Hydraulic redistribution by a dominant, warm-desert phreatophyte: seasonal patterns and response to precipitation pulses

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Summary

1. Hydraulic redistribution may have important consequences for ecosystem water balance where plant root systems span large gradients in soil water potential. To assess seasonal patterns of hydraulic redistribution, we measured the direction and rate of sap flow in tap-roots, lateral roots and main stems of three mature *Prosopis velutina* Woot. trees occurring on a floodplain terrace in semiarid south-eastern Arizona, USA. Sap-flow measurements on two of the trees were initiated before the end of the winter dormancy period, prior to leaf flush.

2 Despite the absence of crown transpiration during the dormant season, sap flow was detected in lateral roots and tap-roots of *P. velutina*. Reverse flow (away from the stem) in the lateral root and positive flow (towards the stem) in the tap-root was observed in one tree, indicating the presence of hydraulic lift. Conversely, reverse flow in the tap-root and positive flow in the lateral root was observed in the second tree, indicating hydraulic descent.

3 Hydraulic descent was induced in the roots of the former tree by wetting the rooting zone in the upper 70 cm of the soil surface with 50 mm of irrigation.

4 Patterns and rates of nocturnal sap flow in roots of a third tree measured during the growing season were similar to those observed during the dormant season. Nocturnal reverse flow in the lateral root and positive flow in the tap-root was observed prior to the onset of the summer monsoon. Hydraulic descent commenced immediately following the first large monsoon rain event, and continued after subsequent rain events. After adjusting for differences in sapwood area, maximum diurnal rates of hydraulic descent in the tap-roots of trees instrumented during the dormant season were 73 and 69% of the maximum night-time rate of hydraulic descent observed during the growing season.

5 Despite very limited potential for direct infiltration, volumetric soil moisture content in deep soil layers (1·5–9·5 m) increased 2–8% by the end of the monsoon (late September), indicating that plant roots were redistributing non-trivial amounts of water to deep soil layers.

6 Roots of *P. velutina* apparently redistribute significant amounts of soil water during the growing season, but also during periods of crown dormancy in winter. In arid regions dormant-season hydraulic descent may buffer plants from water and nutrient deficits during initial stages of the growing season by transferring soil water derived from winter precipitation to deep soil layers and away from zones of evaporation in surface layers and shallow-rooted herbaceous plants.

Key-words: hydraulic descent, hydraulic lift, root sap flow, *Prosopis velutina*, soil moisture redistribution

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Introduction

Plant roots capture, store and transport soil water, and in doing so alter ecosystem water, energy and nutrient balance. One potentially important process facilitated by roots is the passive redistribution of water from moist to dry soil layers. Hydraulic redistribution (*sensu* Burgess *et al.* 1998) occurs during periods of low crown transpiration (such as nocturnal periods) when the water potential of the root xylem rises to values intermediate between root-occupied moist and dry soil layers. Under these circumstances, roots act as conduits for passive transport between soil layers. Hydraulic redistribution has been detected in a wide variety of plant life forms, including grasses (Caldwell & Richards 1989) and succulents (Caldwell, Dawson & Richards 1998), but appears most common in deep-rooted trees and shrubs that can forage for stable water sources across multiple soil layers. The importance of hydraulic redistribution for ecosystem water balance depends largely on its vertical direction, magnitude, duration and seasonality.

Initiation of reverse sap flow in plant roots (flow away from the stem and into surrounding soil) corresponds with measurable changes in soil moisture within the rooting zone (Burgess *et al.* 2000; Brooks *et al.* 2002), establishing a clear connection between reverse flow and hydraulic redistribution. Evidence of hydraulic redistribution from soil moisture data has typically focused on the upward transfer of soil water (hydraulic lift), as soil moisture measurements of subsurface soils are logistically difficult to obtain. However, advancement in soil moisture instrumentation, including frequency domain capacitance probes (Paltineanu & Starr 1997) and cross-borehole ground-penetrating radar (GPR; Eppstein & Dougherty 1998; Alumbaugh *et al.* 2002), can measure very slight changes in diel and seasonal water content in deep soil layers.

