The ecohydrologic significance of hydraulic redistribution in a semiarid savanna

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[1] Recent studies have illuminated the process of hydraulic redistribution, defined as the translocation of soil moisture via plant root systems, but the long-term ecohydrologic significance of this process is poorly understood. We investigated hydraulic redistribution (HR) by *Prosopis velutina* Woot. (velvet mesquite) in an upland savanna ecosystem over a two-year period. Our goal was to quantify patterns of HR by mesquite roots and assess how this affects tree water use and productivity. We used the heat ratio method to monitor bi-directional sap flow, an analog of HR, in both lateral and tap roots. Additionally, we monitored soil water content and used the eddy covariance technique to quantify ecosystem carbon dioxide and water exchange. Mesquite roots redistributed large amounts of water throughout the year, even during periods of canopy dormancy. Dormant season precipitation (November–March) was often taken up by shallow lateral roots and transferred downward in the soil profile by deeper lateral and tap roots. Such a transfer was also apparent when the trees were active and moisture from summer rainfall was plant available in the upper soil layers. As the upper soil layers dried, sap flow moving toward the canopy in the lateral roots diminished and water use from deeper soils increased via the taproots. The relationship between root sap flow and above-canopy fluxes suggested that deeper "stored" water from HR allowed the trees to transpire more in the spring that followed a winter with significant downward redistribution. Patterns of lateral and tap root sap flow also implied that redistribution may extend the growing season of the trees after summer rains have ended and surface soils are dry, thus allowing the trees to photosynthesize through periods of seasonal drought. The large hydrologic magnitude and the ecological effects of HR we studied, along with mounting evidence of this process occurring in many other ecosystems, indicates that HR should be accounted for in many ecohydrologic modeling efforts.

1. Introduction

[2] A growing body of evidence demonstrates that hydraulic redistribution, the transfer of soil water via plant roots, is common in many ecosystems [*Caldwell et al.*, 1998]. Hydraulic redistribution is considered to be a passive process whereby plant roots act as conduits that transport water in response to water potential gradients [*Mooney et al.*, 1980; *Caldwell et al.*, 1998; *Mendel et al.*, 2002], and it occurs in a variety of directions including upwards [termed "hydraulic lift" *Richards and Caldwell*, 1987], downward [*Burgess et al.*, 1998], and even laterally in the soil profile [*Burgess and Bleby*, 2006; *Brooks et al.*, 2002]. Typically, hydraulic redistribution has been observed at night when transpiration is low, but it has also been observed in roots of dormant [*Hultine et al.*, 2004] and even senescent plants [*Leffler et al.*, 2005]. Hydraulic redistribution has been documented in arid to semiarid deserts and rangelands [*Richards and Caldwell*, 1987; *Ryel et al.*, 2002; *Hultine et al.*, 2003a], savannas [*Ludwig et al.*, 2003] and in temperate [*Emerman and Dawson*, 1996], coniferous [*Brooks et al.*, 2002], and tropical forests [*Meinzer et al.*, 2004; *Oliveira et al.*, 2005]. While some studies have shown that the amount of water that plants redistribute on a timescale of days to weeks is large, comparatively little is known about the amount of water that is redistributed on a seasonal to yearly timescale and whether this amount is hydrologically significant.

[3] Many studies have focused on the ecological consequences of hydraulic lift. Hydraulic lift may enhance transpiration and plant growth during rainless periods by storing water in the otherwise dry rhizosphere that can be accessed by lateral roots during the day [*Emerman and Dawson*, 1996; *Caldwell and Richards*, 1989; *Caldwell et al.*, 1998; *Lee et al.*, 2005]. Hydraulic lift may be also beneficial to promoting growth of shallower-rooted understory species which may scavenge some of the lifted water [*Dawson*, 1993; *Zou et al.*, 2005; *Caldwell and Richards*, 1989; *Brooks et al.*, 2002; *Ludwig et al.*, 2003]. In regions frequented by droughts, downward hydraulic redistribution,

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also termed hydraulic descent [*Hultine et al.*, 2003b], may promote plant water conservation by redistributing water deeper in the soil column when it is abundant in near-surface soil layers, where it may otherwise evaporate from the soil surface [*Ryel et al.*, 2004]. Finally, hydraulic redistribution has been hypothesized to improve a deep-rooted plant's nutrient status by increasing the mobility of deep nutrients [*McCulley et al.*, 2004] or maintaining favorable water status for fungi in the near-surface rhizosphere [*Querejeta et al.*, 2007].

[4] Plants have been shown to transport significant amounts of water up and down in the soil profile on a daily to weekly timescale. Around 30% of the water recovered daily from the upper 2 m of soil during the dry season in a northwestern U.S. conifer forests was produced by nocturnal hydraulic redistribution, and this redistribution allowed for maintenance of soil moisture in the upper soil horizons for two to three weeks into a summer drought period [*Brooks et al.*, 2002]. The roots of *Quercus suber* (cork-oak) trees lifted 17–81% of the water used the following day for transpiration [*Kurz-Besson et al.*, 2006]. *Acer saccharum* (sugar maple) hydraulically lifted 102 (±54) l of water daily, about 25% of the transpiration amount [*Emerman and Dawson*, 1996]. In a much drier environment, the daily transpiration in *Artemisia tridentata* (sagebrush) shrubs was reduced by 25 to 50% when nocturnal hydraulic lift was experimentally circumvented [*Caldwell and Richards*, 1989]. Likewise, the amount of water moved via hydraulic descent can be significant when relatively deep soil layers are drier than near-surface ones. In stands of *Artemisia* shrubs, 74–100% of precipitation that had infiltrated below 0.3 m was eventually redistributed even deeper via roots [*Ryel et al.*, 2003]. In some situations, the water potential gradients between soil layers can be greater than between the soil to leaf gradient during transpiration, and this can result in hydraulic descent in deep roots even while transpiration is taking place [*Hultine et al.*, 2003b].

[5] Woody plants can redistribute a significant amount of water during dormancy which may have important ecohydrologic consequences [*Hultine et al.*, 2004]. During wet winters, deeper-rooted plants could redistribute water from moist surface soils to deep soil layers (hydraulic descent), and away from shallow-rooted competitors and direct soil evaporation processes [*Hultine et al.*, 2004]. The "banking" of soil water during dormancy for future use would be beneficial for plants occurring in dryland regions that are typically warm and dry during the early stages of the growing season, such as the southwestern U.S. Likewise, water banking may occur during the active growing season when there is an abundance of near-surface soil water, and this could extend the growing season by providing a source of water after summer rains cease [*Hultine et al.*, 2004; *Ryel et al.*, 2003]. Conversely, dry seasons could produce patterns of hydraulic lift if there is sufficient moisture in the deep rooting zone. This may be beneficial to the "lifter" by enhancing root longevity and activity and nutrient uptake [*Querejeta et al.*, 2007], or it may be detrimental by losing moisture to soil evaporation or co-occurring shallow-rooted understory plants [*Caldwell and Richards*, 1989; *Dawson*, 1993; *Ludwig et al.*, 2003]. In a typical Mediterranean climate (cool wet winters, hot dry summers), *Burgess et al.* [2001a] determined that the amount of stored water in the deep layers would not be enough to support *Eucalyptus spp.* trees for more than several weeks; thus, the banking of water would be unlikely to make a significant contribution to drought avoidance over the summer period. However, they surmise that it may benefit the plants during early spring, following winter rains.

[6] The goal of this study was to determine the ecohydrological significance of hydraulic redistribution in a semiarid savanna ecosystem in southern Arizona. For two years, we monitored the seasonal patterns of root water movement by *Prosopis velutina* Woot. (velvet mesquite), a woody legume that now dominates many savanna ecosystems in the southwest U.S. We used sap flow techniques in order to quantify the water movement through mesquite root systems related to seasonal patterns of hydraulic redistribution. We also monitored the canopy fluxes of water and carbon dioxide using eddy covariance in order to estimate the relative impact hydraulic redistribution has on seasonal fluxes at the stand level.

2. Methods

2.1. Study Site

[7] This study took place on the Santa Rita Experimental Range (SRER), 35 km south of Tucson, AZ USA. Mean annual precipitation (1976–2004) from gages near the site is ~415 mm. About 50% of the rainfall arrives during the months of the summer monsoon (July–September). Winter months (December–March) are cool with occasional nighttime frosts and have around 30% of the annual rainfall. The months of April through June grow increasingly hot, with daytime maximums often exceeding 35°C in June, and usually have little rainfall. Daytime temperatures decrease, and nighttime temperatures increase, somewhat during the months of July through September due to the increased humidity and rainfall during the monsoon. The monsoon typically tapers off in September and rainfall becomes more sporadic through October. The first winter freeze typically occurs in the drier month of November.

