

K. R. Hultine · D. G. Williams · S. S. O. Burgess ·  
T. O. Keefer

## Contrasting patterns of hydraulic redistribution in three desert phreatophytes

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**Abstract** We measured sap flow in taproots, lateral roots and stems within a single individual in each of three co-occurring tree species in a Chihuahuan desert arroyo to assess the seasonality and magnitude of hydraulic redistribution. Nocturnal reverse flow (hydraulic redistribution) was detected in shallow lateral roots of *Fraxinus velutina* and *Juglans major* during periods when surface soils were dry. Reverse flow in the *Fraxinus* lateral root ranged from near zero to  $120 \text{ g h}^{-1}$ , and was inversely correlated with nighttime vapor pressure deficit ( $D$ ), suggesting that nighttime transpiration may have inhibited hydraulic redistribution. Reverse flow in the *Juglans* lateral root ranged from near zero to  $18 \text{ g h}^{-1}$ . There was no relationship between reverse flow and nighttime  $D$  in the *Juglans* lateral root, despite a weak positive relationship between nighttime  $D$  and rates of basipetal flow (flow towards the stem) in the taproot. Reverse flow in *Fraxinus* and *Juglans* ceased when surface soils were wetted by monsoon rains and flooding. We found no reverse flow or seasonal variation in root sap flow in *Celtis reticulata*. However, basipetal sap flow in *Celtis* roots continued throughout most of the evening, even during periods when  $D$  was near zero, and commenced in the morning more than two hours after the onset of sap flow in the main stem. Patterns of nocturnal root sap flow in *Celtis* may have been facilitated by the diurnal withdrawal from, and refilling of above ground storage compartments (i.e. above ground diurnal storage capacity), which may have prevented hydraulic redistribution.

Species differences in nocturnal root function may have significant impacts on ecosystem hydrological fluxes, and should be considered when scaling fluxes to catchment, landscape, and regional levels.

**Keywords** Sap flow · Hydraulic redistribution · Nighttime transpiration · Phreatophytes · Chihuahuan desert

### Introduction

Plants capture, store, redistribute, and transpire water in response to environmental or physiological conditions, and in doing so, affect the temporal and spatial dynamics of water movement at the ecosystem and larger scales. Large woody plants that occur in semi-arid environments often possess dimorphic root systems in which deep roots access groundwater while lateral roots forage for surface moisture and mineral nutrients (Pate et al. 1995). Root systems that span soil layers act as conduits that potentially redistribute water from moist to dry soil layers. The phenomenon termed “hydraulic redistribution” (Burgess et al. 1998) usually occurs nocturnally when reduced transpiration allows xylem water potential ( $\psi_x$ ) of roots in dry soil layers to rise above soil water potential ( $\psi_s$ ). Although previous investigations mostly have focused on the upward transfer of water from moist sub-surface soils to dry surface soils (Richards and Caldwell 1987), water also can be transported downward when surface soils are wetted by precipitation (Burgess et al. 1998, 2001a; Schulze et al. 1998; Smith et al. 1999).

The upward transfer of water to surface soils (hydraulic lift) may increase daily transpiration by storing water in the otherwise dry rhizosphere that can later be acquired by lateral roots (Dawson 1993; Emerman and Dawson 1996). By involving more roots in uptake (i.e. laterals as well as taproots), the total supply capacity of the root system is increased (Simonneau and Habib 1994). However, hydraulic lift does not necessarily enhance a favorable water balance because the redistributed water

K. R. Hultine (✉) · D. G. Williams  
School of Renewable Natural Resources,  
University of Arizona, Tucson, AZ 85721, USA  
e-mail: khultine@ag.arizona.edu  
Fax: +1-520-6218801

S. S. O. Burgess  
Department of Integrated Biology,  
University of California,  
Berkeley, CA 94720–3140, USA

T. O. Keefer  
USDA-ARS Southwest Watershed Research Center,  
Tucson, AZ 85719, USA

can be lost to soil evaporation or to competing plants with shallow root systems (Caldwell and Richards 1989; Dawson 1993). Alternatively, hydraulic lift may play a greater role in fine root longevity and mineral nutrient uptake (Caldwell et al. 1998).

The hydraulic characteristics of vascular plants may impose constraints to hydraulic redistribution. For example, plants with stomata that remain open during the evening may transpire significant amounts of water at night (Matyssek et al. 1995; Donovan et al. 1999). In desert communities, nighttime transpiration would likely be most prevalent in phreatophytic plants that have access to stable water, thereby reducing the requirements for stomatal control of water loss during periods of relatively high evaporative demand. Alternatively, plants that have a large internal storage capacity may continue refilling tissues well into the evening after transpiration ceases or is reduced. Water absorbed by roots may be transported to internal storage compartments as long as there is a water potential gradient ( $\Delta\psi$ ) from the absorbing roots to the refilling storage tissues (Goldstein et al. 1998; Meinzer et al. 2001). Nighttime transpiration, and/or the refilling of storage tissues may indirectly limit, or reduce the magnitude of hydraulic redistribution by creating a stronger sink for water within the plant than exists in the dry soil surrounding the plant roots;  $\psi_x$  of roots thus would remain below  $\psi_s$ , disallowing water efflux.

The heat pulse method has been commonly used to study sap flow in roots and stems (Marshall 1958; Edwards et al. 1996). However, traditional heat pulse methods overestimate sap flow when rates are slow because dissipation of the heat pulse by conduction is more rapid than the movement of the heat pulse by convection (heat transport by sap flow). A modification of the heat pulse method, the heat ratio method (HRM), previously described by Burgess et al. (1998, 2001b) allows for measurements of low sap flow rates in roots and stems. Briefly, the HRM employs temperature probes at equal distances down- and upstream from a heat source. The heat flux to down- and upstream probes is compared, rather than the time required for the probes to read maximum temperature.