Because hydraulic redistribution does not require metabolic energy, plants potentially could redistribute water during periods of dormancy as long as their roots maintain axial (xylem) and radial conductivity and physical contact with the surrounding soil. Hydraulic redistribution throughout extended periods of the dormant season may have important ecological and hydrological consequences. During wet winters, deep-rooted plants could redistribute water from moist surface soils to deep soil layers (hydraulic descent), and away from shallow-rooted competitors and soil evaporative processes. The 'banking' of soil water during dormancy for future use may be particularly beneficial for plants occurring in arid and semiarid regions that are typically warm and dry during the early stages of the growing season, such as in the south-western USA where rainfall is scarce in late spring. Conversely, dry winter years could produce patterns of hydraulic lift if there is sufficient water storage in the deep soil layers of the rooting zone. Dormant-season hydraulic lift may enhance shallow root longevity and activity of not only the deep-rooted 'lifter', but also co-occurring shallow-rooted plants (Richards & Caldwell 1987; Dawson 1993) as long as a significant amount of the hydraulically lifted water is not lost to soil evaporation.

We monitored seasonal patterns of root and stem sap flow, and seasonal fluctuations in soil water content of subsurface soil layers, in a mature stand of velvet mesquite (*Prosopis velutina* Woot.) on a flood-plain terrace of the San Pedro River in south-eastern Arizona, USA. Our goal was to determine if mesquite roots are capable of redistributing soil water during periods of plant dormancy and, if so, how the magnitudes and patterns of dormant-season redistribution compare to those during the growing season.

Materials and methods

SITE DESCRIPTION

The site was located on an alluvial floodplain terrace near the San Pedro River in south-eastern Arizona, USA (31°40′ N, 111°11′ W; 1190 m elevation). Depth to groundwater ranged from 7–11 m. The overstorey vegetation was a mixed-age stand dominated by the leguminous tree *Prosopis velutina*. Stem diameters of *P. velutina* ranged from just a few centimetres to >75 cm, and average leaf area index was ≈1·6 m^2 m^{-2} (Scott *et al.* 2003). The shallow groundwater table was the primary source of transpiration by overstorey vegetation (Scott *et al.* 2003). The understorey vegetation was dominated by the perennial bunchgrass *Sporobolus wrightii* Munro. intermixed with annual herbaceous dicots. The alluvial soils comprised mostly sandy loams interspersed with layers of gravels and clays.

The climate in the upper San Pedro valley is semiarid with temperatures ranging from a mean maximum of 24·8 °C to a mean minimum temperature of 9·9 °C. Night-time temperatures within the riparian corridor are typically 2–8 °C lower than the surrounding valley due to cold air drainage (Scott *et al.* 2004). Air temperature was measured 6 m above the soil surface (mid-canopy height) using a temperature/relative humidity probe (Vaisala, Woburn, MA, USA). Soil temperature was measured at 5 and 15 cm depths with soil thermocouples. Precipitation is bimodal with roughly 60% of the 350 mm mean annual distribution of precipitation falling during the summer monsoon (July–September) and ≈23% falling during the winter months (December–March). Precipitation at the site was measured with a tipping bucket rain gauge.

SAP FLOW MEASUREMENTS

We used the heat-ratio method in this investigation to measure xylem sap flow. The method has been described previously in detail (Burgess *et al.* 2001a, 2001b; Hultine *et al.* 2003a). Briefly, the heat-ratio method employs temperature probes at equal distances up- and downstream from a pulsed heat source. The difference in heat

Table 1. Outside diameter, sapwood thickness and cross-sectional sapwood area of *Prosopis velutina* stems, tap-roots and lateral roots measured for sap flow in 2002 in southeastern Arizona, USA

	Outside diameter (cm)	Sapwood thickness (cm)	Cross-sectional sapwood area (cm²)
Tree 1			
Stem	28·7	1·35	107·0
Tap-root	6·80	1·75	22·5
Lateral root	6·70	1·60	21·5
Tree 2			
Stem	24·1	1·30	77·1
Tap-root	9·85	1·25	28·6
Lateral root	3·95	1·35	7·5
Tree 3			
Stem	34·7	1·90	182·1
Tap-root	19·1	1·90	86·8
Lateral root	8·35	1·20	21·6

carried up- and downstream is proportional to the magnitude of sap flux, and the sign of the difference indicates the flux direction. We measured sap flow in the stems, tap roots and main lateral roots of three *P. velutina* trees in spring, summer and early autumn 2002. Two trees were selected in early March ≈30 m from the river channel to measure root and stem sap flow during periods before and during leaf flush (Trees 1 and 2; Table 1). An additional tree (Tree 3) was selected roughly 400 m from the river in early July for growing-season measurements of sap flow. The close proximity of Trees 1 and 2 to the river allowed for easy extraction of river water to irrigate the trees during the experiment (described below). Soil around the trees was carefully excavated to expose large roots at the base of the trees. The tap-root and one main lateral root were selected on each tree for sensor installation. A single sap-flow sensor was inserted into the xylem of the lateral root, while two sensors were inserted into the larger tap-root on each tree. A single sensor was also inserted into the main stem of each tree. After sensor installation the roots were covered with a tarpaulin to thermally insulate the exposed roots from night-time freezing and to minimize radiant heating during the day by direct sunlight. The sap-flow sensors (Thermal Logic, Pullman, WA, USA) consisted of three 35 mm long stainless steel probes spaced 6 mm apart. The central probe contained an Evanohm 44-Ω line heater, while the outside probes contained three-paired thermocouple junctions spaced to measure heat-pulse velocity at 5, 10 and 20 mm radial depths.

