Hydraulic redistribution by deep roots of a Chihuahuan Desert phreatophyte

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Summary Downward redistribution of soil water through plant roots has important consequences for water and nutrient balance of arid and semi-arid ecosystems. Nevertheless, information on the seasonal patterns and magnitudes of redistribution is lacking for all but a few plant species. We measured sap flow in the taproot and three main lateral roots of a 10-year-old Juglans major Torr. tree, on an ephemeral catchment in southeastern Arizona, to determine how patterns of redistribution respond to pulses of summer precipitation. Groundwater was beyond rooting depth and a hardpan prevented recharge of surface water to deep soil layers. Reverse flow (hydraulic descent) commenced in the taproot and deep lateral roots in early August after a series of moderate precipitation events, and abruptly ceased after all shallow roots were experimentally severed in mid-August. On some days, hydraulic descent continued in the deep lateral roots during periods of daytime transpiration, and the daily volume of hydraulic descent (deep lateral roots plus taproot) ranged from 10 to nearly 60% of daily transpiration. The persistent pattern of reverse flow demonstrates that, in some plants, water potential gradients from soil to leaf during transpiration are often smaller than those between soil layers within the rooting zone. Hydraulic descent may be an important component of the water balance of phreatophytic trees by facilitating root growth in deep soil layers and by transferring water away from shallow-rooted competitors.

Keywords: heat pulse velocity, hydraulic descent, Juglans major, riparian ecosystems, sap flow.

Introduction

Hydraulic redistribution, the nocturnal transfer of soil water through roots, occurs when reduced transpiration (usually at night) allows xylem water potential to exceed water potential in dry soils. The phenomenon is common among plants with dimorphic root systems that extend from shallow to deep soil layers (Caldwell et al. 1998). The significance of hydraulic redistribution to ecosystem hydrologic balance is not fully understood. Its impact on ecosystem processes should be related to the vertical direction in which water is transferred. The upward transfer of water (hydraulic lift) has been observed in several species and life forms (e.g., trees, shrubs, grasses), and across varying environments (Richards and Caldwell 1987, Caldwell and Richards 1989, Dawson 1993, 1996, Hultine et al. 2003). Hydraulic lift potentially facilitates transpiration and nutrient uptake of both the redistributing plant and the co-occurring shallow-rooted plants. More recent investigations have focused on the downward transfer of water (hydraulic descent) after surface soils are wetted by precipitation (Burgess et al. 1998, 2001a, Schulze et al. 1998, Smith et al. 1999). Hydraulic descent may reduce evapotranspiration because water is diverted from shallow-rooted competitors and soil evaporative processes.

Although there is substantial evidence for hydraulic redistribution, information is lacking on the timing, duration, and magnitude of the phenomenon in different environments. Soil texture and water play important roles in observed patterns of hydraulic redistribution (Caldwell et al. 1998, Millikin Ishikawa and Bledsoe 2000, Burgess et al. 2001a). High rates of percolation in sand promote rapid recharge of subsurface soil layers and prevent the establishment of soil water gradients that are conducive to hydraulic descent (Burgess 2001a). Further, long-term soil drying may lead to a reduction in root hydraulic conductivity or root–soil contact, or both, thereby inhibiting hydraulic redistribution (Caldwell et al. 1998). In a recent investigation, hydraulic redistribution in Chihuahuan Desert riparian trees was absent during the summer dry season and was constrained to periods of soil drying following episodic summer rain events (Hultine et al. 2003). Apparently, the fine absorptive roots that are necessary for redistribution of soil water were not produced until after the onset of the summer monsoon. Conversely, hydraulic lift by Quercus douglasii Hook and Arn. was found to continue throughout the dry summer months, suggesting that absorptive surface roots were maintained despite the absence of precipitation (Millikin Ishikawa and Bledsoe 2000).

A recent advance in the heat pulse velocity technique, the
heat ratio method (HRM), allows for sensitive estimates of hydraulic redistribution (Burgess et al. 1998, 2001a, 2001b). As with all heat pulse methods, however, the HRM is extremely sensitive to errors arising from inaccurate probe spacing. Probe spacing errors can be gauged in situ by severing the root or stem to induce a zero sap flow at the conclusion of sap flow experiments. Such assessments are highly destructive, and if the sap flow equipment fails before severing, then corrections by this method are impossible. Thus, alternative methods, such as visual assessments using over-sized probes or X-ray photographs of the inserted probes, would be advantageous.