We deployed the HRM on deep and shallow roots, and a traditional single-sensor (Cohen et al. 1981) heat pulse velocity method (HPV) on the main stems of three co-occurring riparian trees: *Celtis reticulata* Torr., *Fraxinus velutina* Torr., and *Juglans major* Torr. located in a desert arroyo in southeastern Arizona. Seasonal variations in hydraulic redistribution were investigated in relation to groundwater depth, soil moisture, and nighttime vapor pressure deficit. Our goals were to (1) measure the seasonal patterns of hydraulic redistribution in deep and shallow roots, and (2) assess whether hydraulic characteristics of desert phreatophytes may impose constraints on redistribution.

## Materials and methods

### Site description

The study was conducted at the Walnut Gulch Experimental Watershed in southeastern Arizona during the 2000 growing season. The USDA-ARS monitors runoff at several flumes along Walnut Gulch and its main tributaries. This study was conducted near flume no. 2 along the main channel (31°44'N 110°05'W, elevation 1,290 m). Precipitation at Walnut Gulch is bimodal, with about 60% of the 360 mm average annual precipitation falling during the summer "monsoon" (July–September) and 30% falling during the winter (December–March). Groundwater at the site is perched above the regional aquifer by a Schieffelin Granodiorite intrusion, and varies seasonally in depth from approximately 1 to 10 m. Groundwater recharge is from winter and summer rain events. Daily rainfall was collected at the site with a rain gauge, while groundwater depth was monitored with ISCO 2920 water level recorders (ISCO, Lincoln Neb., USA) placed in two pre-existing wells. Atmospheric vapor pressure deficit was calculated from air temperature and humidity data collected at Walnut Gulch. Air temperature and humidity were measured with a Campbell HMP35C sensor (Campbell Scientific, Logan, Utah, USA) every 10 s and averaged at 20 min intervals. Overstory vegetation is dominated by *Prosopis velutina* Woot., intermixed with *C. reticulata*, *J. major*, *F. velutina*, and *Populus fremontii* Wats. The understory is dominated by the perennial C<sub>4</sub> grass *Sporobolus wrightii* Munro. Mature *C. reticulata*, *F. velutina*, and *J. major* trees (one tree per species) were selected for sap flow measurements. *Celtis* and *Juglans* occurred north of the channel where soils consisted of 78% sand, 15% silt, and 7% clay. *Fraxinus* occurred on the south bank of the channel where soils consisted of 84% sand, 14% silt, and 2% clay.  $\psi_s$  was monitored periodically throughout the measurement period with a network of individually calibrated screen cage psychrometers (J.D. Merrill, Logan, Utah, USA). Psychrometers were installed 1.5, 3.0, and 4.5 m from the base of each tree at 20, 35, and 50 cm depths. Measurements were recorded every half-hour with a Campbell CR7X data logger (Campbell Scientific, Logan, Utah, USA). Predawn leaf water potentials ( $\psi_l$ ) were measured on the three study trees periodically throughout the growing season with a Scholander pressure chamber (PMS, Corvallis, Ore., USA).

### Root sap flow measurements

Soil around the base of each tree was carefully excavated to expose the proximal region of large lateral roots (>3 cm diameter) and taproots (*Celtis* did not have a discernable taproot). Heat ratio probe sets were inserted into the xylem of roots a few centimeters from the proximal root collars. A single probe set was inserted into the roots that had diameters of less than 10 cm, while two probe sets were inserted into the larger roots (i.e. diameters greater than 10 cm). In all, one taproot and one to three lateral roots on each tree were instrumented. A stainless steel drill guide was placed over an exposed section of sapwood to ensure accurate placement of the probe sets. The probe sets were constructed by Thermal Logic (Pullman, Wash., USA) and consisted of three 35 mm long stainless steel probes spaced 6 mm apart. The center probe contained an Evanohm 44- $\Omega$  line heater, while the two outside probes contained three chromel-constantan thermocouple sensors spaced 10, 20, and 30 mm from the base of the probe. After probe installation, the roots were covered with a tarpaulin to prevent radiant heating by direct sunlight. Measurements were recorded every half-hour from 7 July (day 189) through 6 August (day 219), and again from 15 August (day 228) through 24 September (day 268) with Campbell Scientific CR10X data loggers and control systems (Campbell Scientific, Logan, Utah, USA). A 6-s heat pulse was produced to heat the sapwood and temperatures were recorded during the period in which the ratios of the down- and upstream temperatures were most constant (between 30 and 90 s after the heat pulse). Measurements were temporarily discontinued between 6 August

and 15 August due to flooding events on 6 August and 11 August (days 219 and 224). The heat pulse velocity ( $V_h$ ;  $\text{cm s}^{-1}$ ) was calculated according to Burgess et al. (1998):

$$V_h = \frac{k}{x} \ln\left(\frac{v_1}{v_2}\right) \quad (1)$$

where  $k$  is the thermal diffusivity of wet wood,  $x$  is the distance between the line heater and the thermocouple sensors, and  $v_1$  and  $v_2$  are the increases in temperature at equidistant points downstream and upstream, respectively,  $x$  cm from the heater. Errors arising from small inaccuracies in probe placement were corrected at the conclusion of the study by severing the roots to stop all sap flow. Probe spacing error was determined according to Burgess et al. (2001b):

