species and plant functional types, including the assumption that the species utilize spatially distinct pools of resources or that they have different resources needs in time (i.e. temporally distinct niches *sensu* Huxman *et al.*, 2008). Most often this idea of a spatial niche is expressed as co-occurrence of vegetation being driven by a relatively distinct utilization of shallow soil water by grasses and of deeper soil water by deeper rooting trees (Walter, 1939, 1971; Holdo, 2013; Ward *et al.*, 2013).

While Kramer (1932, 1933) first established the possibility of water flow from root to soil, it took several more decades to quantify bi-directional flow within shrubs and trees, wherein roots served as preferential low-resistance pathways for water movement between wet and dry soil layers along soil water potential gradients (Schulze *et al.*, 1998). This process of hydraulic redistribution (HR) can result in downward (hydraulic descent; HD) and upward (hydraulic lift; HL) water movement through the plant roots and into the soil, and has been documented in multiple biomes and varied plant functional types (Nadezhdina *et al.*, 2010; Neumann & Cardon, 2012; Prieto *et al.*, 2012). Recent research has demonstrated the impacts of HR on local ecohydrology through field measurements and experiments (Scott *et al.*, 2008; Potts *et al.*, 2010; Verweij *et al.*, 2011; Kulmatiski & Beard, 2013a; Quijano *et al.*, 2013; Yu *et al.*,

2013; Prieto & Ryel, 2014; Prieto *et al.*, 2014) and numerical modeling (Ryel *et al.*, 2002; Amenu & Kumar, 2008; Alton, 2014; Gou & Miller, 2014; Yu & D'Odorico, 2014; Quijano & Kumar, 2015; Fu *et al.*, 2016; E. Lee *et al.*, unpublished). Multiple studies have linked the resulting impact on overstory–understory associations (Ludwig *et al.*, 2004; Armas *et al.*, 2012; Quijano *et al.*, 2012; Cardon *et al.*, 2013; Yu & D'Odorico, 2015; Priyadarshini *et al.*, 2016; Yu & Foster, 2016) and spatial relations in savannas (Zhu *et al.*, 2015). However, studies where HR is measured through manipulation experiments are less common (Schulze *et al.*, 1998; Kulmatiski *et al.*, 2010; Verweij *et al.*, 2011; Kulmatiski & Beard, 2013a,b), and these studies that do exist lack physiological measures of plant function.

Early HR researchers conjectured that nocturnal expression of hydraulically lifted water could be tapped by non-lifting neighbors, potentially affecting plant–plant interactions and community structure, especially in aridland systems (Caldwell & Richards, 1989; Caldwell, 1990; Caldwell *et al.*, 1991). Subsequent research has shown that HL by the overstory can indeed be facilitative in terms of improving understory plant germination (Quijano *et al.*, 2012; Pang *et al.*, 2013) as well as plant nutrient and water status (Cardon *et al.*, 2013; Matimati *et al.*, 2014; Sun *et al.*, 2014). However, other studies question the net benefit of HR on the plant relationships. In contrast to HL, HD by overstory plants can create a detectable competitive effect by limiting understory seedling establishment (Prieto *et al.*, 2011). Given these discrepancies, Dohn *et al.* (2013) examined the role of hydraulic redistribution on plant interactions through the lens of the stress-gradient hypothesis (SGH), which predicts that facilitative mechanisms increase in importance relative to competitive mechanisms with increasing environmental stress. Based on this hypothesis, as the intensity of an abiotic stressor increases along a spatial gradient, facilitative mechanisms should outweigh competitive interactions, leading to a positive change in the response variable (photosynthetic rate, biomass, etc.). Our changing climate could represent an analogy for this gradient evolving in time, particularly in drylands where abiotic stressors of limited moisture and excessive temperatures already exist, making the testing of the validity of this hypothesis important (Ward *et al.*, 2013).

While climatic regimes are currently used to predict current and projected effects on plant and ecosystem processes, an expanded view of the water-based state of an ecosystem's composition and function should augment our abilities to estimate ecohydrological patterns of carbon (C) cycling. Here, we introduce the concept of a hydraulic redistribution regime (HRR) – an ecosystem metric, which captures the balance in downward and upward movement of water (HL relative to HD), the seasonality of these bi-directional flows and the resulting impacts on the understory community. Just as a climate regime describes the external drivers of productivity and function of an ecosystem and the means by which they integrate, an HRR stems from previous work (Schulze *et al.*, 1998; Ryel *et al.*, 2002; Ward *et al.*, 2013) that describes a suite of both benefits and consequences of dynamic water movement by plants. This concept of HRR captures the dynamic heterogeneity of water availability that arises due to water uptake patterns of plant roots that mediate precipitation and groundwater regimes, such that an ecosystem's HRR and climatic regime interact to determine understory and whole ecosystem functioning. Overstory–understory interactions probably exist across a range of HRRs from hydraulic-lift dominated (positive HRR) to hydraulic-descent dominated (negative HRR) that can explain patterns of competition vs facilitation among members of a community. For example, a positive HRR (HL > HD) resulting from root access to groundwater may enhance facilitative dynamics through resource (water and nutrient) sharing (Quijano *et al.*, 2013). By contrast, a negative HRR (HD > HL) may inhibit understory growth or may support a more temporally episodic and spatially intermittent pattern.