In this paper, we report seasonal trends in sap flow in deep and shallow roots of a desert phreatophytic tree species, Juglans major Torr. Our goal was to gain further insight into the timing, duration, magnitude and direction of hydraulic redistribution in desert riparian ecosystems. We conducted an additional study to compare the use of X-ray photographs with the traditional in situ method for determining errors resulting from probe misalignment.

Materials and methods

Site description

The study was conducted at the Walnut Gulch Experimental Watershed along its principal drainage in southeastern Arizona during the 2001 growing season (31°43′ N, 110°03′ W, 1333 m elevation). The seasonal pattern of precipitation at Walnut Gulch is bimodal, with about 60% of the 360 mm mean annual precipitation falling during the summer “monsoon” (July to September) and about 30% falling during the winter (December to March). Daily rainfall was measured with a rain gauge 1.5 km from the field site. Soils at the field site are in the Rillito–Karro series (USDA-SCS, 1970). These soils are a moderately fine, gravelly loam in the upper 20 cm, and have a light clay loam horizon between 20 and 65 cm. Below 65 cm is a 40-cm thick hardpan layer cemented by calcium carbonate (USDA-SCS, 1970). The hardpan effectively limits percolation of water after precipitation or runoff events. Groundwater depth is approximately 50 m at the site. The overstory vegetation was dominated by Prosopis velutina Woot., intermixed with Celtis reticulata Torr., Juglans major and Chilopsis linearis (Cav.) Sweet along the channel. Understory vegetation was dominated by Acacia greggii A. Gray, Baccharis sarothroides Gray and Sporobolus wrightii Munro.

Sap flow measurements

We used the HRM to measure xylem sap flow. The HRM has been described previously in detail (Burgess et al. 1998, 2001a, 2001b, Hultine et al. 2003). Briefly, the HRM employs temperature probes at equal distances up- and downstream from a heat source. The difference in heat carried up- and downstream is proportional to the magnitude of sap flux, and the sign of the difference indicates the direction of sap flow. In this study, a single 10-year-old Juglans major tree was selected along the south terrace of the main channel of Walnut Gulch. Soil around the tree was carefully excavated to expose large roots at the base of the tree. The taproot (14.3 cm diameter, labeled Root 1 in Figure 1) and two large lateral roots (9.0 and 6.7 cm diameter, Roots 2 and 3, respectively; Figure 1) penetrated the hardpan. A single sap flow sensor was inserted into the xylem of each of the two lateral roots, whereas two sensors were inserted into the larger taproot. A fourth root (9.1 cm diameter, Root 4; Figure 1) was also instrumented with a single sensor. This root split into six smaller lateral roots immediately proximal to the point of sensor insertion. The largest of the six roots extended into the hardpan, whereas the other roots remained above the hardpan. After probe installation, the roots were covered with a tarpaulin to prevent radiant heating by direct sunlight. A dense network of surface lateral roots ranging from 2 to 4 cm in diameter was also present, but the roots were too small to instrument with sap flow sensors. The smaller lateral roots were excavated at the conclusion of the study to verify that they did not penetrate the hardpan. The main stem (18.5 cm diameter) was also instrumented with a sap flow sensor, 1.5 m above the soil surface. Sap flow was monitored over a 60-day period from June 21 to August 20, 2001 (Days 172–232). The sap flow sensors (Thermal Logic, Pullman, WA) consisted of three 35-mm long stainless steel probes spaced 6 mm apart. The central probe contained an Evanohm 44-Ω line heater, whereas the outside probes contained three paired thermocouple junctions spaced to measure sap flow at three radial depths. Probes inserted into the taproot and main stem had thermocouples that were spaced 10, 20 and 30 mm from the base of the sensor. Thermocouple spacing of the probes inserted into the smaller roots was 5, 10 and 20 mm from the base.