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

where  $x_1$  and  $x_2$  are distances in centimeter of the down- and upstream probes, respectively, and  $t$  is the median measurement time (in this case, 60 s) after the release of the heat pulse (Marshall 1958). At  $V_h = 0$ , Eq. 2 yields:

$$x_2 = \sqrt{4kt \ln\left(\frac{v_1}{v_2}\right) + x_1^2} \quad (3)$$

where  $x_2$  is designated the incorrectly spaced probe, and  $x_1$  is assumed to be correctly spaced at 6 mm. Because it is unknown which probe is incorrectly spaced, or whether both probes are incorrectly spaced, Eq. 3 was solved for  $x_1$  and  $x_2$  and the two solutions were averaged to generate an intermediate solution for both probes (Burgess et al. 1998). The thermal diffusivity of wet wood ( $k$ ) was calculated empirically from Marshall (1958):

$$k = \frac{k_{\text{gw}}}{\rho c} 10,000 \quad (4)$$

where  $k_{\text{gw}}$  is the thermal conductivity ( $\text{J m}^{-1} \text{s}^{-1} \text{ } ^\circ\text{C}^{-1}$ ),  $\rho$  is the density ( $\text{kg m}^{-3}$ ) (cf. Burgess et al. 2001c) and  $c$  is the specific heat capacity ( $\text{J kg}^{-1} \text{ } ^\circ\text{C}^{-1}$ ) of fresh sapwood. We calculated  $k_{\text{gw}}$  from:

$$k_{\text{gw}} = k_w m_c \frac{\rho_b}{\rho_w} + k_{\text{dw}} \left(1 - m_c \frac{\rho_b}{\rho_w}\right) \quad (5)$$

where  $k_w$  and  $k_{\text{dw}}$  are the thermal conductivities of water ( $6.025 \times 10^{-1} \text{ J m}^{-1} \text{ s}^{-1} \text{ } ^\circ\text{C}^{-1}$ ) and dry wood respectively,  $m_c$  is the moisture fraction of fresh wood ( $\text{kg kg}^{-1}$ ),  $\rho_b$  is the basic density (dry weight/fresh volume) of sapwood, and  $\rho_w$  is the density of water (Swanson 1983; Burgess et al. 2001b).

Drilling holes and inserting probes inevitably cause extensive mechanical damage to xylem tissues. We corrected for wounding using a "finite-element" numerical model generated by Burgess et al. (2001b):

$$V_c = aV_h + bV_h^2 + cV_h^3 \quad (6)$$

where the coefficients  $a$ ,  $b$ , and  $c$ , are derived from numerical analysis of the effect of wounding on  $V_h$  for varying wound widths. (Note that for negative values of  $V_h$ , the form  $V_c = aV_h - bV_h^2 - cV_h^3$  should be used.) Coefficients in Eq. 6 were derived over the measurement time of  $t = 30\text{--}90$  s after the release of the heat pulse. We estimated the wound width by measuring the discoloration of sapwood from the formation of tyloses around the probe insertion points. Wound diameters ranged from 0.19 cm to 0.30 cm.

Corrected values of heat pulse velocity ( $V_c$ ) were converted to sap velocity ( $V_s$ ) ( $\text{cm h}^{-1}$ ) according to Barrett et al. (1995):

$$V_s = \frac{V_c \rho_b (c_w + m_c c_s)}{\rho_s c_s} \quad (7)$$

where  $c_w$  and  $c_s$  are the specific heat of dry wood ( $1,200 \text{ J kg}^{-1} \text{ } ^\circ\text{C}^{-1}$  at  $20^\circ\text{C}$ , Becker and Edwards 1999), and sap (assumed to equal that of water,  $4,182 \text{ J kg}^{-1} \text{ } ^\circ\text{C}^{-1}$  at  $20^\circ\text{C}$ ), and  $\rho_s$  is the density of sap (assumed to equal that of water,  $1.0 \times 10^3 \text{ kg m}^{-3}$ ). Sap flow ( $\text{kg}$

$\text{day}^{-1}$ ) was calculated by multiplying the cross-sectional sapwood area under the bark ( $\pi r^2$ ) by  $V_s$ .

## Stem sap flow measurements

Stem sap flow measurements were conducted to measure whole tree transpiration and to estimate the lag time between the time stem and root sap flow commenced during morning hours. Since we were not concerned with reverse flow in stems, we measured stem sap flow with a less expensive, single-probe heat pulse approach (HPV). The HPV probe sets (Thermal Logic, Pullman, Wash., USA) were similar to the HRM probe sets except that they were without an upstream thermocouple probe (see Schaeffer et al. 2000 for description). Two to four probe sets per tree were inserted at 1.5 m height into exposed sapwood with a stainless steel drill guide. Stem sap flow was measured every half-hour from 7 July (day 189) through 24 September (day 268) with Campbell Scientific CR10X data loggers and control systems (Campbell Scientific, Logan, Utah, USA). An 8-s heat pulse was generated by the up-stream line-heater and temperature was measured for 60 s after the heat pulse by the downstream thermocouples. The time to maximum temperature rise and the maximum temperature difference were recorded. The heat pulse velocity was estimated according to Cohen et al. (1981):

$$V_h = \frac{\sqrt{\chi^2 - 4kt_m}}{t_m} \quad (8)$$

where  $x$  is the distance from the heater,  $k$  is the thermal diffusivity of wet wood, and  $t_m$  is the time required for the temperature sensors to record maximum temperature after the release of the heat pulse. The thermal diffusivity was determined by averaging the time to maximum temperature measurements during lowest flow (assumed to be between 0200 and 0400 hours, Schaefer et al. 2000), and calculated as:

$$k = x^2 / t_{m0} \quad (9)$$

where  $t_{m0}$  is time to maximum temperature at zero flow.