[8] Over the last 100 years, the site has changed from a C4 grassland into a savanna by the encroachment of the woody leguminous tree, *Prosopis velutina* (velvet mesquite). Currently, the mesquite canopy cover is about 35% with canopy heights reaching about 4 m. Velvet mesquite trees on the SRER have a dimorphic root system characterized by a deep taproot and a large number of primary and secondary lateral roots. In the deep sandy loam soils found at our site, mesquites form deep taproots and extensive lateral root systems that can extend more than 15 m beyond the canopy [*Cable*, 1977]. Velvet mesquite roots can extend vertically to great depths [*Phillips*, 1963], and the trees are facultative phreatophytes [*Snyder and Williams*, 2000]. However, on the SRER, the mesquites very likely do not access groundwater due to their location far from the valley bottomlands where the water table is closer to the surface. Also, mesquites form dense woodlands and grow to much greater sizes when they have access to groundwater [*Stromberg et al.*, 1993].

2.2. Sap Flow Monitoring

[9] We used the heat ratio method (HRM) to measure xylem sap flow. The HRM has been previously described and validated in detail [*Burgess et al.*, 2001a, 2001b]. Briefly, the HRM employs temperature probes at equal

distances up and down stream from a pulsed heat source. The ratio of heat carried up- and downstream is proportional to the magnitude and direction of sap flux.

[10] In January, 2004, we carefully excavated around the base of five mature mesquite trees to determine which trees had accessible lateral and taproots. Our sample size was constrained by the need to find trees within a 15 m radius of a data logger and to those trees where we could access the taproot without destroying lateral roots greater than ~2 cm. We found two suitable and medium-sized trees and installed sap flow probes on the main stem, two large lateral roots, and the tap root of each (Table 1). These were kept in operation through January, 2006. In February, 2005, the entire root ball was excavated around one of the trees, and the additional six roots greater than 3.5 cm in diameter were also instrumented. Mesquite species are ring porous. Therefore stem xylem water transport mostly occurs in the outermost region of the woody matrix (i.e., the most recent growth ring). Our previous experience with mesquite transpiration studies is that the HRM grossly underestimates sap flux in stems, likely because of the extreme discontinuity of flow within the stem. On the other hand, xylem transport in mesquite roots occurs through multiple growth rings, likely because the soil insulates the roots from freezing temperatures and subsequent freeze-thaw cavitation cycles. Therefore individual growth rings remain conductive throughout the year, allowing invasive sap flux measurement techniques such as the HRM to produce reasonably accurate data on mesquite roots [Hultine et al., 2004].

Table 1. Diameter and Sap Wood Area (SWA, cm^2) of the Mesquite Stems and All Lateral and Tap Roots (≳2 cm Diameter) for the Two Trees Monitored[a]

	Diameter, cm	SWA, cm^2
Tree 1, canopy area = 15.9 m^2		
Stem	36.6	48.4
Tap roots		
1	15.8	63.9
2	6.0	15.3
3	5.6	14.0
Total		93.2
Lateral roots		
1	8.4	23.2
2	6.5	16.7
3	6.5	16.7
4	10.0	30.0
5	5.9	14.9
6	4.3	11.1
7*	2.7	8.6
8*	1.9	7.7
Total		128.9
Tree 2, canopy area = 22.0 m^2		
Stem	40.1	44.0
Tap roots		
1*	11.5	37.0
2	15.0	58.5
Total		95.6
Lateral roots		
1	6.7	17.2
2	9.5	27.8
3*	4.9	12.5
4*	5.9	14.9
5*	3.8	10.2
Total		82.6

[a]The projected areas of the canopy drip-line are also given. Roots that were not monitored are indicated by an asterisk.

Thus the probes in the stems were only used to detect the presence or absence of tree transpiration.

[11] A single sap flow sensor was inserted into the xylem of each root. After probe installation, the roots were covered with two layers of pipe insulation and the excavated holes around the trees were covered with plywood to thermally insulate the exposed roots from nighttime freezing and to prevent radiant heating during the day by direct sunlight. The sap flow sensors were fabricated following the design of Burgess et al. [2001a]. They consisted of three 35 mm long stainless steel probes spaced 6 mm apart. The central probe contained a Nichrome heater, while the outside probes contained two thermocouple junctions spaced to measure sap flow at 5 and 10 mm radial depths. Because of the design, the thermocouples and heaters of each probe could be replaced independently when they malfunctioned. A data logger (CR-10X, Campbell Scientific, Logan, UT) controlled and measured probe function. Sap flow was measured every 30 m.

[12] After correcting for wounding effect [Burgess et al., 2001b], heat pulse velocity (V_h) was converted to sap velocity (V_s; cm hr^{-1}) according to Barrett et al. [1995]:

$$V_s = \frac{V_h \rho_b (c_w + m_c c_s)}{\rho_s c_s} \qquad (1)$$

where c_w and c_s are the specific heat of dry wood (1200 J kg^{-1} °C^{-1} at 20°C; Becker and Edwards, 1999) and sap (assumed to equal that of water, 4182 J kg^{-1}°C^{-1} at 20°C), and ρ_s is the density of sap (assumed to equal that of water, 1.0×10^3 kg m^{-3}), ρ_b is the measured density of wood, and m_c is the measured moisture content of wood. Positive V_s in the roots indicates sap flow toward the tree base, and negative V_s indicates sap flow away from the tree base.

[13] Volumetric sap flow (L d^{-1}) was calculated after first subtracting the bark thickness from the radius of the root. The heartwood radius was subtracted from gross wood area after it was identified by visual observation of the dark color associated with heartwood. The sapwood area was then divided into concentric bands coinciding with the depth of each thermocouple junction within the probes. Thus estimates of sap flow were weighted by the amount of conducting sapwood of each band. Sapwood and bark thickness was measured on both stems and on a subset of six roots ranging in radial size from 3.7 to 9.3 cm. These properties were then estimated for the remaining roots by using a linear regression of root diameter versus bark thickness ($R^2 = 0.94$) and sapwood thickness ($R^2 = 0.74$).

[14] Because HRM measurements of sap flow are very sensitive to spacing between the temperature probes and the central heating probe, the true spacing between probes must be validated. To ensure zero flow, we drilled two 30 mm deep by 12.5 mm wide holes into the roots on both sides of each probe and then filled them with silicon caulk at the conclusion of the study to stop all flow and keep the xylem around the probe from drying. Spacing between probes was calculated according to Burgess et al. [1998]:

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

where x_2 (mm) is designated the incorrectly spaced probe, x_1 is assumed to be correctly spaced at 6 mm, k is the
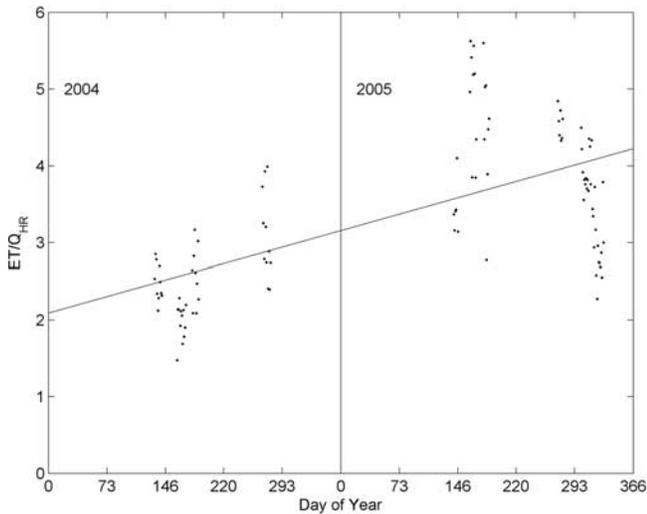
Figure 1. The ratio of ecosystem-scale evapotranspiration (ET) and daily ecosystem-scale tree root water movement (Q_{HR}) during days of the 2004 and 2005 mesquite growing season with minimal understory transpiration and bare-soil evaporation. A regression line reflecting the temporal trend is also shown.

thermal diffusivity of fresh wood (measured from cores of the individual roots and stems), v_1 and v_2 are the increases in temperature at equidistant points downstream and upstream respectively, and t is the median measurement time after the release of the heat pulse (in this case 80 s). Since it is unknown which probe is incorrectly spaced, or whether both probes are incorrectly spaced, equation (2) was solved for x_1 and x_2 and the two solutions were averaged.

[15] In order to compare the magnitude of water moved via hydraulic redistribution to other ecosystem-scale hydrologic fluxes like precipitation and ET, we scaled up our measurements by calculating the volume of water moved by tree roots per unit land surface area, Q_{HR} [mm], as:

$$Q_{HR} = 1000 \frac{\bar{J} A_{SW}}{A_{crown}} f_{tree} \qquad (3)$$

where $\bar{J}$ is the average (lateral or tap root) sap flow per unit sap wood area [$m^3\ m^{-2}\ d^{-1}$], A_{SW} is the total (lateral or tap root) sapwood area of Trees 1 and 2 [m^2, Table 1], A_{crown} is the total canopy area of both trees (m^2, Table 1), $f_{tree} = 0.35$ is the average fractional canopy cover of trees at the site, and 1000 is for unit conversion. Sap flow velocity, $\bar{J}$, for the lateral roots consisted of 3 roots in 2004 and 6 roots in 2005. $\bar{J}$ for the tap roots consisted of 2 roots in 2004 and 5 measurements in 2005 since two additional lateral roots had taproot behavior and an additional probe was added to one taproot. We applied equation (3) after using interpolation across data gaps to compute annual totals for the dormant and potential growing season Q_{HR} in both years. The potential growing season for trees is defined by the typical frost-free period when the trees have green leaves but were not necessarily transpiring (DOY 110–335).