After correcting for wounding effects, heat pulse velocity \( V_s \) was converted to sap velocity \( V_s \) (cm h\(^{-1}\)) according to Barrett et al. (1995):

\[
V_s = \frac{\rho c_s (c_s + m c_s)}{\rho c_s}
\]

Figure 1. Schematic of a 10-year-old Juglans major tree root system instrumented with heat ratio sensors. We instrumented the taproot (14.3 cm diameter, Root 1), two deep lateral roots that penetrated a calcium carbonate hardpan (9.0 and 6.7 cm diameter, Roots 2 and 3, respectively) and a shallow lateral root that split into six smaller roots (9.1 cm diameter, Root 4). The main stem was also instrumented for sap flow measurement. Root and stem diameters were measured at the central point of probe installation.
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), respectively, and $\rho_s$ is sap density (assumed to equal that of water, 1.0 × 10$^3$ kg m$^{-3}$). Sap flow (1 day$^{-1}$) was calculated after subtracting the bark thickness from the radius of the stem or root. Heartwood radius (where present) 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.

Because HRM measurements of sap flow are 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 sap flow. Spacing between probes was calculated according to Burgess et al. (1998):

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

where $x_1$ and $x_2$ are the distances (mm) of the correctly and incorrectly spaced probes, respectively, from the central heating probe ($x_1$ is assumed to be correctly spaced at 6 mm), $k$ is thermal diffusivity of fresh wood (measured from cores of the individual roots), $v_1$ and $v_2$ are the increases in temperature at equidistant points downstream and upstream, respectively, and $t$ is median measurement time after the release of the heat pulse (60 s in this case). Because it was not known which probe was incorrectly spaced, or whether both probes were incorrectly spaced, Equation 1 was solved for $x_1$ and $x_2$ and the solutions were averaged.

Because of technical difficulties, we were unable to obtain a zero measurement for the sensor inserted into Root 4. To estimate the true probe spacing, 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; Figure 2).

Distances between probes were assessed from the X-ray image using the software application NIH Image (version 1.62 for Macintosh). First, the distance between the probes at each thermocouple depth (5, 10 and 20 mm) was measured relative to the central probe from the side view (Figure 2a). Second, the tangential distance (side b) between each probe tip and the probe base was measured from the top view (Figure 2b). The distance from the central probe was then multiplied by the proportional distance along the needle (i.e., 20/35 at the 20 mm thermocouple depth). This required the assumption that the probe remained straight through the wood matrix, which was partially verified from Figure 2a. The actual spacing was calculated by using a right-angled triangle ($a^2 + b^2 = c^2$), where side a is determined from the side view (Figure 2a), side b is calculated from the top view (Figure 2b) and side c (Figure 2c) is the actual spacing between probes. Distances between probes were measured from the center of each probe (black lines in Figure 2). Because errors independent of needle spacing may be present (i.e., thermocouple placement within the probe), a second study was conducted to compare spacing estimates from X-ray analysis with spacing estimates calculated from Equation 1. Seven probe sets were inserted into the ac-

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**Figure 2.** X-Ray radiographs showing a heat ratio sensor inserted into the xylem of a 20-cm diameter Populus fremontii stem. (a) Side view of the probes inserted into the xylem and (b) view of the inserted probes from above. (c) A 3-D representation of the sensor with downstream probe spacing exaggerated for illustration purposes. Probe spacing was calculated by using a right-angled triangle, where side a is determined from the side view, side b is determined from the top view, and side c is the actual spacing between probes. Side b was calculated from the tangential distance between the central probe and the up- or downstream probe, multiplied by the proportional distance along the probe. Distances were calibrated against the known length of the probes (35 mm).
tive xylem of a 20-cm diameter Populus fremontii Wats. stem. The stem was severed and the probe spacing was calculated according to Equation 1. X-Ray radiographs of the inserted probes were obtained and the spacing was calculated by the protocol described above. The results of the two methods were compared by means of a paired $t$-test.

**Results**

**Probe spacing**

Probe spacing errors, determined from Equation 1 and the X-ray radiographs, are reported in Table 1. Mean differences between the two methods of error determination were small, particularly at 5- and 10-mm depths, and yielded no statistically significant differences at any of the three depths ($P = 0.83, 0.85$ and $0.35$, at 5-, 10- and 20-mm depths, respectively). Figure 3 compares the daily course of sap flow in a 20-cm diameter P. fremontii stem, calculated from the mean spacing error values reported in Table 1. Based on the data presented in Figure 3, daily sap flow varied by 8% between the two methods at 5- and 10-mm depths, and 24% at the 20-mm depth.