Distinct wet and dry cycles within drylands offer an opportunity to test the impacts of an HRR on overstory and understory function at multiple timescales as well. The structure, integrity and function of dryland ecosystems are sensitive to the amount and timing of precipitation, disturbance and land-cover change due to woody plant encroachment, putting them at risk of climate and land-use change (Schlesinger *et al.*, 1990; Belnap, 1995; Weltzin *et al.*, 2003; Huxman *et al.*, 2004b; Ogle & Reynolds, 2004; Scott *et al.*, 2006, 2009, 2010). Although globally extensive (Huxman *et al.*, 2004a, 2005; Schwalm *et al.*, 2010; Jenerette *et al.*, 2012; Schaefer *et al.*, 2012; Reichmann *et al.*, 2013), to date, no study has quantified the ecophysiological impacts of overstory HR on understory photosynthetic function at multiple time and spatial (leaf-to-ecosystem) scales within drylands. Therefore, we asked two questions: how do patterns of HR influence overstory and understory plant ecophysiological function? How do these patterns vary across timescales of an individual precipitation pulse to an entire growing season?

To address these questions, we experimentally manipulated tree understory plots in a savanna dominated by mesquite (*Prosopis velutina*) to eliminate the effects of mesquite HR on soil water. We hypothesized that periods of HD during which the surface soils were wet (after precipitation events and in the wet seasons) would largely result in competition between the overstory trees and the understory grasses as both groups maximized surface soil-water use. Contrastingly, dry periods characterized by HL would yield facilitation between the overstory and understory (Fig. 1) because understory grasses, which only have shallow roots, would have no other access to soil moisture.

Materials and Methods

Study site and species

The site is located in the Santa Rita Experimental Range (SRER; 31.8214°N, 110.8661°W, elevation: 1116 m) south of Tucson (AZ, USA). Soils here are deep loamy sands (Scott *et al.*, 2009). Mesquite (*Prosopis velutina* Woot.) cover at this site is *c.* 35%, with vegetation of the intercanopy space dominated by a mosaic of perennial C_4 bunchgrasses and seasonally bare soil. Intercanopy plant cover of perennial grasses, forbs and sub-shrubs is *c.* 22% (Scott *et al.*, 2009; Hamerlynck *et al.*, 2012). Mesquite averaged 2.5 m in height, and the mean
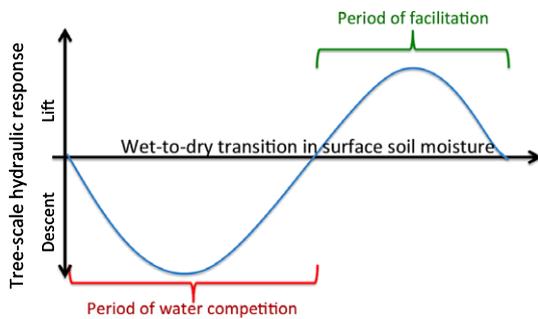
Fig. 1 Illustration of potential rates and direction of hydraulic redistribution in overstory trees (hydraulic descent (HD) vs hydraulic lift (HL)) and the resulting effect on understory plants. HD by a tree, driven by a gradient of shallow wet to deep dry soil water potentials, creates a period of competition for water amongst the tree and understory plants. Alternatively, periods of HL, in response to deep wet and dry shallow soil water potentials, may facilitate understory plant function during periods of otherwise moisture stress. The *x*-axis represents time through a wet-to-dry transition. The axis is dimensionless because this may represent a period of time around a rain event or across an entire growing season of relatively available moisture and then drought.

depth to groundwater exceeds 100 m beyond the average rooting depth of these mesquite, as nearby wells measured depths to groundwater of 100 and 154 m. Mean annual precipitation (1937–2007) is 380 mm, with *c.* 50% falling between July and September during the North American Monsoon and *c.* 30% falling during the winter (Scott *et al.*, 2009). Daily precipitation and atmospheric vapor pressure deficit (VPD) were obtained from meteorological instrumentation used in ongoing long-term eddy-covariance monitoring of landscape-scale C and water fluxes on a tower located *c.* 300 m from the study site (for full description of all aspects, see Scott *et al.*, 2009). We measured volumetric soil water content using soil moisture probes (CS616-L, Campbell Scientific, Logan, UT, USA) installed at 5, 10, 20, 30, 50, 70 and 100 cm depths beneath a mesquite tree near the flux tower, as part of a longer-term monitoring project, and at centimeter depths in a pair of trenched and control mesquite trees in the experimental area. Measurements were recorded every 30 min and stored on a data logger (CR-1000, Campbell Scientific).

On 15 May 2015, we identified eight mesquite trees of average height, and we established a $1.0 \times 1.0 \, \text{m}^2$ plot under the south-facing canopy portion of each mesquite with *c.* 0.5 m buffer around each plot. We inserted a rebar post at each of two opposing corners of each plot to ensure repeat measurements through time were on the same plot position. Four of these trees and associated plots served as controls. The plots associated with the four remaining trees all had potential for HR into the plot blocked when we created a 1 m deep × 2 m long trench along the south side of tree trunk and severed all mesquite lateral roots that approached the plot area, similar to the techniques used by Verweij *et al.* (2011). Ultimately, a 2 m long trench represents *c.* 20% of the understory area, resulting in minimal impact on the overstory tree function, but a complete elimination of the connectivity between overstory and understory roots. We then lined this trench with ground cover fabric (DeWitt Sunbelt weed

fabric, Sikeston, MO, USA) to allow water and air to pass through it and to prevent regrowth of roots into the treatment plot.