The numerical model used to correct for mechanical wounding from the HRM sensors could not be applied to the HPV sensors. Therefore, wounding corrections were estimated from Swanson and Whitfield (1981). However, since the corrections reported by Swanson and Whitfield do not apply directly to our probe configuration (thermocouples placed 0.6 cm downstream from heater), there may be small errors (less than 10%) in the absolute stem sap flow values reported in the present study.

HPV, through numerical analysis, has been shown to be less accurate at low sap velocities than at high sap velocities (Swanson and Whitfield 1981, Barrett et al. 1995). Therefore, velocities below  $5 \text{ cm h}^{-1}$  were not evaluated in the final analysis (Swanson and Whitfield 1981; Schaefer et al. 2000). Heat pulse velocity was converted to sap flow velocity using Eq. 7, and was scaled to sap flow ( $\text{kg day}^{-1}$ ) using the method described above. Since sap flow varies proportionally with cross-sectional sapwood area, large differences arise between the various sized roots and the stems. Therefore, data comparisons between large and small roots and between roots and stems were presented in terms of sap velocity.

## Root distribution measurements

After root sections containing the probes were excised, the remainder of the lateral roots was excavated. Roots that remained in the upper 1 m of the soil profile were classified as shallow roots, whereas roots that extended below 1 m were classified as deep lateral roots. We assumed that the taproots extended into stable groundwater, as there was no evidence of lateral roots emerging from the taproots within the upper 1 m of the soil profile. *Fraxinus* and *Juglans* displayed typical dimorphic root distributions, with a network of shallow lateral roots and deep roots. Roots that demonstrated reverse flow in both species remained in the upper

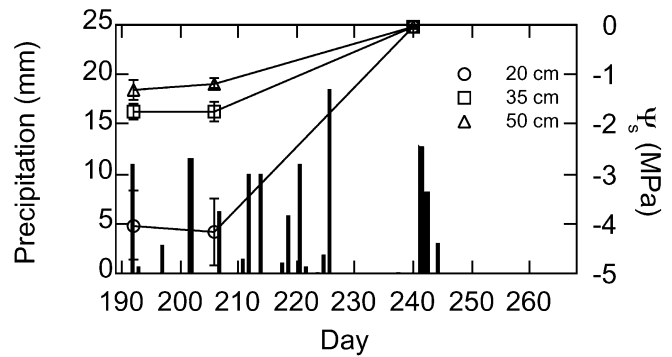
75 cm of the soil profile. Conversely, *Celtis* did not have a discernable taproot and all the lateral roots contained sinker roots that extended below 1 m, and secondary lateral roots that remained above 1 m.

#### Wood density and wood saturated water content

The density and saturated water content of stem wood were measured on each tree using five 5×30 mm stem cores. Cores were collected from the base of each tree with an increment bore, and were immediately placed in aluminum foil and sealed in vials. The cores were saturated in deionized water for 48 h, and were weighed to the nearest 0.001 g after they were briefly air-dried. The cores were oven-dried for 48 h at 90°C and re-weighed. Saturated water content was determined by dividing the saturated mass minus the dry mass by the dry mass. Wood density was determined by dividing the dry mass by the volume of the core.

## Results

Because there was no correlation between  $\psi_s$  and distance from tree base, data from all the psychrometer installations were pooled. At the beginning of the sap flow experiments (9 July),  $\psi_s$  ranged from  $-4.0$  MPa at 20 cm to  $-1.2$  MPa at 50 cm, and demonstrated little change from 9 July to 25 July, despite a series of moderate rain events between the two measurement periods (Fig. 1).  $\psi_s$  changed dramatically after two large flow events on 6 August and 11 August (days 219 and 224) topped the channel banks and flooded the terraces on both sides of the channel. On 27 August (day 240),  $\psi_s$  was near zero at all depths (Fig. 1). Diel fluctuations in  $\psi_s$  that are often associated with hydraulic lift were not observed during this study.  $\psi_1$  remained high in all study trees throughout the growing season. On 1 June before the onset of the summer monsoon season,  $\psi_1$  ranged from  $-0.4$  MPa in *Celtis* and *Fraxinus* to  $-0.45$  MPa in *Juglans*. Measurements of  $\psi_1$  were slightly higher in *Celtis* and *Juglans* ( $-0.3$  MPa) on 17 July after moderate rainfall, but were unchanged in *Fraxinus*. On 27 August, 16 days after the second flood,  $\psi_1$



**Fig. 1** Daily rainfall at Walnut Gulch in southeastern Arizona between 7 July 2000 and 24 September 2000 (days 189–268), and profiles of soil water potential ( $\psi_s$ ) on 9 July, 25 July and 27 August 2000, (days 191, 207, and 240 respectively) determined from individually calibrated screen cage psychrometers ( $n=12$  psychrometers at each depth)

in the three trees was  $-0.15$  MPa, indicating that moisture in the rhizosphere remained high after flooding.