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

$$V_s = [V_h \rho_b (c_w + m_c c_s)]/\rho_s c_s \qquad \text{eqn 1}$$

where c_w and c_s are the specific heat of dry wood (1200 J kg^{-1} °C^{-1} at 20 °C; Becker & 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, 998 kg m^{-3} at 20 °C), ρ_b is the density of wood, and m_c is the moisture content of wood. Volumetric sap flow (l day^{-1}) was calculated after first subtracting the bark thickness from the radius of the stem or root. The heartwood radius was subtracted from gross wood area after it was identified by visual observation of the dark colour 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.

Because heat-ratio 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 validate a zero flow, we severed the roots and stem at the conclusion of the study to stop all flow. Spacing between probes was calculated according to Burgess *et al.* (1998):

$$x_2 = \sqrt{4kt \ln(v_1/v_2) + x_1^2} \qquad \text{eqn 2}$$

where x_2 (mm) is designated the incorrectly spaced probe, x_1 is assumed to be correctly spaced at 6 mm, k is the 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 release of the heat pulse (in this case, 60 s). As it is not known which probe is incorrectly spaced, or whether both probes are incorrectly spaced, equation 1 was solved for x_1 and x_2 and the two solutions were averaged.

In some cases we were unable to obtain a zero measurement to correct for probe misalignment. In these cases, X-ray radiographs were taken of the inserted probes from the side and top to obtain a three-dimensional view inside the root segment (Diagnostic X-ray Laboratory, University of Arizona Medical Center). This approach has previously shown comparable results with the traditional *in situ* method for probe-spacing corrections (Hultine *et al.* 2003b). Distances between probes were measured from the X-ray image using the software application NIH IMAGE (ver. 1·62 for Macintosh) and the protocol described by Hultine *et al.* (2003b).

IRRIGATION EXPERIMENT

Eleven days after sap-flow measurements were initiated during the dormant winter period, we applied 50 mm irrigation to Trees 1 and 2 to assess the potential response of sap flow in deep and shallow roots to pulses of dormant-season precipitation. The ground surface within a 5 m radius around each tree was cleared, and a gas-powered pump was used to deliver river water to the cleared area (78·53 m²) of each tree at a rate of 20 l min^{-1}. Runoff from the plots was absent due to the

relatively low application rate coupled with the high infiltration rate of the coarse sandy loam soil. Care was taken to avoid applying water near the base of the trees where the roots were instrumented with sap-flow sensors. Water content reflectometers (WCR) (CS615, Campbell Scientific, Logan, UT, USA) were installed in a vertical profile in one of the irrigation plots at 10, 20, 30, 50, 70 and 90 cm depths to assess the rate and depth of infiltration after irrigation. Two WCR probes were installed at each depth, except at 70 and 90 cm where single probes were installed.

VADOSE ZONE SOIL MOISTURE MEASUREMENTS

Volumetric soil water content (θ) of deep soil layers (1·5–9·5 m depths) was estimated periodically near Tree 3 using cross-borehole GPR (see Alumbaugh *et al.* 2002 for details). Briefly, cross-borehole GPR yielded the travel time of the direct wave from source to receiver using a centre frequency of 50 MHz along a 0·25 m incremental depth sampling interval. The travel times in combination with the known separation between two adjacent, PVC-lined boreholes (1·72 and 2·13 m) were used to estimate profiles of the dielectric constant. Profiles of volumetric water content were computed using the dielectric values via a well known empirical relationship (Topp *et al.* 1980). Total moisture was calculated for each sampling interval by multiplying the volumetric water content of each interval by its length (0·25 m).