Determination of hydraulic redistribution regime through sap flux measurements

We used the heat-ratio method (HRM), which uses temperature probes at equal distances up- and downstream from a pulsed heat source to allow for measures of high, low and reverse flow rates within the xylem (Burgess *et al.*, 2001a,b; Hultine *et al.*, 2003, 2004; Scott *et al.*, 2008). We used the SFM1 Sap Flow Meter (ICT International, Armidale, NSW, Australia) to measure the heat transmitted up- and downstream along the root, as this has been shown to be proportional to the magnitude of sap flux (sap flow per unit time). We installed sap flow sensors in the taproot, two lateral roots and the stem of each of the four control trees, and we installed the sensors in the taproot and stem of the four trenched treatment trees. The SFM1 sap flow sensors consist of three 35 mm stainless steel probes, each spaced 5 mm apart. A filament in the center probe produces heat, and the resultant heat flux is measured by two thermistors in the outer two probes. The two measurement probes have thermistors located at 7.5 and 22.5 mm from the tip of the probe. Sap flux was measured every 10 min.

HRM measurements of sap flux are sensitive to the spacing between heater and measurement probes. By imposing zero flow conditions, the *in situ* distance between probes can be inferred, accounting for both thermal and physical asymmetry in the installation (Becker, 1998). We imposed zero flow conditions by drilling 35 mm deep × 13 mm wide holes upstream and downstream from the sap flux sensors and filling the holes with silicon caulk at the end of the study. The *in situ* probe spacing was computed according to Burgess *et al.* (1998), such that when the measured heat pulse velocity differed from 0, Eqn 1 was used to compute the actual probe spacing:

$$x_2 = \sqrt{4kt \ln\left(\frac{v_1}{v_2}\right) + x_1^2} \qquad \text{Eqn 1}$$

where x_2 (cm) denotes the incorrectly spaced probe, k is the thermal diffusivity constant (measured mean value of $0.002455 \, \text{cm}^2 \, \text{s}^{-1}$), t is the median measurement time (80 s), v_1 and v_2 are increases in temperature from initial temperatures at measurements probes, and x_1 is assumed to be correctly spaced at 0.05 cm. After the probe spacing of x_2 was computed, we used Eqn 2 to correct heat pulse velocity for probe misalignment:

$$V_m = \frac{4tV_h x_1 - x_2^2 + x_1^2}{2t(x_1 + x_2)} \qquad \text{Eqn 2}$$

where V_m (cm s^{-1}) denotes misalignment-corrected heat pulse velocity, V_h (cm s^{-1}) is uncorrected heat pulse velocity and x_1 is, again, the assumed spacing (0.05 cm in our case). Because it is not known which of the probes is incorrectly spaced, Eqn 1 was

also solved for x_1, assuming that x_2 is correctly spaced. We then evaluated Eqn 2 with the computed value of x_1 and the assumed value of x_2 and averaged the two estimates of V_m, thereby producing an estimate of sap flux that is not biased in either the positive or the negative direction.

We corrected for the 'wounding effect' according to Burgess *et al.* (2001a):

$$V_c = bV_m + cV_m^2 + dV_m^3 \qquad \text{Eqn 3}$$

where V_c (cm s^{-1}) denotes corrected heat pulse velocity and b, c and d are coefficients based on measured wound width and the specific meter installation (Burgess *et al.*, 2001a). After correcting for probe misalignment and wounding effect, corrected heat pulse velocity, V_c, was converted to sap velocity, V_s (cm s^{-1}), according to Barrett *et al.* (1995):

$$V_s = \frac{V_c \rho_b (c_w + m_c c_s)}{\rho_s c_s} \qquad \text{Eqn 4}$$

where V_s denotes sap velocity, ρ_b (0.99460716 g cm^{-3}) is the measured density of wood (DW/green volume), c_w (1200.0) and c_s (4182.0) are the specific heat capacity per unit mass (J K^{-1} kg^{-1}) of material of the wood matrix and sap, respectively, m_c (0.582986495 g g^{-1}) is the water content of the sapwood and ρ_s (1 g cm^{-3}) is the density of water.

The sign of the difference indicates the direction of sap flux (Table 1), where positive values indicate movement towards the stem and canopy of the tree. In lateral roots, these positive values signify root-water uptake. Positive values in the taproot coupled with negative values in the lateral roots indicate HL of deep water out into the shallower soil, whereas negative values in the taproot sap flux indicate HD. To distinguish positive sap flux, which also supports transpiration, from that which signifies HL, we examined nighttime data independent of the full diel data set, as nocturnal expression of water via lateral roots is the hallmark of hydraulic lift (Caldwell & Richards, 1989).

Leaf-level physiological measurements of CO_2 and water exchange

Measurements of leaf-level net photosynthesis (A_{net}) were conducted using an LI-6400 portable photosynthesis system (Li-Cor, Lincoln, NE, USA). A red–blue light source (LI-6400-02b) attached to the leaf cuvette provided constant irradiance of 1500 µmol m^{-2} s^{-1}, with cuvette [CO_2] held constant at 400 ppm across all measurement dates. Cuvette air temperature was set to match that of ambient conditions on each measurement date. All measurements were conducted between 09:00 and 12:00 h Mountain Standard Time (MST) on fully unfurled, south-facing leaves of similar age. Once chamber conditions and gas exchange rates of A_{net} had stabilized, the two infrared gas analyzers within the instrument were matched, and gas-exchange data were logged five times across a 1 min period and averaged. For each of the eight

plots, we measured the overstory mesquite and one individual of the two dominant C_4 bunchgrasses: bush muhly (*Muhlenbergia porteri* Scribn. ex Beal) and plains bristlegrass (*Setaria leucopila* (Scribn. & Merr.) K. Schum.). All leaves that were within the 2×3 cm cuvette for gas exchange measurements were harvested after measurements and stored 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. We obtained wet leaf mass, and then sample leaf area was determined using an LI-3100C area meter (Li-Cor). Samples were then air-dried to obtain dry leaf mass (Barron-Gafford *et al.*, 2012, 2013).