[16] Following an approach similar to *Williams et al.* [2004], we compared total daily lateral and tap root Q_{HR}

with ET during carefully selected rain-free and low soil moisture periods of the spring and fall months. During these times, the understory vegetation was likely senesced and soil evaporation was negligible so it was reasonable to assume that total daily Q_{HR} = ET. However, we found that our scaled sap flow underestimated ET during these periods (Figure 1), with the degree of underestimation tending to increase through the two year monitoring period. Also, there was considerable variation in ET/Q_{HR} within each period, which we suspect was due not only to the inaccuracy of Q_{HR} but also to the accuracy of quantifying low ET rates and the assumption that T = ET. Scaled sap flow measurements may be underestimated due to sap flow measurement problems including: 1) the underestimation of wounding and subsequent tylosis [*Swanson and Whitfield*, 1981], 2) a failure to measure sap flux in the most active region of the xylem that is generally located near the cambium [*Swanson*, 1994], or 3) an underestimation of sap flux at depths beyond which our sensors were designed to measure (in this case, 10 mm) [*Fernández et al.*, 2001]. Additional scaling errors may have resulted from an underestimation of total sap wood area (including the omission of all roots < 0.02 m diameter) or an overestimation of crown area. The increase of the underestimation in time suggests that either wounding increased throughout the investigation (i.e., reason #1) or radial growth after the probes were installed resulted in high sap flux rates in regions not captured by our sensors (i.e., reason #2). Unfortunately, these potential errors are unavoidable when using accepted, invasive sap flux approaches during multiyear studies. Furthermore, lysimeter tests of HRM in mesquite stems (unpublished data) indicate that the ring porous nature of mesquite xylem may also lead to an underestimation of the flow velocity in the roots. Nevertheless, this lysimeter study and the results of *Williams et al.* [2004] suggest that multiplying Q_{HR} by a correction factor results in a reasonable estimation of total tree water use. To account for this underestimation, we multiplied Q_{HR} by the underestimation trend line (Figure 1). This correction resulted in an $R^2 = 0.76$ (p < 0.001).

2.3. Micrometeorological and Soil Moisture Monitoring

[17] Thirty meters west of the trees with sap flow instrumentation, we used the eddy covariance technique to quantify ecosystem evapotranspiration (ET) and the net ecosystem exchange of CO_2 (NEE). A 3-dimensional, sonic anemometer (Model CSAT-3; Campbell Scientific Inc., Logan UT) and an open-path infrared gas analyzer (LI-7500, LI-COR Inc., Lincoln, NE) were mounted at 7 m height (approximately twice the vegetation height) to measure the three components of the wind velocity vector, sonic temperature and concentrations of water vapor and carbon dioxide. Data were sampled at 10 Hz and the 30-min covariances were recorded by a data logger (CR5000, Campbell Scientific Inc., Logan UT). Every one-to-two months, IRGAs were zero- and span-calibrated using a CO_2/H_2O –free gas, a standard [CO_2] gas and a dew point generator. Fluxes were later calculated off-line, after performing a two-dimensional coordinate rotation and accounting for density fluctuations [*Webb et al.*, 1980].

[18] The flux data were filtered for spikes and instrument malfunctions (representing, 6.4% of the ET and 7.2% of NEE data). Also, we applied a friction velocity or u*-filter (u* =

0.15 m s^{-1}) to omit fluxes when there was not sufficient turbulence to make representative flux measurements, which occurred about 10% of the time [*Malhi et al.*, 1998]. Daily average ET values were calculated by first filling the gaps in the 30 min data. Gaps were filled using 30-min averages of PAR and 14-day look-up tables of ET values averaged over 100 μmoles m^{-2} s^{-1} intervals [*Falge et al.*, 2001].

[19] To compute weekly averages of gross primary production of CO_2 (GPP), we first calculated composite diurnal NEE curves for each week, and these were used to calculate weekly average NEE. Thirty minute respiration values were determined by fitting an exponential function to air temperature and nighttime NEE data over a 5-day moving window [*Reichstein et al.*, 2005]. This model was then used to fill missing nighttime data and model daytime respiration. The 30-min data were then averaged up to determine weekly average respiration, R. Finally, weekly average GPP was determined by:

$$GPP = R - NEE \qquad (4)$$

[20] We measured volumetric soil water content (θ) using commercial soil moisture probes (CS616-L, Campbell Scientific, Logan, UT) at 5, 10, 20, 30, 50, 70, 100, and 130 cm depths in a profile located in an inter-mesquite-canopy position immediately to the west of the monitored trees and beneath a large mesquite tree about 10 m north of the monitored trees. Measurements were recorded every 30 min and stored on a data logger (CR-10X, Campbell Scientific, Logan, UT). In these profiles, the soils were fairly uniform sandy loams with no observable changes in soil texture. Thus the gradients of soil moisture across the different measurement depths are likely representative of similar gradients in soil water potential, the driving force for hydraulic redistribution.

3. Results

[21] During the two-year study period, maximum air temperatures were around 40°C and occurred during the dry summer period prior to the onset of the monsoon (Figure 2). While minimum air temperatures occasionally dipped below freezing, even shallow soil temperatures remained above 5°C.

[22] Using the remotely sensed Enhanced Vegetation Index (EVI, level MOD13Q1, NASA MODIS Terra satellite, *Huete et al.*, 2002) as a surrogate for vegetation greenness, the green leaf-area at our savanna site generally had two peaks during each year (Figure 3). The first increase in greenness occurred in April with a more prominent increase in mid-summer. The spring peak can be mainly attributed to the mesquite canopy leaf flush, which occurs in April regardless of winter/spring rainfall [*Cable*, 1977] though there can be some understory green-up mainly in annual forbs and understory shrubs following wet winters. The larger summer peak is due to the monsoon rainfall and largely reflects the growth of the perennial grasses; the change in mesquite canopy greenness is much smaller based on measurements of tree LAI (data not shown).

[23] The trend in annual vegetation greenness was generally tracked by the behavior of ET ($R^2 = 0.62$, p < 0.001, Figure 3). Ignoring the spikes in ET due to the high evaporation that followed precipitation events, ET peaked during the monsoon (the time with greatest vegetation growth and soil moisture availability), but there was also a sustained level of ET in the spring of 2004. This elevated level of ET in spring was well-correlated with greenness and thus probably indicative of mesquite transpiration. This was not the case, however, in the spring of 2005 when the leaf flush of the trees was not associated with an increased and sustained ET rate.

[24] Reverse flow was evident in the taproots of both trees before leaf flush and after a number of significant rainfall events in the spring of 2004 (Figure 4a). Conversely there was positive flow (flow toward the stem) in the lateral roots, indicating that shallow soil moisture was being redistributed to deep soil layers (i.e., hydraulic descent). Similar behavior was also seen in the other roots of Tree 1 and 2 (data not shown). Prior to ∼DOY 100 the canopy was leafless, and there were generally no strong and regular diurnal fluctuations in the root sap flow (Figure 4a). At this time, the flow in the lateral and tap roots was strongly negatively correlated (Tree 2-R^2 = 0.64, p < 0.001; Tree 1-R^2 = 0.49, p < 0.001). The reverse flow in the tap and positive flow in the lateral root tapered off toward the end of canopy leaf flush. During the active transpiration period, root sap flow occurred with large, obvious diurnal fluctuations, and flow in the roots at night gradually transitioned from hydraulic descent (see around DOY 115−117) to a small amount of hydraulic lift (negative flow in the lateral root and positive flow in the tap) as near-surface soils dried. The roots reacted similarly to rain events in summer (Figure 4b) except that flow in the tap root was generally positive in the daytime as well, indicating that all or most of the roots were supporting transpiration. Hydraulic descent was mainly confined to nighttime periods following a large amount of rain which led to hydraulic descent even during the daytime in some of the roots.

[25] Average sap velocities for all lateral and tap roots of both trees indicate that hydraulic redistribution was a common occurrence both in the dormant and active-growing season (Figure 5, upper panels). The gradient between deep and shallow soil moisture was strongly correlated with (R^2 = 0.61, p < 0.001) and mirrored the direction of the flow in the taproots (Figure 5, lower panels). Hydraulic descent occurred after most rainfall events, especially during dormancy (before ∼DOY 110 or after ∼DOY 330) but also during the height of the monsoon when transpiration was at its peak. Positive flow in the taproots occurred mainly during the summer prior to or after the peak of the monsoon rains.