**Root sap flow**

Despite the occurrence of some precipitation, the shallow roots contributed little to daily plant transpiration from July 3 to August 3 (Days 184 to 215); sap flow in the deep roots equaled transpiration from the canopy over this period (Figure 4). The shallow roots appeared to contribute a measurable amount of water to canopy transpiration only after a 10-mm precipitation event on August 5 (Day 217). After this event, the daily contribution of water to canopy transpiration from deep roots declined (Figure 4). Nocturnal reverse flow was detected in Roots 1, 2 and 3 after August 5 (Figures 5 and 6). Between August 5 and 11 (Days 217–223), nocturnal reverse flow in all deep roots ranged from 10 to 15% of daily transpiration. After a 22-mm rain event on August 11 (Day 223), reverse flow increased from 30 to 60% of daily transpiration (Figures 4 and 5). On many days after the 22-mm rainfall, daytime sap flow in Roots 2 and 3 continued in the reverse direction (Figure 6), and daytime sap flow in Root 1 decreased to about 50% of pre-August 5 values despite substantial transpiration in the crown (Figures 4 and 5). All shallow lateral roots (including Root 4) were severed on August 18 (Day 230). After severing, reverse flow in the deep roots immediately ceased, and daytime sap flow in the deep lateral roots increased to rates comparable with those before reverse flow was detected (i.e., before Day 217; Figures 5 and 6). Unlike the other roots, nocturnal reverse flow was detected in Root 4 throughout the measurement period until sensor failure disrupted sap flow measurements on August 5 (Day 217). Precipitation modified the pattern of sap flow by reducing daytime

Table 1. Deviation from the intended 6-mm spacing between probes of individual sensors inserted into the sapwood of a 20-cm diameter Populus fremontii tree. Calculated values were derived from Equation 2 and measured values were determined from X-ray images of the inserted sensors. A standard paired $t$-test yielded no significant differences between the methods at any thermocouple depth. Numbers in parenthesis represent standard errors of the mean ($n = 7$). Spacing errors of up- and downstream probes were averaged, because it is impossible to determine which probe was incorrectly spaced, or whether both were.

<table>
<thead>
<tr>
<th>Thermocouple depth (mm)</th>
<th>Probe spacing $P$</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Equation 2 (mm)</td>
</tr>
<tr>
<td>5</td>
<td>0.171 (0.050)</td>
</tr>
<tr>
<td>10</td>
<td>0.147 (0.042)</td>
</tr>
<tr>
<td>20</td>
<td>0.264 (0.082)</td>
</tr>
</tbody>
</table>

Figure 3. An example of the daily course of sap flow at 5, 10 and 20 mm thermocouple depths in a 20-cm diameter Populus fremontii stem corrected for probe spacing errors (based on Equation 1 or X-ray images of sensors) reported in Table 1. Sap flow was calculated by multiplying the sap flow velocities (corrected for probe spacing error) by the cross-sectional sapwood area at each thermocouple depth.
net basipetal flow (flow toward the crown) to near zero, whereas the magnitude of nocturnal reverse flow remained unchanged (Figure 7).

Discussion

The observed patterns of root sap flow are consistent with those reported in previous studies (Burgess et al. 1998, 2001a, Smith et al. 1999). However, sap flow patterns reported in our study differ from those reported by Hultine et al. (2003) on a similar sized *J. major* tree located 5 km downstream from our study site. Hultine et al. (2003) found no evidence of reverse flow in deep roots after surface soils were wetted by precipitation, and concluded that the presence of a perched groundwater table coupled with coarse soils prevented the “inverse” water potential gradient necessary for hydraulic descent. Such constraints to hydraulic descent were absent in our study, because depth to groundwater was likely beyond the rooting zone and a shallow hardpan prevented surface water from quickly recharging subsurface soil layers. These studies suggest that soil and geomorphic conditions moderate the potential for hydraulic redistribution over relatively small spatial
Daytime reverse flow after Day 223 occurred often in Roots 2 and 3 despite appreciable daytime transpiration from the canopy. In these cases, water potential of the rooting zone presumably remained lower than leaf water potential during transpiration. Daytime hydraulic redistribution is possible during periods when transpiration is reduced as a result of clouds. In clear weather, daytime hydraulic redistribution may still occur in plants that are highly vulnerable to xylem cavitation; critical xylem water potentials (xylem water potentials in which runaway xylem cavitation occurs) may be higher than soil water potential in the driest portions of the active root zone. In the present study, canopy transpiration was typically high during periods when daytime reverse flow was observed in Roots 2 and 3, strongly suggesting that patterns of daytime reverse flow were not caused by cloudy conditions.