These protocols were repeated across multiple campaigns throughout the growing season to capture the full spectrum of environmental conditions including the spring (day of year (DOY) 135), pre-monsoon drought (DOY 148, 169), monsoon peak (DOY 202, 232, 238) and post-monsoon dry-down (DOY 261, 298) in 2015 and in the subsequent spring (DOY 97) of 2016. We also repeated these measurements just before and for multiple days after an individual precipitation event in the wet season to quantify overstory and understory responses around a rain pulse (DOY 249–262).

Understory whole-ecosystem measures of CO_2 exchange

We repeated understory ecosystem CO_2 flux measurements across the eight 1.0×1.0 m^2 plots described in the section above, according to the schedule described in the section above. Following techniques similar to Hamerlynck *et al.* (2011, 2012) and others (Huxman *et al.*, 2004b; Potts *et al.*, 2006b), we measured each plot with a $1.0 \times 1.0 \times 1.0$ m^3 chamber of tightly sewn polyethylene held taut by a PVC pipe tent frame (Shelter Systems, Santa Cruz, CA, USA). A small fan was placed over the plot to ensure atmospheric mixing within the chamber. After placing the chamber on the plot, we sealed the chamber base with a chain. This polyethylene material allowed c. 90% of photosynthetically active radiation (PAR) to pass onto the plots (Hamerlynck *et al.*, 2012). We estimated net ecosystem exchange of CO_2 (NEE, in units of µmol CO_2 m^{-2} ground area s^{-1}) by measuring changes in [CO_2], [H_2O] and air temperature (T) through time using an open-path infrared gas analyzer (LI-7500; Li-Cor). We allowed air to mix within the chamber for 30 s and then logged the data every second over a 90 s flux measurement period. After this, we removed the chamber, aerated it for c. 1 min, replaced and sealed the chamber over the same plot, and shaded it with a blanket to repeat measurements in the dark to estimate ecosystem respiration (R_{eco}). All understory ecosystem measurements were conducted between 09:00 and 12:00 MST. We estimated gross ecosystem productivity (GEP; in units of µmol CO_2 m^{-2} ground area s^{-1}) from these measurements, where GEP $= -1 \times$ (NEE $- R_{eco}$). Such late morning measurements are good predictors of daily integrated values, and can be extrapolated across several days' activity (Huxman *et al.*, 2004b; Potts *et al.*, 2006a; Hamerlynck *et al.*, 2012).

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 life (HL) vs hydraulic descent (HD)) of the overstory mesquite

Taproot sap flux sign	Lateral root sap flux sign	Direction of net water movement	Ecohydrologic outcome	Pre-monsoon (%)	Monsoon (%)	Post-monsoon (%)	Spring (%)
+	+	Upward and inward	Plant soil-water extraction: water being pulled from deep and shallow soil layers	41	0	0	20
−	+	Downward and inward	HD: water being pulled in laterally and moved down vertically	25	97	99	78
+	−	Upward and outward	HL: water being moved up vertically and expressed out laterally	18	0	0	0
−	−	Downward and outward	Soil plant-water extraction: water being pulled from plant into soil	16	3	1	2

Data are summarized for distinct seasonal periods of the pre-monsoon (day of year (DOY) 142–185), monsoon (DOY 186–275), post-monsoon and autumn (DOY 276–60), and the following spring (DOY 61–109).

Measurements of soil CO_2 efflux

Measurements of rates of soil CO_2 efflux to the atmosphere (F_{soil}; in units of µmol CO_2 m^{-2} ground area s^{-1}) were conducted using an LI-8100 automated soil gas flux system outfitted with the 10 cm survey chamber (8100-102; Li-Cor). Within each of the eight plots described above, we permanently installed two soil-gas flux measurement collars. Each collar had a diameter of 10.2 cm and was installed to a depth of 5 cm. At each collar, we measured soil moisture integrated over a 12 cm depth using a handheld water content sensor (HydroSense system, Campbell Scientific), and soil temperature integrated over a 10 cm depth using a temperature probe (Temp-100, Oakton Instruments, IL, USA), as described by Barron-Gafford *et al.* (2011, 2014). To capture the full suite of soil conditions and to link with understory C dynamics, we repeated measurements of R_{soil} at all of the same time points as leaf-level measures of A_{net} and understory NEE.

Statistical analysis

A split-plot, repeated-measures ANOVA (RM-ANOVA; Statistix v. 8.0, Analytical Software, Tallahassee, FL, USA) was used to test for differences in leaf-level A_{max} within the overstory mesquite and understory bunchgrass individuals, understory GEP, and soil CO_2 efflux between the treatment (presence of HR (control vs trenched)), multiple sampling periods and plant species. The between-treatment, whole-plot effect was the different species (mesquite, bush muhly and plains bristlegrass), using the species-by-replicate interaction as the whole-plot error term and an α of 0.05. The within-treatment, sub-plot effects were the various measurement periods, which spanned pre-monsoon, monsoon, post-monsoon and the following spring. We tested for a species-by-measurement period interaction, which would indicate if the species had different responses to seasonal periods, using the species-by-measurement-period-by-replicate interaction as the sub-plot error term.