[26] Figure 6 shows the cumulative sap flux of a single lateral root and the taproot of Tree 2, where daytime (nighttime) totals were summed for all periods with PAR > 5 (< 5) μmol m^{-2} s^{-1}. In early 2004, a large quantity of water was moved downward in the soil profile via the taproot during dormancy. Next, in early summer, the large swing to positive taproot flow and its co-occurrence with an increase in GPP provides evidence that the water redistributed during dormancy may have facilitated early summer growth. There is also evidence for a small amount of nocturnal hydraulic lift during this time (negative lateral root flow and positive tap root flow). The peak in GPP during the monsoon summer
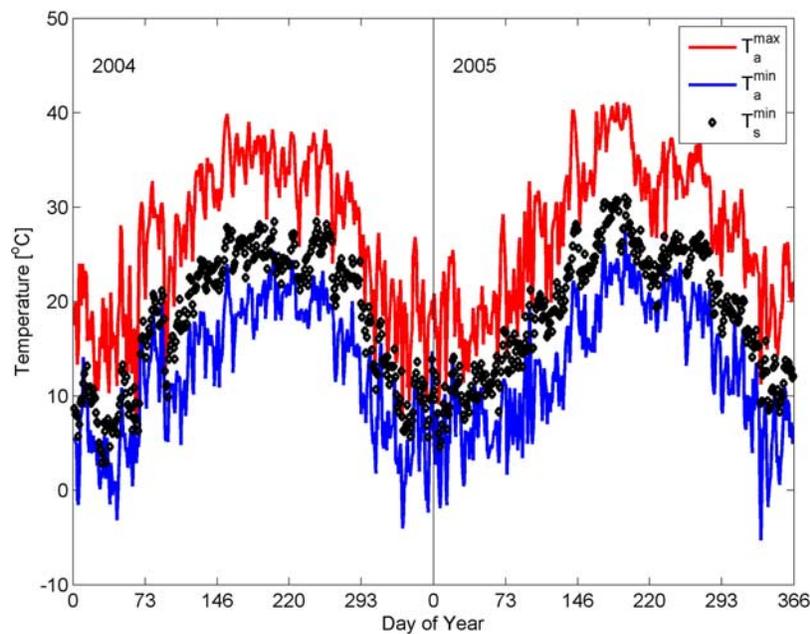
Figure 2. Daily maximum and minimum air temperature at 2 m height (T_a) along with daily minimum soil temperature at 5 cm depth (T_s).

coincided with nocturnal periods of positive lateral root flow and negative taproot flow (hydraulic descent), but growth at the end of the monsoon coincided with positive flow mainly by the taproot. In the winter of 2005, there was less "banking" of soil water, and early summer GPP (Figure 6, bottom panels) was small. From around DOY 1–60 in 2005, the slightly positive taproot flow and positive lateral root flow during the daytime gives some evidence of transpiration loss despite the lack of canopy leaves, which might indicate some loss via the tree's stem and branches. Small, but regular, diurnal fluctuations with positive flow both in tap and lateral roots during the dry periods in winter

provided additional evidence of transpiration during dormancy (data not shown). Then, from around DOY 60–100, the negative flow in the lateral root showed that some of the banked water was transported to the upper soil layers via hydraulic lift. Much of the hydraulic lift appeared to have ended upon leaf flush (~DOY 115) with a small amount of positive flow in the taproot supporting tree transpiration. The behavior in the two roots from the monsoon to the end of year in 2005 was similar to 2004, although the quantity of water moved was greater due to a higher volume of precipitation.
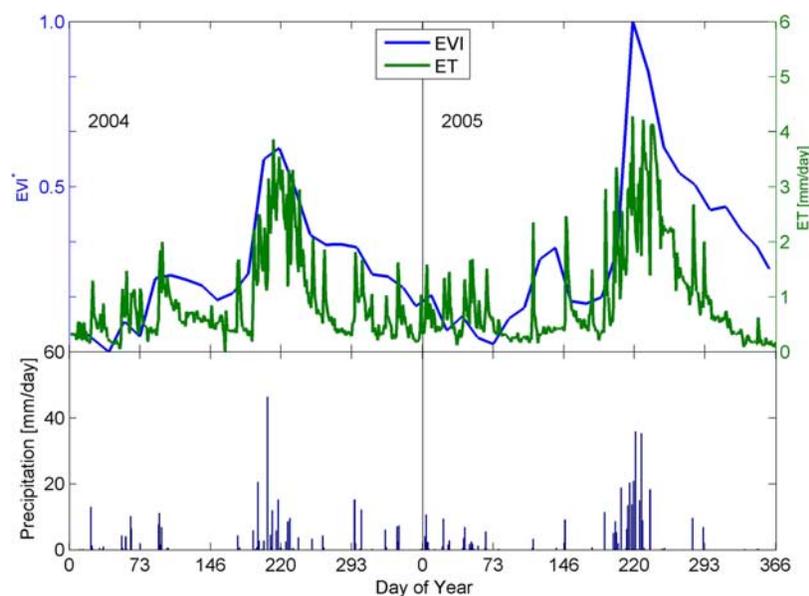
Figure 3. MODIS Enhanced Vegetation Index (EVI*, normalized between 0 and 1), daily total evapotranspiration from eddy covariance (ET), and precipitation. EVI data are the average of 3 × 3 (1 km) pixels centered over the site.
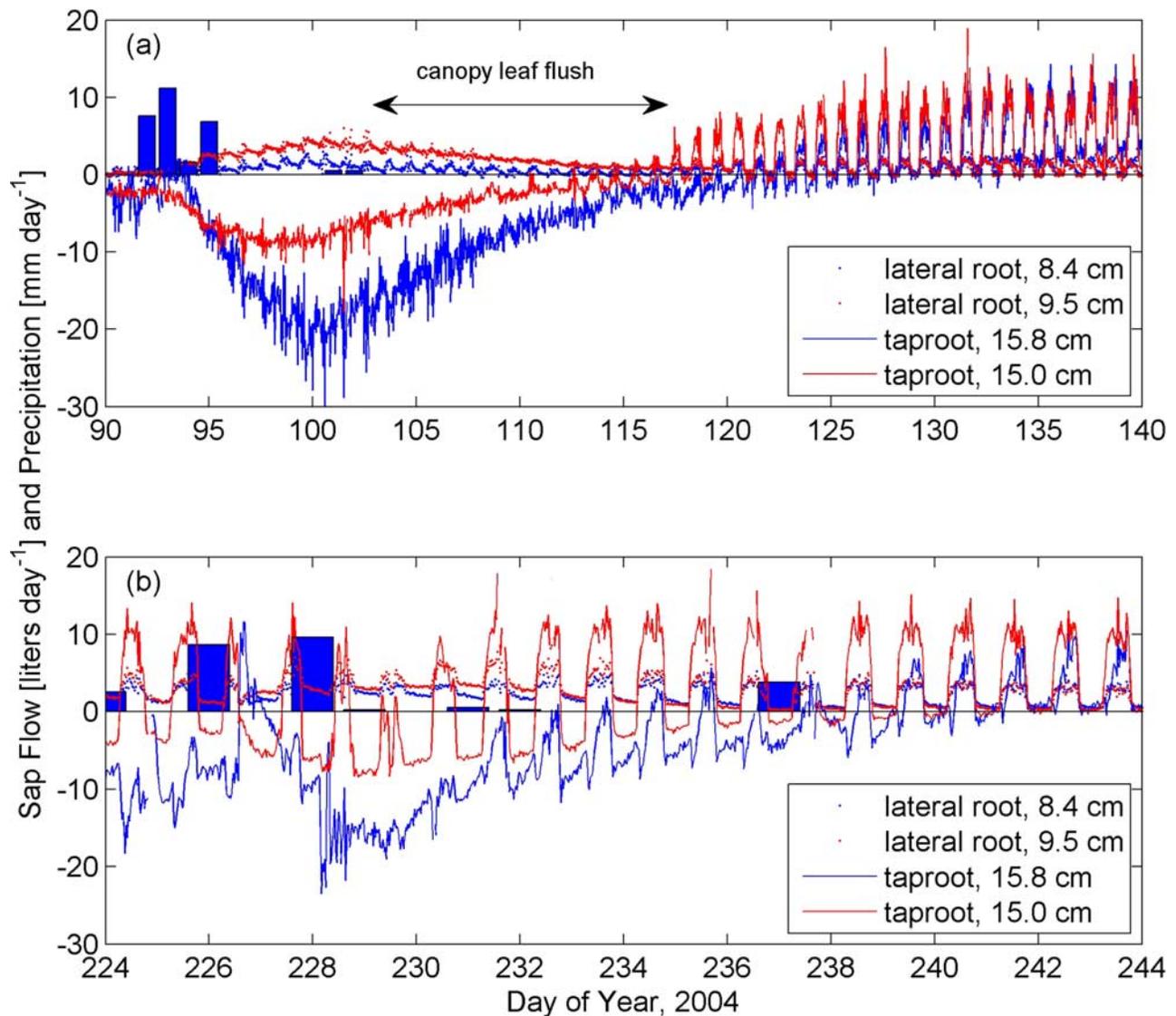
Figure 4. Daily precipitation and volumetric sap flow for a spring (a) and summer (b) period on a lateral and tap root on Tree 1 (grey) and Tree 2 (black). Positive sap flow in the roots indicates flow toward the tree base, and negative sap flow indicates flow away from the tree base.