STATISTICAL ANALYSIS

Linear regression analysis (ANOVA) was used to test whether patterns of root sap flow varied with time following experimental irrigation. Linear regression was also performed to test the relationship in the direction and magnitude of sap flow between the tap-root and lateral root of each tree. Statistical analysis was performed using JMP 4·0 (SAS Institute, Inc., Cary, NC, USA).
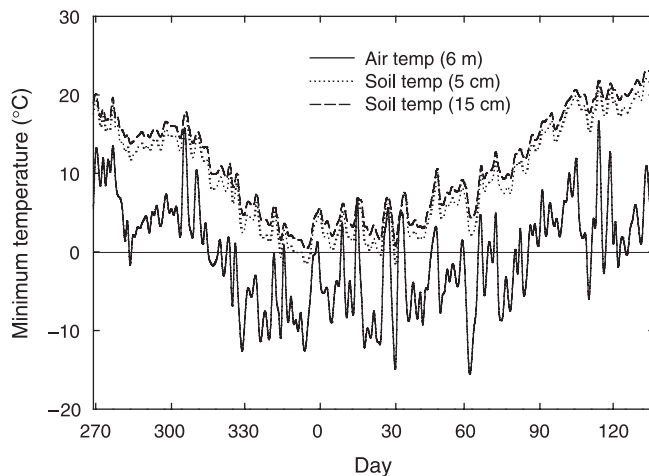
Fig. 1. Air temperature at 6 m above the soil surface and soil temperatures at 5 and 15 cm depths during the dormant period between the 2001 and 2002 growing seasons.

Results

DORMANT-SEASON HYDRAULIC REDISTRIBUTION

Minimum diurnal air temperatures during the dormant season ranged from −15 to +15 °C at the study site (Fig. 1). Despite the freezing air temperatures, soil temperatures at 5 cm depths only briefly dropped below zero in late December, and again in early February. Soil temperatures at 15 cm depth never dropped below 1 °C, suggesting that *P. velutina* roots probably were not subjected to freeze–thaw cycles that would induce xylem embolism.

Positive rates of sap flow (toward the stem) in the tap-root of Tree 1 ranged from 0·5 to 1·8 l day^{-1} (Fig. 2a) prior to irrigation. Sap flow decreased slightly in this root between day-of-year (DOY) 64 and 74; however, the pattern was not significant ($P = 0·328$). After 50 mm irrigation was applied, soil water content in the upper 30 cm of the profile increased within 12 h, while infiltration at 50 and 70 cm depths took ≈48 and 96 h, respectively (Fig. 2b). There was little or no infiltration at 90 cm. After irrigation the direction of sap flow in
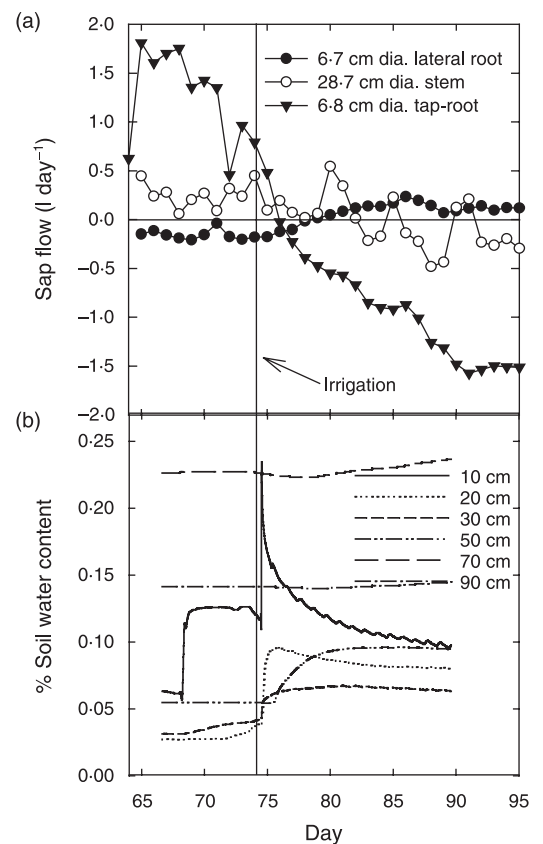
Fig. 2. (a) Total daily sap flow of the stem, tap-root and lateral root of a mature, single-stemmed *Prosopis velutina* tree (Tree 1) measured from 5 March (DOY 64) to 30 May (DOY 95). Sap-flow values were calculated from half-hourly measurements from 0 : 00 to 23 : 30 h. Irrigation (50 mm) was applied on day 74. Negative values represent reverse flow (away from the crown). (b) Percentage soil water content measured by water-content reflectometry probes at 10, 20, 30, 50, 70 and 90 cm soil depths. Irrigation (50 mm) was applied on DOY 74.
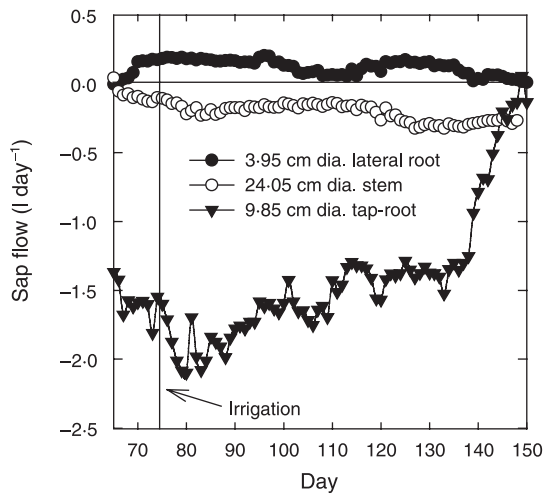
Fig. 3. Total daily sap flow of the stem, tap-root and lateral root of a mature, single-stemmed *Prosopis velutina* tree (Tree 2) measured from 5 March (DOY 64) to 30 May (DOY 150). Sap-flow values were calculated from half-hourly measurements from 0 : 00 to 23 : 30 h. Irrigation (50 mm) was applied on DOY 74. Negative values represent reverse flow (away from the crown).