Results

Cumulative precipitation in 2015 was 475 mm, with 61% coming within the summer monsoon period, yielding the bimodal precipitation pattern typical of the southwestern USA (Fig. 2a). Soil moisture declined throughout the hot pre-monsoon (*c.* DOY 120–180, Fig. 2c–e). Throughout this hottest part of the year when VPDs were at their maximum, average diel (day and night) sap flux within the taproot was largely positive, with two periods of daily lateral-root flux approaching zero, indicating flow towards the base of the tree (i.e. HL; Table 1). This period of HL was well correlated with times when there was greater soil moisture deeper in the soil profile (0.5–1.0 m) than at the near surface (0.05–0.3 m; Fig. 3a,b), but the significance of the correlation varied by season. We detected a positive correlation between a soil moisture gradient with deeper soil moisture at depth and taproot flux velocity within the pre-monsoon ($r^2 = 0.7$) and the monsoon ($r^2 = 0.4$; DOY 200–275), but there was no correlation within the cooler post-monsoon and autumn periods ($r^2 = 0.01$; DOY 276–365). Average daily lateral-root sap flux was almost always positive, indicating flow from the root tips towards the base of the tree (Fig. 3a). By examining nighttime sap flux alone, we found that once the monsoon season brought precipitation to the savanna, there was limited evidence of HL (i.e. negative nocturnal lateral root sap-flux; Table 1; Fig. 4f); In fact, nighttime sap flux through taproots was consistently negative, indicating sustained nocturnal removal of surface water through HD.

A_{net} differed across seasonal measurement periods ($F_{5,80} = 36.24$; $P \leq 0.0001$), and we detected a significant two-way species-by-measurement period interaction ($F_{10,80} = 8.35$; $P \leq 0.0001$). Rates of A_{net} within the overstory mesquite were similar before the onset of our trenching treatment that reduced the potential for HR (Fig. 4a). However, after we imposed the trenching treatment, A_{net} rates were significantly lower in treatment trees throughout the dry pre-monsoon than those in control plots. Rates were, again, similar between control and treatment trees once the steady rains increased available soil moisture and reduced VPD within the monsoon growing season and in the next spring following winter rains.

Understory GEP differed significantly across seasonal measurement periods ($F_{4,32} = 14.55$; $P \leq 0.0001$). During the pre-monsoon dry period, understory GEP was similar among trenched plots and those under control trees (Fig. 4b). However, as the monsoon rains began, rates of bulk understory productivity within the treatment plots (where HR was eliminated) were

significantly greater than those in the control plots. There was no difference during the post-monsoon cool period, but this same pattern of elevated rates of GEP within trenched plots returned in the spring following winter rains. The differences in whole-understory productivity were not due to differences in the functional capacity of individual grasses, as we did not find any significant differences in leaf-level rates of A_{net} between grasses in the control and trenched plots, nor did we detect differences in this trend between the two most common species (Fig. 4c, d). Similarly, differences in whole-understory C fluxes were not due to differences in rates of soil CO_2 efflux, as we did not detect a treatment effect in F_{soil} at any point through time (Fig. 4e).

However, at the scale of an individual precipitation pulse, we did find significantly greater photosynthetic rates within bunchgrasses in trenched plots freed from root water competition with overstory mesquite (Fig. 5). Whereas grasses within control and trenched treatment plots were similar just before a rain event, we detected significantly elevated A_{net} in grasses within the treatment plots for the subsequent 10 d (Fig. 5b,c). Soil moisture remained elevated in these trenched treatment plots relative to the control plots for this 10 d period as well (Fig. 5d).

Discussion

A long-standing goal in biogeography, ecology and ecosystem science has been to understand the relationship between the structure of an ecosystem and the processes that generate the community composition and the function of that ecosystem. Here, we linked measures of water movement within the stem and roots, meteorological data, and measurements of leaf- and understory-ecosystem-scale CO_2 exchange to examine an ecosystem's hydraulic redistribution regime.
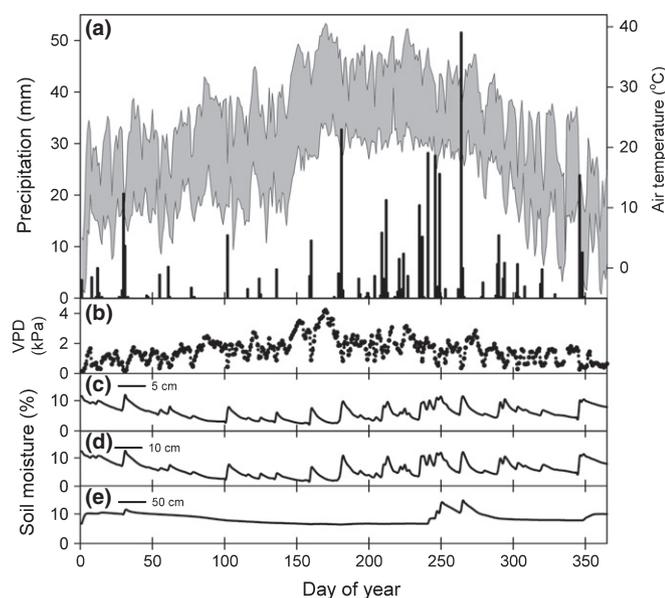

Fig. 2 (a) Daily maximum and minimum air temperatures and daily cumulative precipitation. (b) Vapor pressure deficit (VPD) and (c–e) soil moisture at 5, 10 and 50 cm depths at the study site in 2015.
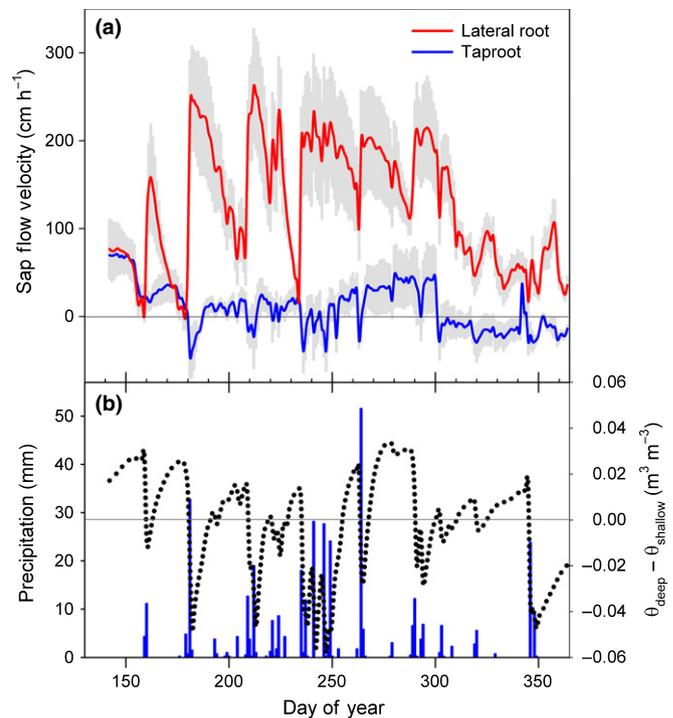