[27] The total contribution of ecosystem-scale lateral and tap root sap flow (Q_{HR}) during the daytime varied considerably throughout the two years (Figure 7). Q_{HR}, summed over the daytime and when the canopy had leaves, resulted in an estimate of tree transpiration. In 2004, transpiration in the pre-monsoon period of the growing season (DOY 110–190) was mainly supported by the taproots even though deeper soil layers showed little influence from precipitation events and remained quite dry. At the peak of monsoon ET, tree transpiration was supported mainly by lateral roots with a greater contribution being added by taproots as the rainy season waned. In the 2005 pre-monsoon period, there was less of a sustained period of ET and also less tree transpiration (the sum of the lateral and tap root Q_{HR}) and taproot flow than in 2004. During the 2005 monsoon, transpiration was again first supplied mainly by the lateral roots, with roots at both depths contributing equally toward the end of the monsoon. Average soil moisture conditions from the under-tree and open profiles were similarly dry in the pre-monsoon period (Figure 7, lower panels). The wetter monsoon of 2005 resulted in infiltration going beyond 100 cm (but less than 130 cm-data not shown) while in 2004, probes at 100 cm recorded no changes.

[28] The net amount of water acquired by lateral roots was 28% of annual precipitation in 2004 and 49% in 2005 (Table 2). Estimating total tree transpiration as the sum of daytime Q_{HR} during the growing season, the trees transpired 78 mm in 2004 and 131 mm in 2006 which represents about 27% of annual ET in 2004 and 39% in 2005. In the dormant season of 2004, daytime and nighttime totals were similar, and a total of 12 mm of water was moved toward the stems in the lateral roots while 38 mm was moved downward in the taproots, indicating a lack of balance in the measurements though the standard errors of these estimates were considerable. If this moisture was later used to support transpiration or lost via hydraulic lift during the subsequent
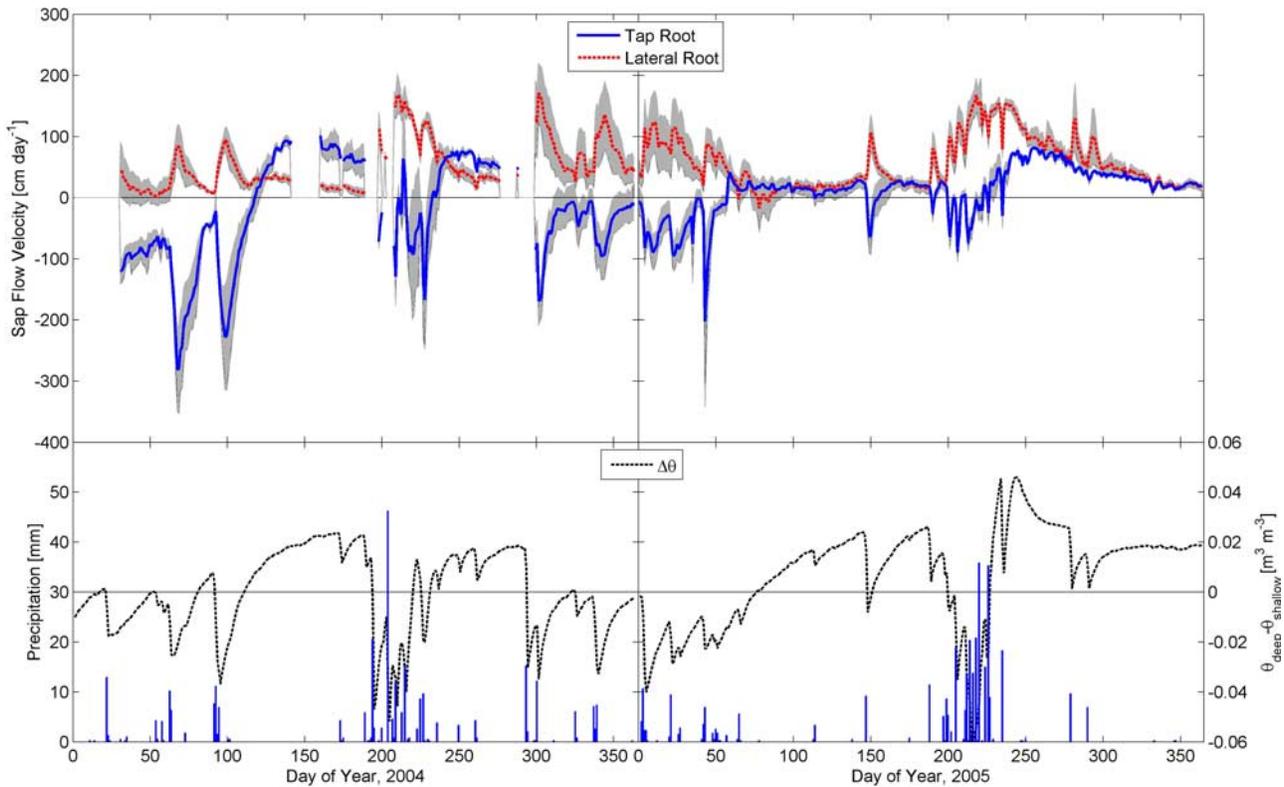
Figure 5. 2004–2005 average lateral and tap root sap flow velocity ±S.E. (upper panels) along with daily precipitation and the difference between average deep (0.5–1.0 m) and shallow (0.0–0.3 m) soil moisture. Positive sap flow in the roots indicates flow toward the tree base, and negative sap flow indicates flow away from the tree base.

season(s), this represents 15–49% of the estimated transpiration in 2004 (using the lateral and tap root totals, respectively). In the dormant season of 2005, net lateral root Q_{HR} implied that 48 mm was taken in, but this was not balanced in net taproot Q_{HR}. However, nighttime totals were in good agreement so the larger, positive daytime flows are another indicator that water may have been lost in aboveground tissues. The −15 mm of water transported downward in the taproot represents 11% of the estimated transpiration in 2005. Total 2004 growing season flow in the taproots was 21 mm, 17 mm less than the −38 mm of estimated "banked" water. It is possible that this excess moisture was carried over to 2005 which would help explain the decreased amount of hydraulic descent in the winter of 2005 and that the taproots' net flow during the 2005 growing season was 17 mm more than was banked in the winter.

4. Discussion

[29] We found that velvet mesquite trees in a semiarid savanna ecosystem redistribute soil water upwards and downward in the soil profile throughout the year including periods of canopy dormancy. Root activity probably continues throughout the year due to the non-freezing soil temperatures (Figure 2) even though winter air temperatures can fall below zero [Hultine et al., 2004]. The direction of flow in the taproots (and some deep lateral roots) displayed good correspondence with soil moisture gradients (Figure 5), which likely mirrored water potential gradients because of the uniform soil profiles [Caldwell et al., 1998]. During the

dormant winter season, hydraulic descent occurred during times when shallow soil moisture was elevated due to recent and sufficiently large precipitation events and when the canopy was not actively transpiring (Figures 4–6). When significant winter "storage" occurred, the start of the tree growing season was supported largely by the taproots with only a small contribution from lateral roots (Figures 6, 7). During this pre-monsoon summer period, winter moisture in the shallow soil layers has been largely appropriated by understory evapotranspiration (Figure 7) because the mesquites generally leaf out much later than the understory [Cable, 1977]; thus, the taproots were the primary source for canopy transpiration. Also during this time, hydraulic lift was occurring as evapotranspiration dried the shallow soils thereby providing a water potential gradient from the moist, deep soil layers to the dry, shallow soil layers (Figures 4, 6). During the monsoon season the shallow soil layers were wet, and transpiration was supported mainly by the lateral roots (Figures 5–7), which has also been shown in mature floodplain velvet mesquite trees [Snyder and Williams, 2000]. Nocturnal hydraulic descent also occurred during this period (Figure 6). After the peak of the monsoon, transpiration was increasingly supported by the taproots as the shallow soil layers again became dry (Figure 7).