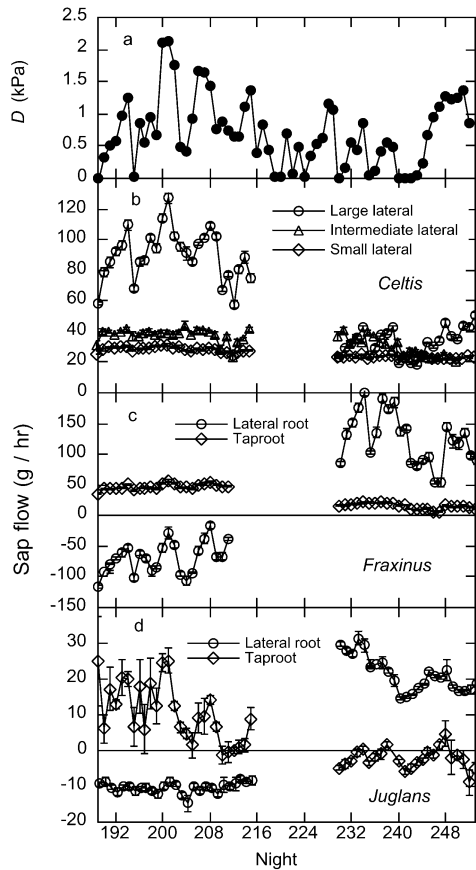
As expected, total daily transpiration determined from sap flow measurements at the main stem was correlated with stem diameter; *Fraxinus* had the highest daily transpiration and the largest stem diameter, followed by *Celtis* and *Juglans* (Table 1). *Fraxinus* transported almost twice as much water per day in July ( $501 \text{ kg day}^{-1}$ ) than in August ( $266 \text{ kg day}^{-1}$ , Table 1). Daily transpiration in August was also lower than in July for *Juglans* and presumably *Celtis* (stem sap flow was not measured in July), where total root sap flow measured in August was 36% lower than in July (Table 1).

Because the traditional heat pulse method used in the stems was not sensitive enough to detect low rates of sap flow (i.e. rates below  $5 \text{ cm h}^{-1}$ ), we used root sap flow measurements to assess the relationship between nocturnal vapor pressure deficit ( $D$ ) and nighttime transpiration. Reverse flow was observed in the lateral roots of *Fraxinus*

**Table 1** Outside diameter, cross-sectional sapwood area, and average pre-flood, and post-flood sap flow of roots and stems of three phreatophytic trees at Walnut Gulch in southeastern Arizona.

	Outside diameter (cm)	Cross-sectional sapwood area (cm <sup>2</sup> )	July sap flow (kg day <sup>-1</sup> ) % contribution		August sap flow (kg day <sup>-1</sup> ) % contribution	
<i>Celtis</i>						
Small lateral	6.05	25.07	3.13		2.05	1.89
Intermediated lateral	7.40	36.32	5.37		4.50	4.14
Large lateral	14.95	139.98	18.51		12.20	11.24
Stem	23.50	363.05			108.55	–
<i>Fraxinus</i>						
Shallow lateral	15.60	116.90	19.66	3.92	30.35	11.41
Taproot	14.80	128.68	6.34	1.26	3.32	1.25
Stem	49.50	1,171.37	501.59	–	266.03	–
<i>Juglans</i>						
Shallow lateral	4.65	10.35	1.08	1.79	4.50	8.07
Taproot	12.00	95.03	7.47	12.38	7.35	13.18
Stem	17.90	179.08	60.34	–	55.76	–

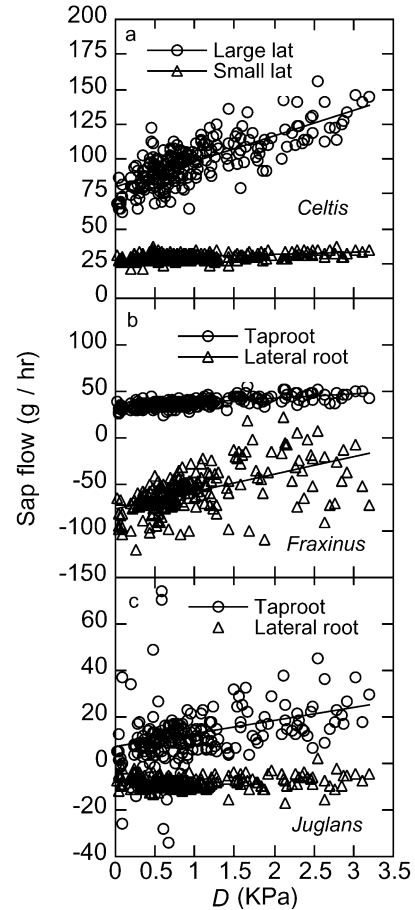
The relative (%) contribution is the amount of water contributed by the root to the total daily transpiration measured in the stem



**Fig. 2** a Patterns of mean nighttime vapor pressure deficit ( $D$ ) calculated from temperature and humidity data between 2130 and 0530 hours. b Patterns of nighttime sap flow in three lateral roots of a single *Celtis reticulata* tree. c Nighttime sap flow in the taproot and shallow lateral root of a single *Fraxinus velutina* tree. d Nighttime sap flow in the taproot and shallow lateral root of a single *Juglans major* tree. Sap flow values are mean nightly rates calculated from measurements taken every half-hour between 2130 and 0530 hours

and *Juglans* before flooding, indicating hydraulic lift (Fig. 2c, d). Mean nightly rates of reverse flow in the *Fraxinus* lateral root ranged from 20 g h<sup>-1</sup> to 120 g h<sup>-1</sup> (Fig. 2c), while reverse flow in the smaller *Juglans* lateral root ranged from 8 to 13 g h<sup>-1</sup> (Fig. 2d). Sap flow measurements were temporarily interrupted on 6 August (day 219) due to flooding. When measurements resumed on 15 August (day 228), *Fraxinus* and *Juglans* lateral roots displayed nocturnal basipetal flow (flow towards the crown) (Fig. 2c, d). Nocturnal basipetal flow was strongly evident in the *Celtis* lateral roots throughout the experiment. Patterns of nocturnal flow in the large *Celtis* lateral root ranged from 60 to 120 g h<sup>-1</sup> before flooding and 20 to 60 g h<sup>-1</sup> after flooding. Nocturnal flow was less variable in the intermediate and small lateral roots, and ranged from 20 to 40 g h<sup>-1</sup> in the two roots (Fig. 3b).