Fig. 4. An example of the 24 h pattern of sap flow in the tap-root, lateral root and stem of Tree 1 during the dormant season. Measurements were recorded on DOY 65.

the tap-root immediately shifted from positive to reverse, and significantly increased in magnitude between day of irrigation and DOY 92 by an average of 0·11 l day⁻¹ ($R^2 = 0.91$, $P < 0.0001$, $n = 17$ days, from ANOVA). Reverse flow (away from the stem) levelled off at ≈1·5 l day⁻¹ after DOY 92. Sap flow in the smaller lateral root was much lower than in the tap-root, but consistently flowed in the direction away from the stem prior to irrigation, the pattern expected with hydraulic lift. After irrigation the direction of nocturnal sap flow in the lateral root shifted toward the stem, and remained positive throughout the remainder of the experiment. Rates of sap flow in the lateral root and tap-root were inversely correlated on a daily time-step, consistent with that expected during hydraulic redistribution ($R^2 = 0.59$, $P < 0.0001$, $n = 32$ days, from ANOVA).

The direction of sap flow in the roots of Tree 2 was different from that in Tree 1 prior to irrigation; reverse flow was detected in the tap-root while positive flow was detected in the lateral root (Fig. 3a). After irrigation, rates of reverse sap flow in the tap-root increased continuously from ≈1·5–2·2 l day⁻¹ until DOY 80. Afterwards, reverse flow declined steadily until leaf flush on DOY 138. After leaf flush, sap flow in the tap-root consistently increased until the amount of daytime positive sap flow equalled nocturnal reverse flow at the conclusion of the measurements. Response to irrigation in the lateral root was barely detectable. Nevertheless, daily sap-flow rates in the lateral root and tap-root were weakly and inversely correlated between DOY 65 (beginning of the observations) and DOY 138 (beginning of leaf flush) ($R^2 = 0.20$, $P < 0.0001$, from ANOVA).

There was no consistent diurnal pattern of root or stem sap flow in either tree (Fig. 4). Likewise, there was no consistent correlation between patterns of root and
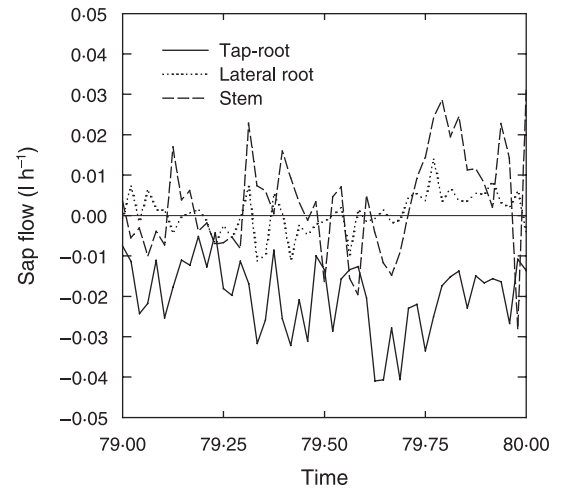
stem sap flow during the dormant season, suggesting that flow patterns in the roots were not related to water loss from the stem.