[30] It is important to reiterate that there is a large degree of uncertainty in our ecosystem-scale estimate of root water movement. This uncertainty results from a small sample size of roots and trees in the ecosystem, the correction factor (Figure 1), and a lack of an in-depth laboratory validation of
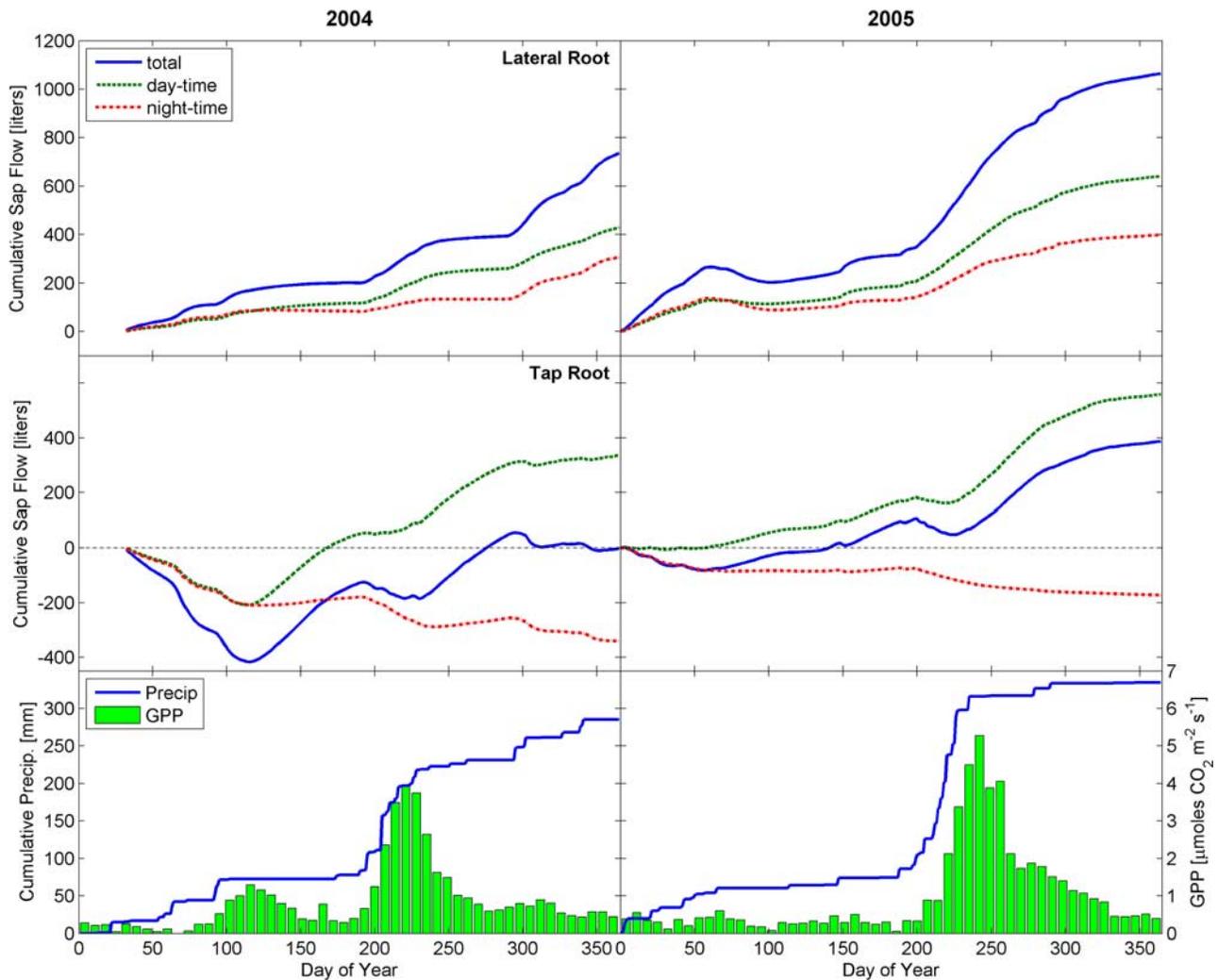
Figure 6. Yearly cumulative daily, daytime, and nighttime volumetric sap flow in a large (9.5 cm diameter) lateral root and (15.0 cm) tap root on Tree 2 for 2004 and 2005. Also, shown in the lower panels is cumulative precipitation and weekly average gross primary production (GPP). Negative (positive) sap flow indicates flow away from (toward) the tree base.

the HRM in mesquite roots. Nevertheless, we felt it was important to derive an estimate (albeit, a crude one) to compare with the major hydrologic fluxes in the ecosystem (i.e., ET and P). Although the errors of ecosystem-scale sap flow estimates are large (Table 2), the magnitude of soil water that was moved in their dormant and growing seasons was comparable, and water moved downward in the soil profile by the taproots was a considerable fraction of estimated tree transpiration (Figure 7) and likely boosted subsequent transpiration (Figure 7). For the roots that we monitored we found that hydraulic descent was a far more detectable phenomenon than hydraulic lift (Figures 5, 6), perhaps due to flow being more concentrated in the taproot. The larger lateral roots did show direct evidence of nocturnal reverse flow during the growing season (Figure 4) and even a net negative daily flow in the dormant season (Figure 6).

[31] Root sap flow at the beginning of 2005 showed that there was less banking of dormant-season precipitation than in 2004 (Figures 5, 6 and Table 2). While our estimate of deep (0.5–1.0 m) to shallow (0.025–0.30 m) soil moisture gradient was equally as strong in early 2005 (Figure 5,

lower panels), the taproots undoubtedly extended beyond 1.0 m [*Cable*, 1977; *Phillips*, 1963] and were responsive to water potential gradients that we did not quantify. Also, the winter precipitation events were larger in 2004 and would have promoted deeper infiltration of rainwater to the lateral roots; we found that lateral roots generally did not respond to smaller rainfall events that had infiltration less than ~0.25 m (data not shown). Ecosystem water and CO_2 fluxes also support the notion that there was more banking of precipitation in early 2004. ET had a more sustained rise and decay in the spring of 2004 while it rose and fell much more quickly in response to rainfall, likely indicative of mainly bare soil evaporation during the same period in 2005 (Figure 3). Likewise, photosynthesis (GPP) in the spring of 2005 was virtually undetected (Figure 6) even though there was measurable positive flow in both lateral and tap roots (Figure 6, right side). Perhaps this small amount of spring sap flow supported cell expansion during leaf flush and wood development that occurs concurrently in ring-porous species such as mesquite.
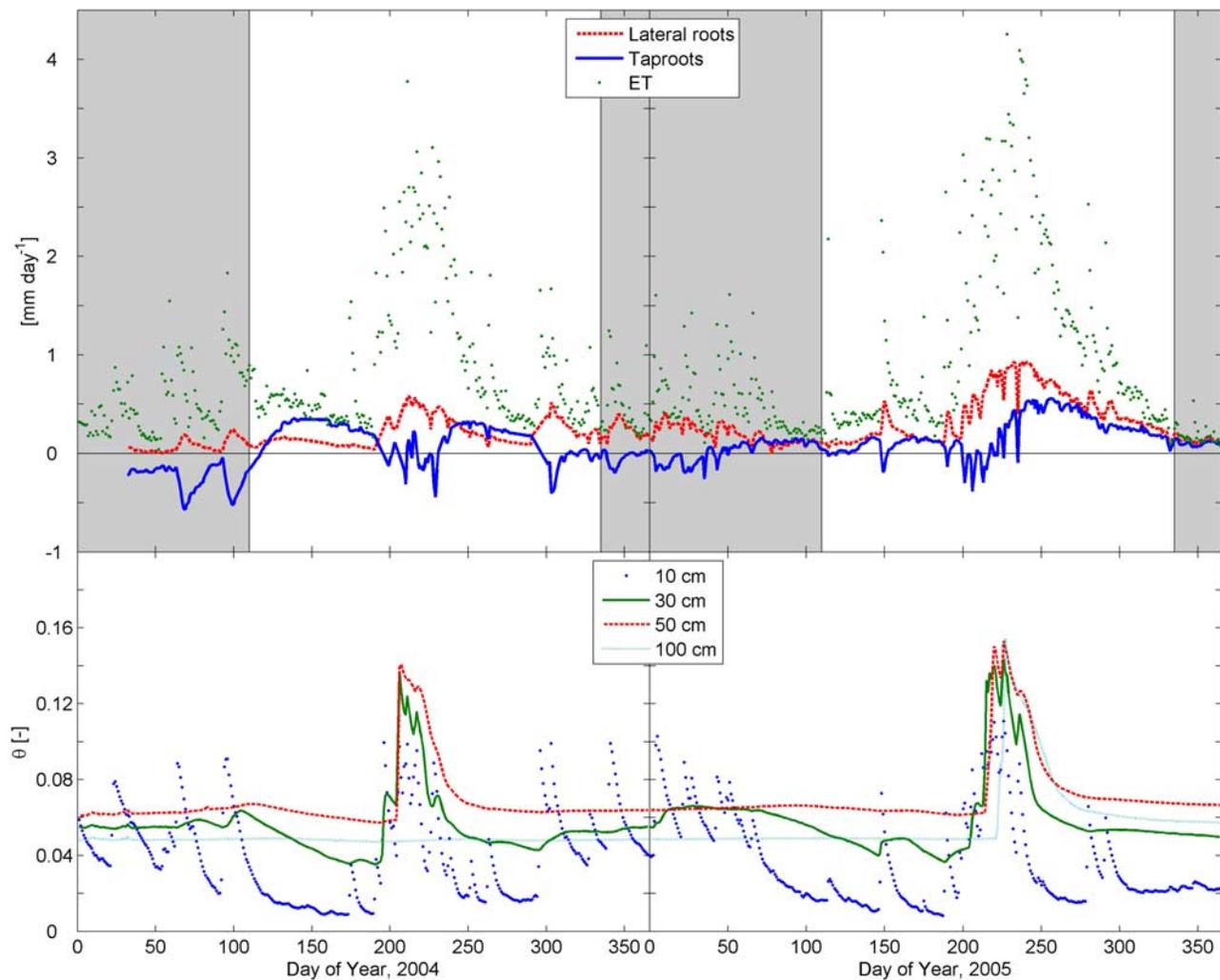
Figure 7. 2004–2005 ecosystem-scale, daytime lateral and tap root total sap flow (Q_{HR}, equation (3)) and ET from eddy covariance (upper panels). Shaded areas indicate tree canopy senescence. Also shown is the average daily volumetric soil moisture (θ) at 10, 30, 50, and 100 cm (lower panels).