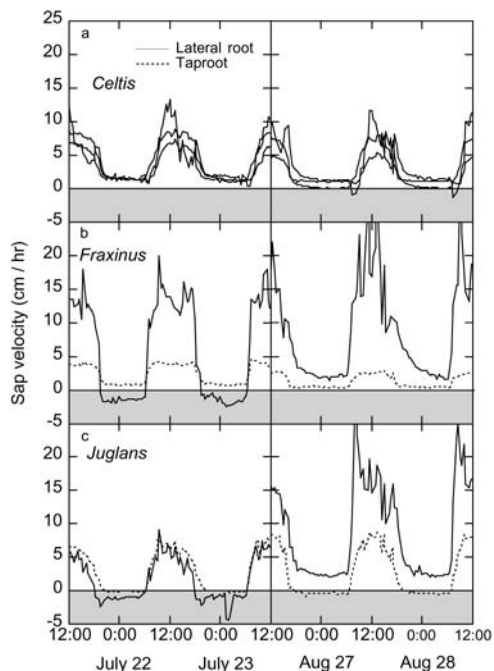
Before flooding, nocturnal sap flow rates in the large *Celtis* lateral root were highly correlated with nocturnal  $D$  ( $r^2=0.60$ ,  $n=231$ ,  $P<0.0001$ , Fig. 3a), suggesting that significant nighttime transpiration was present. Basipetal



**Fig. 3** a, b The relationship between nighttime sap flow and nighttime vapor pressure deficit in the roots of a single *C. reticulata*, *F. velutina*, and *J. major* tree between 7 July (day 189) and 6 August (day 219) 2000. Sap flow and vapor pressure deficit values are mean nightly rates calculated from measurements taken every half-hour between 2130 and 0530 hours. a *Celtis* large lateral root, sap flow (g h<sup>-1</sup>) = 79.4 + 18.5  $D$  (kPa),  $r^2=0.60$ ,  $n=231$ ,  $P<0.0001$ , and small lateral root, sap flow = 28.6 + 1.32  $D$ ,  $r^2=0.14$ ,  $n=231$ ,  $P<0.0001$ . b *Fraxinus* taproot, sap flow (g h<sup>-1</sup>) = 32.8 + 4.94  $D$  (kPa),  $r^2=0.49$ ,  $n=231$ ,  $P<0.0001$ , and shallow lateral root, sap flow = -76.6 + 18.9  $D$ ,  $r^2=0.32$ ,  $n=220$ ,  $P<0.0001$ . c *Juglans* taproot, sap flow (g h<sup>-1</sup>) = 7.46 + 5.50  $D$  (kPa),  $r^2=0.07$ ,  $n=204$ ,  $P=0.0002$ , and shallow lateral root,  $n=204$ ,  $P=0.29$

flow continued during periods when  $D$  was near zero kPa, at a mean rate of 79.4 g h<sup>-1</sup> (i.e. the intercept in Fig. 3). Sap flow in the small lateral root had a similar, but weaker relationship with  $D$  ( $r^2=0.14$ ,  $n=231$ ,  $P<0.0001$ , Fig. 3a), and also showed flow towards the crown during periods of zero  $D$  (28.6 g h<sup>-1</sup>). There was no relationship between nighttime sap flow in the intermediate lateral root and nighttime  $D$  ( $n=231$ ,  $P=0.33$ , data not shown), although nighttime basipetal flow was present throughout the experiment. After flooding, the relationship between nighttime sap flow and  $D$  was much weaker (data not shown), as nighttime  $D$  was generally much lower after flooding (Fig. 2a).

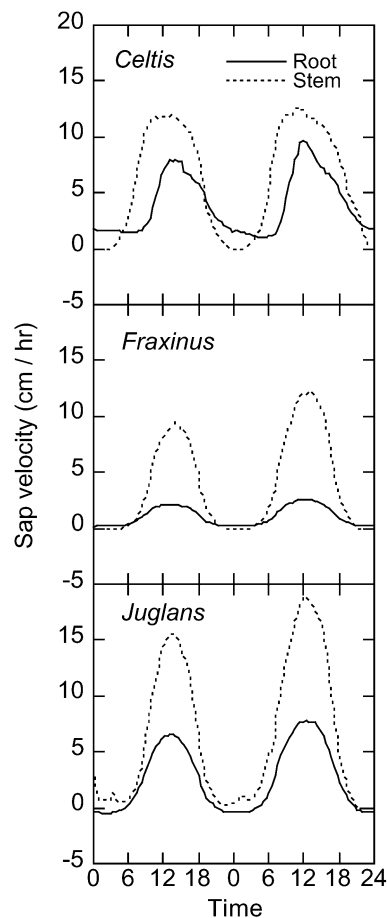
Nocturnal sap flow in the two *Fraxinus* roots showed a strong relationship with nighttime  $D$ ; sap flow increased



**Fig. 4** An example of the diurnal patterns of sap velocity in the roots of *C. reticulata*, *F. velutina*, and *J. major* before flooding on 6 August and 11 August 2000 (days 219 and 224), and after flooding. Negative flow indicates flow away from the crown

with  $D$  in the taproot ( $r^2=0.49$ ,  $n=231$ ,  $P<0.0001$ , Fig. 3b), while reverse flow in the lateral root declined as  $D$  increased ( $r^2=0.32$ ,  $n=220$ ,  $P<0.0001$ , Fig. 3b), suggesting that reverse flow was inhibited by nighttime transpiration. During periods when nighttime  $D$  was zero, mean rates of basipetal flow in the taproot were  $32.8 \text{ g h}^{-1}$  before flooding, while mean rates of reverse flow in the lateral root were  $-76.6 \text{ g h}^{-1}$ . Sap flow in the *Juglans* taproot was weakly correlated with  $D$  before flooding ( $r^2=0.07$ ,  $n=204$ ,  $P=0.0002$ , Fig. 3c), however, unlike *Fraxinus*, there was apparently not enough nighttime transpiration to inhibit hydraulic lift, as there was no relationship between nighttime sap flow and nighttime  $D$  in the lateral root ( $n=204$ ,  $P=0.29$ , Fig. 3c).