Fig. 3 (a) Daily average lateral (red) and taproot (blue) sap flux velocity in 2015. Positive sap flux in the roots indicates flow toward the tree base, and negative sap flux indicates flow away from the tree base. Standard errors around the mean are shown in gray. (b) Daily precipitation (bars) and the difference between average deep (0.5–1.0 m) and shallow (0.05–0.3 m) soil moisture (dotted line), where positive values indicate more water in deeper layers and negative values indicate more water in shallow layers.

Impacts of hydraulic redistribution on overstory function

The ratio of HD relative to HL was disproportionately in favor of HD (net downward movement of water), and the seasonality of hydraulic activity was very episodic by season (Table 1). We found that HL in overstory mesquite trees was largely constrained to the hot and dry pre-monsoon period (DOY 140–182, Fig. 3e). Thus, during this time, overstory C uptake is probably enabled by connectivity to deep soil water resources, derived either from deep infiltration of cool-season rains (e.g. DOY 27–30, Fig. 2a, e), or late-monsoon or cool-season water stored through hydraulic descent (e.g. DOY 300–360, Fig. 3a). Model simulations for this site also suggest strong evidence for HL to be concentrated within the dry pre-monsoon (E. Lee *et al.*, unpublished). Access to water from deeper profiles eased mesquite sensitivity to drought conditions, so that initial rates of A_{net} in mesquite (DOY 135) were nearly equal to those attained over the wet monsoon. Scott *et al.* (2006, 2014) had previously noted that a connectivity to subsurface water could decouple tree function from precipitation within a semi-arid riparian setting. Our findings suggest evidence of such reduced coupling in upland settings as well. As the pre-monsoon drought deepened (DOY 150–180) there was a more pronounced indication of nocturnal HL, as evidenced by greater frequency of positive taproot and negative lateral root nocturnal sap fluxes (Fig. 4f), which
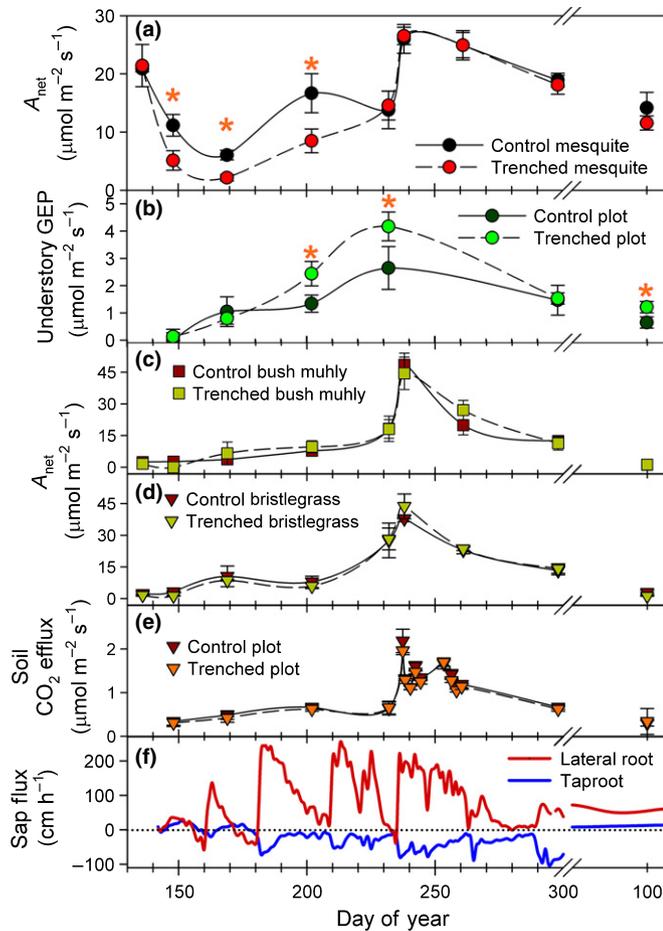
Fig. 4 Daily average (a) net leaf-level photosynthesis (A_{net}) rates in overstory mesquite trees, (b) understory plot gross ecosystem productivity (GEP), A_{net} of understory (c) bush muhly and (d) plains bristlegrass bunchgrasses, and (e) soil CO_2 efflux within control and trenched plots where hydraulic redistribution was physically blocked throughout 2015 and the spring of 2016. Bars represent $\pm$ 1 SE around the mean, and asterisks indicate significant difference ($P < 0.01$). (f) Average nighttime sap flux within control tree lateral roots and the taproots are shown to indicate patterns of nighttime hydraulic lift vs descent.