[32] In addition to its hydrologic significance, we also found that hydraulic redistribution likely played an important ecological role in this ecosystem. Banked soil moisture would almost certainly be exploited during the dry early summer so long as the water does not diffuse too far away from the emitting roots (Figures 4–6). Likewise, reverse flow in the taproots during the time when monsoon rains were most abundant and then the subsequent return of upward taproot flow after the monsoon (Figures 4, 6) implies that hydraulic redistribution can lead to an extension of the growing season [*Lee et al.*, 2005; *Ryel et al.*, 2004]. However, the magnitude of GPP and ET during these "extensions" of the mesquite growing season was considerably smaller than during their peak in the summer rainy season. Thus our data suggest that hydraulic redistribution extends the period over which woody plants grow, providing them a means to compete with the grass-dominated understory which more quickly and more efficiently responds to summer rains [*Ryel et al.*, 2004; *Mendel et al.*, 2002; *Burgess et al.*, 2001a].

[33] Root sap flow data from the current study are consistent with previous investigations that report rapid response by mesquite roots to relatively small monsoon precipitation pulses [*Fravolini et al.*, 2005]. Hydraulic lift and a small amount of canopy transpiration throughout the dry early summer, coupled with the high cavitation resistance previously reported in shallow mesquite roots at this site [*Hultine et al.*, 2006], may prolong fine root activity and allow these trees to rapidly respond to summer moisture [*Fravolini et al.*, 2005; *Meinzer et al.*, 2004]. Likewise, seasonal patterns of hydraulic redistribution by mesquite roots are likely facilitated by the avoidance of both freeze-induced cavitation in winter, and drought-induced cavitation in summer. By maintaining at least some hydraulic conductivity throughout the year through cavitation resistance, root systems may remain in hydraulic contact with the soil, allowing for the passive movement of water between soil layers even during dormancy.

[34] These previously unsuspected activities whereby plants affect soil moisture contents even when dormant have important implications for vegetation change and subsequent impacts on soil hydrology. As mentioned earlier, the encroachment of woody plants in the western U.S. and much of the Earth's semiarid areas [e.g., *Archer*, 1994; *McPherson*, 1997] has potential large-scale ramifications for both carbon [*Archer*

Table 2. Ecosystem-Scale Dormant (Prior Year DOY 336–365 & DOY 1–109) and Potential Growing (Day 110–335) Season Total Lateral Root and Taproot Sap Flow for 2004 and 2005 [mm, Equation 3][b]

	2004		2005	
	Mean	Std. Err	Mean	Std. Err
Dormant Season[a]				
Lateral roots				
Day	6	3	28	11
Night	5	4	20	14
Total	12	7	48	24
Taproots				
Day	−20	6	1	10
Night	−18	5	−16	7
Total	−38	11	−15	17
Growing season				
Lateral roots				
Day	48	11	89	13
Night	20	8	28	13
Total	68	19	116	25
Taproots				
Day	30	16	42	12
Night	−9	10	−9	6
Total	21	24	32	15
Evapotranspiration	285		332	
Precipitation	286		334	

[a]Data available for only DOY 31–109 in 2004.
[b]Also, annual total precipitation and savanna ET from eddy covariance [mm].

et al., 2001; *Pacala et al.*, 2001; *Jackson et al.*, 2002] and water cycling [*Wilcox*, 2002; *Huxman et al.*, 2005]. Given the considerable evidence that hydraulic redistribution in woody plants is a common phenomenon, our findings clearly point to the need to account for this process in ecohydrologic modeling efforts [*Guswa*, 2005]. Many modeling efforts include only the effect of soil physics on soil moisture redistribution [e.g., *Guswa et al.*, 2002]. Our findings, along with an ever-growing body of evidence, show that woody plant roots routinely facilitate the rapid redistribution of soil moisture through a network of roots that readily transmit significant quantities of water across soil water potential gradients.

[35] Savanna ecosystems like the one we studied are common throughout the world [*Huntley and Walker*, 1982]. In many of these, some partitioning of the plant-available soil water is thought to occur with shallower-rooted understory grasses relying primarily on near-surface moisture and trees relying mainly on water that has infiltrated deeper into the soil profile [*Walter*, 1971]. In much of the southwest U.S., it is likely that the source of plant water for the woody and understory plants is not as clearly partitioned because of the relatively shallow depths of infiltration [*Cable*, 1980; *Scott et al.*, 2000]. However, hydraulic redistribution by mesquite and other woody plants likely facilitates such a partitioning [*Zou et al.*, 2005] during periods when hydraulic descent occurs. Likewise, hydraulic redistribution would lead to an even greater enhancement of moisture for the trees in wetter savanna ecosystems where a "two-source" partitioning can occur [*Porporato et al.*, 2003].

[36] Results from this investigation show that mature mesquite trees (*Prosopis* spp.) redistribute a significant amount of water throughout the year, and that HR may have considerable consequences on tree, ecosystem and regional level ET and CO_2 fluxes. Hydraulic redistribution allows deeply rooted plants such as mesquite to involve most, if not all of their root systems in water uptake even when moisture is spatially limited throughout much of the growing season. The propensity to redistribute water, particularly during dormancy may be an important competitive advantage in regions where summer, monsoonal rains may become increasingly more uncertain during climate change. The improved water status via HR, may, in part facilitate the pervasive encroachment of mesquite throughout much of the southwestern United States, northern Mexico, and other warm-temperate and subtropical zones. One can imagine that if the trees only had lateral roots in the shallow soil layers, their growing season would be limited to the rainy season when these soil layers were wet. However, because of a deep root system, the mesquite effectively store precipitation via hydraulic descent during the winter dormant period and during the wettest parts of the summer rainy season. This, in effect, likely increases the productivity and fitness of these deeply rooted plants both spatially and temporally.

References

Archer, S. A. (1994), Woody Plant Encroachment into Southwestern Grasslands and Savannas: Rates, Patterns and Proximate Causes, in *Ecological Implications of Livestock Herbivory in the West*, M. Vavra, W. Laycock and R. Pieper (eds), Society for Range Management: Denver, Colorado, 13–68.

Archer, S. A., T. W. Boutton, and K. A. Hibbard (2001), Trees in Grasslands: Biogeochemical Consequences of Woody Plant Expansion, in *Global Biogeochemical Cycles in the Climate System*, pp. 115–138, Academic Press, Durham, NC.

Barrett, D. J., T. J. Hatton, J. E. Ash, and M. C. Ball (1995), Evaluation of the heat pulse velocity technique for measurement of sap flow in rainforest and eucalypt forest species of south-eastern Australia, *Plant Cell and Environ.*, 18, 463–469.

Becker, P., and W. R. N. Edwards (1999), Corrected heat capacity of wood for sap flow calculations, *Tree Physiol.*, 19, 767–768.

Brooks, J. R., F. C. Meinzer, R. Coulombe, and J. Gregg (2002), Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests, *Tree Physiol.*, 22, 1107–1117.

Burgess, S. S. O., and T. M. Bleby (2006), Redistribution of soil water by lateral roots mediated by stem tissues, *J. Exp. Bot.*, 57, 3283–3291.

Burgess, S. S. O., M. A. Adams, N. C. Turner, and C. K. Ong (1998), The redistribution of soil water by tree root systems, *Oecologia*, 115, 306–311.

Burgess, S. S. O., M. A. Adams, N. C. Turner, D.A White, and C. K. Ong (2001a), Tree roots: Conduits for deep recharge of soil water, *Oecologia*, 126, 158–165.

Burgess, S. S. O., M. A. Adams, N. C. Turner, C. R. Beverly, C. K. Ong, A. A. H. Khan, and T. M. Bleby (2001b), An improved heat pulse method to measure slow and reverse flow in woody plants, *Tree Physiol.*, 21, 589–598.

Cable, D. R. (1977), Seasonal use of soil water by mature velvet mesquite, *J. Range Manage.*, 30, 4–11.

Cable, D. R. (1980), Seasonal patterns of soil water recharge and extraction on semidesert ranges, *J. Range Manage.*, 33, 9–15.

Caldwell, M. M., and J. H. Richards (1989), Hydraulic lift: Water efflux from upper roots improves effectiveness of water uptake by deep roots, *Oecologia*, 79, 1–5.

Caldwell, M. M., T. E. Dawson, and J. H. Richards (1998), Hydraulic lift: Consequences of water efflux from the roots of plants, *Oecologia*, 113, 151–161.

Dawson, T. E. (1993), Hydraulic lift and water use by plants: Implications for water balance, performance and plant-plant interactions, *Oecologia*, 95, 565–574.

Emerman, S. H., and T. E. Dawson (1996), Hydraulic lift and its influence on the water content of the rhiozosphere: An example from sugar maple, Acer saccharum, *Oecologia*, 1, 273–278.

Falge, E., D. Baldocchi, R. Olson, et al. (2001), Gap filling strategies for long term energy flux data sets, *Agric. For. Meteorol.*, 107, 71–77.