Before flooding, nighttime  $V_s$  typically ranged from  $-1.5$  to  $-3.0 \text{ cm h}^{-1}$  in both the *Fraxinus* and *Juglans* lateral roots (Fig. 4b, c). The *Fraxinus* taproot showed nighttime basipetal flow that corresponded with reverse flow in the lateral root (Fig. 4a). The *Juglans* taproot showed basipetal flow during the early evening, but did not correspond to patterns of reverse flow in the lateral root throughout the night (Fig. 4c). After flooding, nighttime patterns of  $V_s$  shifted in the *Fraxinus* and *Juglans* lateral roots and demonstrated significant basipetal flow (Fig. 4b, c). Unlike the other two species, the *Celtis* lateral roots had nighttime basipetal flow throughout the study and ranging from 1 to  $3 \text{ cm h}^{-1}$ . Further, sap flow in the *Celtis* roots commenced a minimum of 2 h after sap flow commenced in the stem (Fig. 5a), strongly indicating that water was being withdrawn from internal storage reservoirs early in the day. By contrast, daytime



**Fig. 5** Diurnal measurements of sap velocity in the main stems and lateral roots of *C. reticulata*, *F. velutina*, and *J. major* measured on 18 and 19 August 2000 (days 231 and 232)

root and stem sap flow commenced simultaneously in *Fraxinus* and *Juglans* throughout the investigation (Fig. 5b, c).

Wood density and saturated water content were measured to account for properties associated with diurnal storage capacity (Stratten et al. 2000). Stem wood density varied slightly among the three species ranging from  $0.55 \text{ g cm}^{-3}$  in *Celtis*, to  $0.56 \text{ g cm}^{-3}$  in *Fraxinus* to  $0.61 \text{ g cm}^{-3}$  in *Juglans*. Saturated water content of stem wood was substantially higher in *Celtis* (104%) than *Fraxinus* and *Juglans* (91 and 94% respectively). There was no apparent relationship between wood density and percent wood saturated water content.

## Discussion

Several recent studies have investigated patterns of nocturnal root sap flow (Burgess et al. 1998, 2001a; Smith et al. 1999). However, few studies have investigated correlation between patterns of hydraulic redistribution and nighttime transpiration and diurnal storage capacity, two plant hydraulic characteristics that poten-

tially could restrain the magnitude or pattern of hydraulic redistribution. We found evidence for hydraulic redistribution from deep roots to shallow roots in *Fraxinus* and *Juglans* before shallow soils were saturated by monsoon rains and flooding. Rates of redistribution were highest in *Fraxinus* when nighttime  $D$  was at or near zero. Conversely, basipetal flow continued in *Celtis* roots throughout the evening regardless of nighttime  $D$ , and was accompanied by large time lags between the onset of root and stem sap flow after sunrise.

Reverse flow was observed in the lateral roots of *Fraxinus* and *Juglans* and was of the order of 1.5–3.0 cm h<sup>-1</sup>, which was similar in magnitude to rates of reverse flow reported by Burgess et al. (1998). Typically roots that are active in absorption will allow water to move into the soil if  $\psi_s$  is more negative than root  $\psi_x$  (Caldwell et al. 1998). However, plant roots may continue to absorb water throughout the evening if the canopy transpires significant quantities of water at night. This would indirectly limit or reduce the magnitude of hydraulic redistribution since the process prevents nighttime  $\psi_x$  from rising above  $\psi_s$ . We did not measure  $\psi_x$  of roots and we were unable to assess directly the magnitude of nighttime transpiration. However, rates of reverse flow in *Fraxinus* were greatest during periods when  $D$  was at or near zero strongly suggesting that nighttime transpiration at least partially inhibited hydraulic redistribution. Despite a weak relationship between nighttime  $D$  and nighttime sap flow in the *Juglans* taproot, rates of reverse flow in the lateral root showed no relationship with  $D$ , suggesting that there was not enough nighttime transpiration to significantly reduce redistribution from the lateral root in this species.

Nighttime transpiration has been observed in several tree and shrub taxa (Matyssek et al. 1995; Assaf and Zieslin 1995; Donovan et al. 1999). However, in desert communities, one might expect nighttime transpiration to be most common in phreatophytic plants that have relatively stable access to water, thereby reducing the requirements for highly resistive stomatal control during periods of high  $D$ . In the present study, depth to groundwater was never deeper than 4.1 m during the growing season (data not shown), and  $\psi_1$  during the driest portion of the growing season (early June) ranged from -0.45 to -0.40 MPa in the three plants ( $\psi_s$  in the rhizosphere may have been higher than measured values of  $\psi_1$  due to the possible presence of nighttime transpiration, Donovan et al. 1999), suggesting that all three species maintained roots that extended to the shallow groundwater table throughout the growing season.