GROWING-SEASON HYDRAULIC REDISTRIBUTION

Growing-season sap-flow measurements were initiated before the onset of the monsoon. There had been no significant precipitation for 149 days prior to the study, so the shallow soil layers were extremely dry at the beginning of the study. Before the onset of the monsoon, nocturnal reverse flow was strongly evident in the lateral root of Tree 3, and was accompanied by positive flow in the tap-root (Fig. 5a). After two moderate precipitation events on DOY 197 and 198, root sap-flow patterns in Tree 3 shifted dramatically; nocturnal reverse flow commenced in the tap-root, while night-time positive flow was detected in the lateral root. This pattern was enhanced by large rain events on DOY 232 and 251 (Fig. 5a), with maximum rates of reverse flow in the tap-root approaching 9 l night⁻¹ (Fig. 5b). Rates of nocturnal sap flow in the tap-root and lateral root were inversely correlated on a half-hourly time-step ($R^2 = 0.85$, $F = 9498$, $P < 0.0001$, from ANOVA).

SOIL MOISTURE OF SUBSURFACE SOIL LAYERS

Cross-borehole GPR measurements were made for the two adjacent vadose-zone profiles (−1·5–9·5 m) located near Tree 3 on 17 June (DOY 168, pre-monsoon), 15 August (DOY 227, mid-monsoon), 25 September (DOY 268, late-monsoon), and 20 November (DOY 324, post-monsoon) 2002. Soil moisture increased during the monsoon, particularly late monsoon where moisture in the deep soil layers was 2–8% higher than before the monsoon (Fig. 6). In fact, total moisture within the
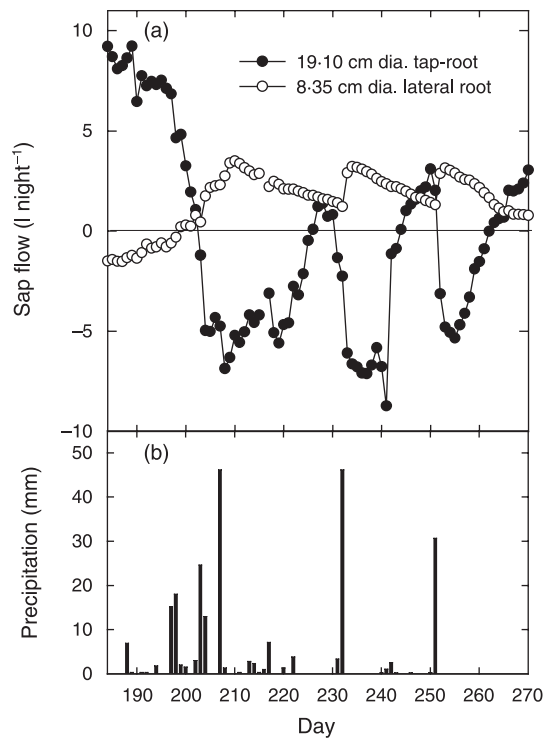
Fig. 5. (a) Total daily nocturnal sap flow of the stem, tap-root and lateral root of Tree 3 calculated from half-hourly measurements from 20.00 h to 05.30 h during the 2002 growing season. Negative values represent reverse flow (away from the crown). (b) Daily precipitation totals (mm day⁻¹) at the field site during the study.

Fig. 6. Relative change in soil-water content after initial measurements on 17 June 2002. Measurements were conducted with cross-borehole ground-penetrating radar. Values are the mean from two adjacent vertical transects.

vertical profile increased between 17 June and 25 September (DOY 168–268) by 318 mm. Soil moisture decreased between late-monsoon and post-monsoon periods, but remained higher after than before the monsoon (Fig. 6).

Discussion

Previous studies indicate that when transpiration is reduced (usually at night), plant roots transport water from moist soil layers to drier regions of the soil profile (Richards & Caldwell 1987; Burgess *et al.* 1998, 2000, 2001a; Smith *et al.* 1999; Hultine *et al.* 2003a, 2003b). This phenomenon, termed hydraulic redistribution, occurs in a wide range of ecosystems and plant life forms (Caldwell, Dawson, & Richards 1998). However, to our knowledge no previous investigation has reported the phenomenon occurring during periods of plant dormancy. Our study shows that roots of the woody legume *P. velutina* redistributed a significant amount of water in early spring prior to leaf flush (typically early November to mid-May) at rates comparable to those observed during the summer growing season.