Fernández, J. E., M. J. Palomo, A. Díaz-Espejo, B. E. Clothier, S. R. Green, I. F. Girón, and F. Moreno (2001), Heat-pulse measurements

of sap flow in olives for automating irrigation: Tests, root flow and diagnostics of water stress, *Agric. Water Manage.*, 51, 99–123.

Fravolini, A., K. R. Hultine, E. Brugnoli, R. Gazal, N. B. English, and D. G. Williams (2005), Precipitation pulse use by an invasive woody legume: The role of soil texture and pulse size, *Oecologia*, 144, 618–627.

Guswa, A. J. (2005), Soil-moisture limits on plant uptake: An upscaled relationship for water-limited ecosystems, *Adv. Water Resour.*, 28, 543–552.

Guswa, A. J., M. A. Celia, and I. Rodriquez-Iturbe (2002), Models of soil moisture dynamics in ecohydrology: A comparative study, *Water Resour. Res.*, 38(9), 1166, doi:10.1029/2001WR000826.

Huete, A., K. Didan, T. Miura, E. Rodreguez, X. Gao, and L. Ferreira (2002), Overview of the radiometric and biophysical performance of the MODIS vegetation indices, *Remote Sens. Environ.*, 83, 195–213.

Hultine, K. H., D. G. Williams, S. S. O. Burgess, and T. O. Keefer (2003a), Contrasting patterns of hydraulic redistribution in three desert phreatophytes, *Oecologia*, 135, 167–175.

Hultine, K. H., W. L. Cable, S. S. O. Burgess, and D. G. Williams (2003b), Hydraulic redistribution by deep roots of a Chihuahuan Desert phreatophyte, *Tree Physiol.*, 23, 353–360.

Hultine, K. R., R. L. Scott, W. L. Cable, D. C. Goodrich, and D. G. Williams (2004), Hydraulic redistribution by a dominant, warm desert phreatophyte: Seasonal patterns and response to precipitation pulses, *Functional Ecol.*, 18, 530–538.

Hultine, K. R., D. F. Koepke, W. T. Pockman, A. Fravolini, J. S. Sperry, and D. G. Williams (2006), Influence of soil texture on hydraulic properties and water relations of a dominant warm-desert phreatophyte, *Tree Physiol.*, 26, 313–324.

Huntley, B. J., and B. H. Walker (1982), Introduction, in *Ecology of Tropical Savannas*, B. J. Huntley and B. H. Walker (eds.), Ecological Studies 42, Springer-Verlag, pp. 1–2.

Huxman, T. E., B. P. Wilcox, D. D. Breshears, R. L. Scott, K. A. Snyder, E. E. Small, K. R. Hultine, W. T. Pockman, and R. B. Jackson (2005), Ecohydrological implication of woody plant encroachment, *Ecology*, 86, 308–319.

Jackson, R. B., J. L. Banner, E. G. Jobbagy, W. T. Pockman, and D. H. Wal (2002), Ecosystem carbon loss with woody plant invasion of grasslands, *Nature*, 418, 623–626.

Kurz-Besson, C., D. Otieno, and R. Lobo Do Vale et al. (2006), Hydraulic lift in cork oak trees in a savannah-type Mediterranean ecosystem and its contribution to the local water balance, *Plant Soil*, 282, 361–378.

Lee, J. E., R. S. Oliviera, T. E. Dawson, and I. Fung (2005), Root functioning modifies seasonal climate, *PNAS*, 102, 17,576–17,581.

Leffler, A. J., M. S. Peek, R. J. Ryel, C. Y. Ivans, and M. M. Caldwell (2005), Hydraulic redistribution through the root systems of senesced plants, *Ecology*, 86, 633–642.

Ludwig, F., T. E. Dawson, H. Kroon, F. Berendse, and H. H. T. Prins (2003), Hydraulic lift in Acacia tortilis trees on an East African savanna, *Oecologia*, 134, 293–300.

Malhi, Y., A. D. Nobre, J. Grace, B. Kruijt, M. G. P. Pereira, and A. Culf (1998), Carbon dioxide transfer over a Central Amazonian rain forest, *J. Geophys. Res.*, 103, 593-31, 612.

McCulley, R. L., E. G. Jobbágy, W. T. Pockman, and R. B. Jackson (2004), Nutrient uptake as a contributing explanation for deep rooting in arid and semi-arid ecosystems, *Oecologia*, 141, 620–628.

McPherson, G. R. (1997), *Ecology and management of North American savannas*, University of Arizona Press, Tucson, AZ.

Meinzer, F. C., J. R. Brooks, S. Bucci, G. Goldstein, F. G. Scholz, and J. M. Warren (2004), Converging patterns of uptake and hydraulic redistribution of soil water in contrasting woody vegetation types, *Tree Physiol.*, 24, 919–928.

Mendel, M., S. Hergarten, and H. J. Neugebauer (2002), On a better understanding of hydraulic lift: A numerical study, *Water Resour. Res.*, 38(10), 1183, doi:10.1029/2001WR000911.

Mooney, H. A., S. L. Gulmon, P. W. Rundel, and J. Ehleringer (1980), Further observations on the water relations of Prosopis tamarugo of the Northern Atacama Desert, *Oecologia*, 44, 177–180.

Oliveira, R. S., T. E. Dawson, S. S. O. Burgess, and D. C. Nepstad (2005), Hydraulic redistribution in three Amazonian trees, *Oecologia*, 145, 354–363.

Pacala, S. W., G. C. Hurtt, and D. P. Baker, et al. (2001), Consistent land- and atmosphere-based US carbon sink estimates, *Science*, 292, 2316–2320.

Phillips, W. S. (1963), Depth of roots in soil, *Ecology*, 44, 424.

Porporato, A., F. Laio, L. Ridolfi, K. K. Caylor, and I. Rodriguez-Iturbe (2003), Soil moisture and plant stress dynamics along the Kalahari precipitation gradient, *J. Geophys. Res.*, 108(D3), 4127, doi:10.1029/2002JD002448.

Querejeta, J. I., L. M. Egerton-Warburton, and M. F. Allen (2007), Hydraulic lift may buffer rhizosphere hyphae against the negative effects of severe soil drying in a California Oak savanna, *Soil Biol. Biochem.*, 39, 409–417.

Reichstein, M., et al. (2005), On the separation of net ecosystem exchange into assimilation and ecosystem respiration: Review and improved algorithm, *Global Change Biol.*, 11(9), 1424–1439.

Richards, J. H., and M. M. Caldwell (1987), Hydraulic lift: Substantial nocturnal water transport between soil layers by Artemisia tridentata roots, *Oecologia*, 73, 486–489.

Ryel, R. J., M. M. Caldwell, C. K. Yoder, D. Or, and A. J. Leffler (2002), Hydraulic redistribution in a stand of Artemisia tridentate: Evaluation of benefits to transpiration assessed with a simulation model, *Oecologia*, 130, 173–184.

Ryel, R. J., M. M. Caldwell, A. J. Leffler, and C. K. Yoder (2003), Rapid soil moisture recharge to depth by roots in a stand of Artemisia tridentata, *Ecology*, 84, 757–764.

Ryel, R. J., A. J. Leffler, M. S. Peek, C. Y. Ivans, and M. M. Caldwell (2004), Water conservation in Artemisia tridentata through redistribution of precipitation, *Oecologia*, 141, 335–345.

Scott, R. L., W. J. Shuttleworth, T. O. Keefer, and A. W. Warrick (2000), Modeling multiyear observations of soil moisture recharge in the semiarid American southwest, *Water Resour. Res.*, 36, 2233–2247.

Snyder, K. A., and D. G. Williams (2000), Water sources used by riparian trees varies among stream types on the San Pedro River, Arizona, *Agric. For. Meteorol.*, 105, 227–240.

Stromberg, J. C., S. D. Wilkins, and J. A. Tress (1993), Vegetation-hydrology models: Implications for management of Prosopis velutina (velvet mesquite) riparian ecosystems, *Ecol. Appl.*, 3, 307–314.

Swanson, R. H. (1994), Significant historical developments in thermal methods for measuring sap flow in trees, *Agric. For. Meteorol.*, 72, 113–132.

Swanson, R. H., and D. W. A. Whitfield (1981), A numerical analysis of heat pulse velocity and theory, *J. Exp. Bot.*, 32, 221–239.

Walter, H. (1971), *Ecology of Tropical and Subtropical Vegetation*, Oliver & Boyd, Edinburgh.

Webb, E. K., G. I. Pearman, and R. Leuning (1980), Correction of flux measurements for density effects due to heat and water vapor transfer, *Q. J. R. Meteorol. Soc.*, 106, 85–100.

Wilcox, B. P. (2002), Shrub control and streamflow on rangelands: A process-based viewpoint, *J. Range Manage.*, 55, 318–326.

Williams, D. G., et al. (2004), Evapotranspiration components determined by stable isotope, sap flow and eddy covariance techniques, *Agric. For. Meteorol.*, 125, 241–258.

Zou, C. B., P. W. Barnes, S. Archer, and C. R. McMurtry (2005), Soil moisture redistribution as a mechanism of facilitation in savanna tree-shrub clusters, *Oecologia*, 145, 32–40.

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