Fig. 5 Average net leaf-level photosynthesis rates in (a) overstory mesquite and understory (b) bush muhly and (c) plains bristlegrass bunchgrasses within control (untrenched) plots. Data are shown for just before a 25 mm precipitation event in September 2015 and throughout the soil dry-down. Bars represent $\pm$ 1 SE around the mean, and asterisks indicate significant difference ($P < 0.01$). (d) Average soil moisture at 10 cm depth across control and treatment plots of both species. Standard errors around the mean are shown in gray.

were concurrent with higher A_{net} in untrenched control mesquite (Fig. 4a). These lower rates of daytime assimilation in the mesquite overstory agree with prolonged dry-period measurements in previous studies (Potts *et al.*, 2008; Hamerlynck *et al.*, 2010; Barron-Gafford *et al.*, 2013, 2014). Thus, even as daily rates of HR were declining over this period (Fig. 3a), our findings demonstrate that HL still served to help sustain mesquite C acquisition over the prolonged hot and dry pre-monsoon period.

During the summer monsoon, average daily taproot sap flux was more dynamic and probably tied to the episodic nature of precipitation in drylands (Noy-Meir, 1973; Ward *et al.*, 2013; Yu & D'Odorico, 2014), which triggers pulses of plant transpiration (positive daytime taproot sap flux) and photosynthetic uptake. After the monsoon growing season initiated around DOY 180 (Fig. 2a), there was limited evidence of HL (i.e. negative nocturnal lateral root sap-flux), and nighttime sap flux through taproots was invariably negative, indicating sustained
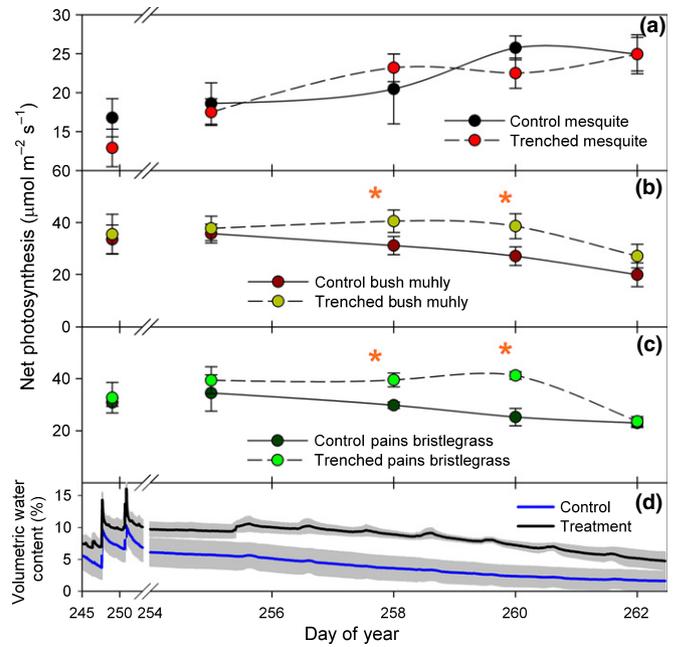
nocturnal HD (Fig. 4f). This sustained nocturnal HD probably contributed to the several days where even daily average taproot fluxes were negative, which was concurrent with invariably positive daily average lateral root sap-fluxes (Fig. 3a). This suggests the initially higher A_{net} in untrenched control mesquite (Fig. 4a) was driven largely by soil water extracted by lateral roots. The subsequent convergence in A_{net} between control and trenched trees probably originates from increasing storm frequencies that led to soil moisture conditions sufficient to support similar A_{net} between these treatments (Fig. 2a) or an increase in fine root biomass to capture these water resources.

Impacts of overstory hydraulic redistribution on understory C fluxes

At the annual scale, we found evidence of a competitive interaction between the overstory trees and understory grasses. Grasses within the control plots, where the trees still have lateral roots that access this same soil space, experienced reduced A_{net} relative to grasses not experiencing this competition (Fig. 4b). This does not support Walter's two-layer hypothesis (Walter, 1971), which suggests differential water use among soil layers (shallow and deep) for different plant functional types. Also, our findings differ from the modeled predictions of Yu & D'Odorico (2015) for a savanna system in the Kalahari, which suggest that HL may be a mechanism that supports tree-grass coexistence across dry and wet savannas. This is noteworthy in that their results were obtained from sandy, well-drained soils with marginal cambic

and calcic horizon development (D'Odorico *et al.*, 2007), which are very similar to soils at the SRER site, and are soils that would facilitate strong root/soil contact that enhance expression of HL water compared with soils with large subsurface rocky clasts (Yoder & Nowak, 1999a,b). Thus, the contrasting HR regime results between the Kalahari and our location do not reflect differences in surface and sub-surface soil horizon development, which are known to have marked impacts to plant rooting distribution, ecophysiological performance, community structure and ecosystem function (McAuliffe, 1994; Hamerlynck *et al.*, 2000, 2002; Hamerlynck & McAuliffe, 2008, 2010; Duniway *et al.*, 2010). One primary difference between the Kalahari Transect in southern Africa and this research is the structure of the ecosystem. Average woody plant rooting depth was *c.* 1.8 m in the Kalahari Transect, whereas mesquite can have roots deeper than 50 m, with more than 20% of the total root biomass being below 1 m depth (Heitschmidt *et al.*, 1988; Canadell *et al.*, 1996). Perhaps rooting depth, and therefore below-ground storage capacity of HD-driven water pools, yields significant variation in tree–grass interactions in terms of above-ground function? Moreover, it is likely that the apparent lack of two-layer partitioning arises from an absence of a constant source of deep water from infiltration. Deep soil water infiltration is limited to cool season and winter periods, a source of precipitation with extremely high inter-annual variability in the south-western US (Scott *et al.*, 2000; McAfee & Russell, 2008). Thus, mesquite in our system store deep soil moisture by way of HD in order to have it available for utilization outside of the summer monsoon (D'Odorico *et al.*, 2007; Yu & D'Odorico, 2015; E. Lee *et al.*, unpublished).