After adjusting for differences in sapwood area among the tap-roots of the three trees, maximum rates of reverse flow (l day⁻¹) in the two trees instrumented during the dormant period were 69 and 73% of the maximum nightly rate of reverse flow observed in the tap-root of a third tree during the summer, while
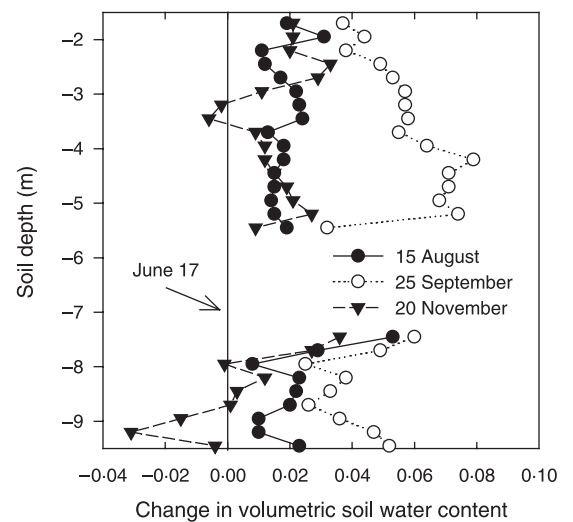
nocturnal reverse flow in the tap-root of the third tree was 25–50% of daytime positive flow during transpiration (cluster not shown). Based on these observations, 3–6 days' reverse flow during the dormant season potentially could supply the tap-root with enough moisture to meet the transpiration for 1 day during the growing season. We caution against strict conclusions based on a few individual trees. Nevertheless, given that crown dormancy in *P. velutina* at this site typically lasts about 5 months, hydraulic descent during wet winters could supply the tap-root with several days, or even several weeks, of water for growing-season consumption as long as a water-potential gradient is maintained within the root zone.

The relative importance of hydraulic descent to plant water balance depends on the fate of shallow soil water if it is not otherwise redistributed by the root system. Soil water from winter precipitation apparently does not recharge deep soil layers along the alluvial river terrace (Scott *et al.* 2004), nor at other upland sites in this region (Scott *et al.* 2000). Thus much of the water that remains in shallow soil layers is either taken up early in the growing season by co-occurring shallow-rooted plants such as the perennial tussock grass *Sporobolus wrightii*, or is potentially lost to evaporation, as potential evapotranspiration during the winter and early spring remains relatively high in semiarid climates. The ability to 'bank' water during winter dormancy for later consumption presents a win–win scenario for deep-rooted plants, as there is a very small carbon investment to maintain the fine-root systems that act as conduits for redistribution during winter dormancy (Widen & Majdi 2001; Burton *et al.* 2002). Nevertheless, the significance of hydraulic descent to the water balance of mature mesquite plants in floodplain ecosystems is an open question, as mature plants have access to groundwater throughout the growing season (Scott *et al.* 2003).

Dormant-season hydraulic descent may play a much greater role in the water balance of mesquite growing in upland habitats where groundwater is not available within the rooting zone, or in young plants in the flood-plain that have not yet grown roots into groundwater.

During years of little or no winter precipitation, the balance of redistribution is towards the upper soil layers (hydraulic lift). Hydraulic lift during extended periods of the dormant season provides water storage in the upper soil layers that can be rapidly extracted during spring leaf flush, as the upper soil layers generally contain the highest root-length densities (Jackson *et al.* 1996). However much of the water that is deposited from deep soil layers to shallow soils may be lost to evapotranspiration before leaf flush, or to other co-occurring plants. Further work is needed to establish a clear connection between dormant-season hydraulic lift and whole-plant water balance.

Regardless of its role in plant and ecosystem water balance, dormant-season hydraulic redistribution has several potentially important implications for plant nutrient balance (Richards & Caldwell 1987). Mineral nutrients are generally most abundant in the upper soil layers. However, the early growing season in most of the south-western USA is characterized by warm daytime temperatures with little or no precipitation until the onset of the monsoon (usually mid-July). For *P. velutina* trees at our field site, this represents between 80 and 120 days between spring leaf flush and the onset of the monsoon. Thus the mobility of nutrients in the dry shallow soils is potentially low before the monsoon, and diffusion to roots is inhibited. Hydraulic lift during the dormant season can prolong the life span of fine roots and micro-organisms and thereby enhance nutrient ion mobility and uptake during the dry periods of the growing season. Likewise, the dormant-season transfer of mineral nutrients with hydraulic descent to deeper soil layers can potentially smooth the spatial heterogeneity of nutrients, and therefore, enhance plant nutrient uptake during the early growing season when water extraction is primarily from deep soils (Emerman 1996; Burgess *et al.* 2001a).