Hydraulic redistribution not only can facilitate water transport from shallow surface soils to sub-surface layers, but the magnitude is often greater in the downward direction (Burgess et al. 1998, 2001a; Smith et al. 1999). The shallow groundwater table and sandy soils at our study site likely inhibited downward hydraulic redistribution. The deep roots very likely had access to groundwater (see above). Further, downward hydraulic redistribution is unlikely to occur in sandy soils with high

hydraulic conductivity and percolation rates since inverse gradients in  $\psi_s$  would only be maintained for a few hours.

Since sap flow measurements do not directly confirm that water is moving back into the soil, and since diurnal variation in  $\psi_s$  was not observed, we cannot rule out the possibility that reverse flow might result from refilling of root storage reservoirs. However, the temporal patterns of reverse flow suggest that this was not the case. Refilling of tissues would induce the highest rates of reverse flow in the early evening when tissue water deficits are highest, and would likely complete refilling before transpiration commences the following day (Burgess et al. 1998). Reverse flow remained fairly constant throughout the evening, suggesting that water continued to move into the soil until sunrise the following morning. Further, values of  $\psi_s$  at lateral rooting depths (between 20 and 50 cm) were within the range in which hydraulic redistribution has previously been reported (Millikin Ishikawa and Bledsoe 2000). However, it is likely that the measurement zone of the psychrometers (a few cubic centimeters) was too localized to detect small diurnal changes in  $\psi_s$  of the rhizosphere (Caldwell et al. 1998).

Hydraulic redistribution may facilitate whole plant water uptake, particularly in systems where there is a high degree of spatial and temporal heterogeneity in plant available water. For example, on some days, hydraulic redistribution increased transpiration by over 20% in a stand of *Artemisia tridentata* (Ryel et al. 2002). In the present study, hydraulic redistribution likely had a small, if any direct influence on whole plant transpiration; nocturnal reverse flow in both the *Fraxinus* and *Juglans* lateral roots typically amounted to less than 1% of whole transpiration the following day. Certainly, other roots that were not instrumented with sap flow sensors were also involved in hydraulic lift. However, in cases where phreatophytic plants have access to groundwater, the direct contribution of hydraulic lift to whole plant water use is likely insignificant.

Even if the direct effect on whole plant transpiration is small, hydraulic lift may still have important indirect consequences on whole plant water balance and the acquisition of other resources. The redistribution of water may facilitate the production and maintenance of fine absorptive roots that are necessary for water and nutrient uptake (Richards and Caldwell 1987). The maintenance of an active root system allows for a rapid response to small rain events. Further, hydraulic lift may facilitate mineral uptake by the plant, since mineral nutrients are mostly located in upper soil layers (Caldwell et al. 1998). As soils dry, ion mobility is rapidly lost, and ion diffusion to roots is inhibited. Hydraulic lift can reverse the process by supplying water to upper soil layers, thereby improving ion diffusion to roots (Emerman 1996; Caldwell et al. 1998).

Unlike *Fraxinus* and *Juglans*, we found no evidence of hydraulic redistribution in *Celtis* roots. One explanation is that the root distribution pattern in *Celtis* was considerably different than the two species in which hydraulic lift was detected. We found that all of this species' roots

developed sinkers that extended below one meter, and possibly into groundwater, thereby preventing hydraulic lift. Caution should be taken, however, in that one tree may not represent the general rooting pattern for this species at this site. Further, we cannot rule out the possibility that smaller roots that were not instrumented with sap flow sensors, or that segments of the roots that were instrumented were acting as conduits for hydraulic lift.

Alternatively, nocturnal gradients in  $\psi$  from soil to shoot may have been sustained within *Celtis* by nighttime transpiration and/or diurnal storage capacity. Nocturnal sap flow in *Celtis* roots increased linearly with nighttime  $D$ . However, significant nocturnal sap flow continued during saturated air conditions in all the *Celtis* roots we measured, demonstrating that another mechanism was involved in maintaining nocturnal sap flow in the roots. One possible explanation is that above ground internal storage compartments were being refilled throughout the evening by the nocturnal uptake of soil water (i.e. diurnal storage capacity). In this study, we define diurnal storage capacity as the amount of water that can be withdrawn between two points along the transpiration stream during the day and replaced over a 24 h cycle (Goldstein et al. 1998). *Celtis* demonstrated a significant time lag between morning onset of root and stem sap flow suggesting that water was removed from the stem long before water was withdrawn from the soil. Conversely, there was no apparent lag time between root and stem sap flow in *Fraxinus* or *Juglans*. Measurement of stem wood saturated water content, a surrogate of storage capacity (Stratten et al. 2000) supports this assertion; saturated water content of the *Celtis* stem was more than 10% higher than that in stems of *Fraxinus* and *Juglans*. As with nighttime transpiration, a gradient in  $\psi$  along the transport pathway may be maintained nocturnally in plants with high diurnal storage capacities, and may indirectly limit, or reduce the magnitude of hydraulic redistribution since the process inhibits nighttime  $\psi_x$  of roots from rising above  $\psi_s$ . Thus, it is plausible that storage capacity in the *Celtis* stem inhibited hydraulic lift during periods of the growing season when shallow soil layers were unsaturated.

The nocturnal uptake and transport of soil water by root systems may have important consequences to catchment hydrology and ecosystem processes. In habitats where plant roots extend vertically to the water table, plant-level processes such as hydraulic lift and nighttime transpiration have the potential to enhance groundwater decline and reduce stream discharge, beyond what is otherwise predicted from most models (Jackson et al. 2000). Information on species differences in root functioning will improve the parameterization of models that link plant-level phenomena with larger-scale processes.

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