Importantly, this savanna system in southern Arizona experiences distinct dry pre-monsoon, warm monsoon and wet winter periods. Precipitation in the cool autumn, winter and spring seasons within temperate savannas percolate and recharge deeper soil layers as opposed to rain that falls within the peak growing season when herbaceous plants are physiologically active and evaporative demand is high (Scott *et al.*, 2000; E. Lee *et al.*, unpublished). Dohn *et al.* (2013) therefore note that deep-rooted trees in temperate savannas may benefit from singular access to soil moisture below the herbaceous root zone. Downward movement of water through prolonged periods of HD by the overstory only compounds this transfer of moisture to deeper layers. This represents a spatial and temporal asymmetry of resource availability within temperate savannas that has complicated previous estimations of the competitive or facilitative nature of tree–grass systems in the absence of measurements.

We found that baseline physiological functional capacities of the grasses were equal between treatment and control plots (on a per-unit area basis in green leaves). Therefore, the elevated GEP we found within the understory of treatment plots was not due to an enhanced capacity for photosynthesis (Fig. 5). Rather, higher GEP probably reflects the development of greater photosynthetic biomass than in the control plots where the understory was experiencing competition for water. This is consistent with Hamerlynck *et al.* (2011) who found that intercanopy grasses (those less linked to the HD of overstory trees) grew in soils with higher volumetric water content, and had plant canopy areas greater than

grasses in the understory. The higher plant canopy area noted here could have resulted from more available soil moisture or improved access to soil nutrients because our treatment also eliminated nutrient absorption by mesquite, and all of their roots were eliminated from the trenched treatment plots. We postulate that these patterns in the structure of the understory reflect our newly illuminated understanding in the hydraulic advantage of the trees that enables their competitive water grabs.

Furthermore, we found evidence of a competitive interaction between the trees and grasses at the scale of a single precipitation event (Fig. 5a). The steeper decline in volumetric water content in control vs treated plots in the days after a rain event documented here suggests that the trees were actively depleting near-surface moisture resources through HD. Having sole access to incident rain water yielded greater photosynthetic rates per unit leaf area in grasses free of competition with mesquite compared to those in a shared below-ground hydraulic regime. These elevated rates of A_{net} lasted nearly 10 d after a single rain, which translates into a significantly greater cumulative C uptake per volume of precipitation in grasses not linked to the HD dynamics of overstory trees. Again, this does not support Walter's two-layer hypothesis, as we see both mesquites and understory utilizing the same shallow soil water pool in control plots. This greater than 50% C gain by grasses within trenched plots over control plots could partially explain the greater individual biomass (canopy area and height) documented by Hamerlynck *et al.* (2011) for intercanopy grasses, which experience less hydraulic competition than their understory counterparts.

Implications under a changing climate

Dohn *et al.* (2013) note that HR within overstory neighbors might be a more important driver of grass growth in drier regions where water is more limited than in wetter areas where rainfall is more abundant. Similarly, modeling work by Fu *et al.* (2016) stresses that the impacts of HR are greatest in ecosystems with pronounced dry seasons. Yu & D'Odorico (2014, 2015) note that drylands with rainfall regimes with more rare storms tend to yield more hydraulic lift by the overstory. How might we consider these spatial patterns as a correlate for a projected global climate change that will yield drier conditions for many savannas? Our results within an upland temperate savanna suggest that the episodic nature of precipitation and the relative abundance of moisture outside of the growing season (winter) vs within the period of shared physiological activity among overstory and understory plants may modulate any predictions of facilitation due to prolonged decline in precipitation. This narrative matches that postulated by Yu & D'Odorico (2014), which also noted that rainfall distribution (size and timing of events) should affect net direction (HL vs HD) and rates of HR. But what about the effects of any increased HL by the tree on interactions with understory grasses?

With respect to our hypothesized Fig. 1, we found that regardless of whether looking across an entire growing season or an individual precipitation pulse, there was a dominant competitive interaction between the overstory and understory. The net

movement of water within the lateral roots of the overstory tree was nearly always positive, implying that very little of the hydraulically lifted water is lost to understory transpiration. This was true whether that HL occurred in the early spring before the grasses were physiologically active or during the growing season of peak grass activity. This pattern of HD and HL being contained within the overstory tree itself is contrary to our previous understandings. The SGH suggests that under progressively drier conditions this interaction would become more facilitative for the understory grasses (Dohn *et al.*, 2013), but this assumes that the overstory is not utilizing all lifted water. Indeed, in more water-limited North American desert ecosystems, woody plants that conduct HL typically extract all annually available rooting zone soil water (Yoder & Nowak, 1999a,b). Why, then, do we find such an abundance of grass establishment under woody plants in dryland savannas?

This work suggests that alleviating water stress is not the reason; instead, other stresses, such as excessive light and temperature, are being ameliorated for these grasses (see Hamerlynck *et al.*, 2011; Quijano *et al.*, 2012). As such, both the two-layer model and the SGH need to be refined. The two-layer model would actually only be affected by HR if the trees and grasses had similar phenologies, and this is not the case in this semi-arid savanna system. Rather, the variable phenologies in overstory and understory species support temporal resource niche partitioning more than the more spatially determined two-layer model (Huxman *et al.*, 2008). We posit that the SGH is operating primarily in terms of the 'ancillary' stresses such as high light and extreme temperatures, and not the main ecological forcing variable that actually determines productivity, at least as it relates to water limitations and the resulting hydraulic redistribution regime. This may be because in truly water-limited systems, woody plants are using up all the water available to them on an annual basis. Comparative studies within dry, average and wet years at a single site are needed to determine how plastic these responses actually are in response to climatic change.

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Author contributions

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

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