For plant roots to redistribute water between soil layers, they must maintain axial (xylem) hydraulic conductivity (K_x). In many regions xylem conduits in above-ground tissues typically become dysfunctional during the winter due to freeze–thaw cavitation (Cochard & Tyree 1990; Sperry 1993; Pockman & Sperry 1997). Conversely, xylem conduits in roots may not completely embolize where soils insulate roots from freezing temperatures. In the present study, *P. velutina* roots in the upper 50 cm of soil maintained 35% of maximum conductivity during winter, and 70% during summer before the onset of the monsoon (data unpublished). The relatively high xylem conductivities in winter are not surprising considering soil temperatures at 15 cm never reached freezing, despite the fact that minimum air temperatures at mid-canopy reached −15 °C during the winter. *Prosopis velutina* roots at the site are rarely found near the soil surface above 15 cm depth, particularly in the intercanopy spaces where high temperatures in the upper top few centimetres of soil during the growing season are lethal to living root tissues.

Soil moisture levels in deep soil layers (−1·5 to −9·5 m) increased during the monsoon. Observed soil moisture changes were probably due to hydraulic redistribution; moisture throughout the vertical transect increased 318 mm between 17 June and 25 September (DOY 168–268). Calculated values of capillary rise from groundwater fluctuations and direct infiltration from summer precipitation could account for only 45 mm of moisture within the GPR profile (R.L.S. and co-workers, unpublished data). Even if all precipitation inputs (248 mm) were transferred below −1·5 m (highly unlikely), the combined inputs from capillary rise and direct infiltration still would not explain the observed change in moisture in the deep soil layers. Moreover, Scott *et al.* (2004), using profiles of soil moisture probes in the upper 1·0 m of soil at this site, report that infiltration of precipitation below 0·5 m rarely occurred during 2001 and 2002. Only one infiltration event was observed below 0·5 m, and this resulted in only a 2% change in soil moisture content at 0·7 m.

The above argument requires reasonably accurate estimates of vadose zone θ. Although a site-specific calibration of apparent dielectric constant *vs* soil moisture content has not yet been established, Alumbaugh *et al.* (2002) argued that the precision error for this type of cross-borehole GPR measurement is ≈0·5% in moisture content estimation. Therefore the changes seen in the profile are arguably significant. Water content changes between ≈5·75–7·25 m depth could not be estimated as there was too much attenuation of the waveform for an accurate estimation of the travel time. At this depth interval, well logs reveal a thick layer of clayey material.

After the onset of the monsoon, nocturnal reverse flow in the tap-root was typically lower in magnitude than its daytime flow towards the stem, suggesting that the water content of deep soil layers should still be depleted (although at a lower rate) after precipitation wetted the upper soil layers. However, water content increased during the monsoon in the deep soil layers despite the absence of direct recharge of precipitation below 1 m. It is likely that lateral roots, fine roots and root hairs extend from the tap-root in relatively dry soil layers as well as the shallow groundwater table or capillary fringe. Thus the bulk of daytime positive flow in the tap-root was probably derived from the extraction of groundwater, and nocturnal reverse flow was a consequence of redistribution to the dry soil layers above the water table. Unfortunately, measurements of root sap flow alone cannot detect the source or fate of water that moves through woody roots.

There were substantial differences between Trees 1 and 2 in the pattern and direction of root sap flow during the dormant season prior to irrigation. Sap in the tap-root of Tree 1 flowed towards the stem, while sap

in the lateral root flowed away from the stem. Before irrigation we found reverse flow in the tap-root, and positive flow in the lateral root of Tree 2. Differences in root sap flow between trees were probably caused by differences in the vertical distribution of roots within the various soil layers. Lateral roots of *P. velutina* at our site often extend vertically beyond the recharge zone (personal observation) and therefore, unlike shallow lateral roots, do not respond to pulses of moisture. In fact, sap-flow patterns in the tap-root of Tree 2 suggest that some lateral roots were in deeper, wetter soil layers than the tap-root. Hence it is possible that the source of water supplied to the tap-root of Tree 2 was from deep soil layers before irrigation, and from shallow (and possibly deep) soil layers after irrigation was applied.

We found evidence that plants redistribute a non-trivial amount of water during winter dormancy. The magnitude and vertical direction of redistribution probably depends on the amount and intensity of winter precipitation, and the vertical distribution and activity of fine roots. Potential benefits of redistribution include reducing water and nutrient deficits, particularly if the balance of redistribution over the dormant season occurs in the downward direction and away from evaporative processes in the shallow soil layers. Hydraulic redistribution could play an important role in the ratio of ecosystem evaporation to transpiration on a diurnal, seasonal and annual time-step. Future work will focus on the relative impacts of hydraulic redistribution on soil hydraulic properties within the vadose zone, the water table, and stream discharge.

Acknowledgements

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