After shallow roots were severed, reverse flow in deep roots ceased and daytime basipetal sap flow increased substantially. In a similar experiment, hydraulic descent ceased in the deep roots of *Grevillea robusta* A. Cun. after the lateral roots were severed, and daytime basipetal sap flow in the deep roots was substantially higher than on previous days (Smith et al. 1999). Both experiments demonstrate that plants with dimorphic root systems are capable of rapidly switching water sources, and provide further evidence that water redistributed by deep roots is supplied by the roots in shallow soil layers.

Root 4 had a different sap flow pattern than the other roots; reverse flow was detected throughout the measurement period and daytime basipetal sap flow decreased after early season rain events. Sap flow patterns in Root 4 were somewhat unexpected considering that most of the root system remained above the hardpan. Previous studies have shown that lateral roots often develop sinkers that span multiple soil layers, thereby allowing parts of the root system to access abundant water, whereas other lateral roots remain in contact with dry soil (Dawson and Pate 1996, Burgess et al. 2000, Hultine et al. 2003). Root 4 split into six small roots immediately proximal to the sap flow sensor insertion point. The largest of these small roots appeared to penetrate the hardpan, whereas the other roots spanned multiple layers above the hardpan, making sap flow patterns difficult to interpret.

The presence of reverse sap flow does not necessarily confirm that water is moving back into the soil. It is possible, or even likely that some water transported by reverse flow may be utilized to refill internal storage compartments, or used for cell expansion during root growth (Smith et al. 1999). However, Burgess et al. (2001a) observed that reverse sap flow is redistributed into deeper soils. They found nocturnal increases in soil water content in association with reverse flow measured in a *Eucalyptus camaldulensis* Dehn. taproot. The diameter of the *J. major* taproot and the magnitude of reverse flow in our study were similar to those reported by Burgess et al. (2001a). Therefore, it seems likely that a significant amount of reverse flow measured in *J. major* was redistributed to the deep soil layers.

Is hydraulic descent important to ecosystem and hydrological processes? Hydraulic descent may improve whole-plant water uptake by removing water from shallow soils and away from evaporation and shallow-rooted competitors (Burgess et al. 2001a). The acquisition of mineral nutrients may be enhanced by mineral uptake associated with the reabsorption of redistributed water. Further, hydraulic descent may play an important role in the establishment of juvenile phreatophytes by providing a wetting front for roots to follow as they extend through dry soils until they reach the water table (Schulze et al. 1998, Smith et al. 1999). In regions where infiltration is inhibited by hardpans or soils with low permeability, hydraulic redistribution may be the primary method of wetting deep soil layers. Thus, hydraulic descent may reduce water logging, erosion and runoff in some environments.

It is unclear why the shallow roots did not respond to precipitation early in the growing season. It is possible that the shallow soil layers were inadequately wetted. Because we did not measure soil water content, we cannot discount the possibility that soil water availability remained low at rooting depth. However, competition from shallow-rooted plants was minimal early in the summer rainy season, suggesting that available water was greater during this period than in August when the shallow roots responded to precipitation. Alternatively, the activity of shallow roots may have been inhibited by high soil temperatures early in the summer “monsoon” season. High soil temperatures have been shown to inhibit fine root development and maintenance (Kramer and Kozlowski 1979, Nobel et al. 1991). Ehleringer et al. (1991) demonstrated that

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**Figure 7.** Patterns of sap flow in a *Juglans major* lateral root (Root 4) during two different seasons; June 21–25 (Days 202–206), and August 1–6, 2001 (Days 213–217). Sap flow was calculated by multiplying the sap velocity by the cross-sectional sapwood area. Shaded bars are daily rainfall totals.
some species on the Colorado Plateau responded to rain in the spring and late summer, but not during midsummer when soil temperatures were highest. Likewise, cold desert shrubs and trees in Utah took up more irrigated water when temperatures were lower in late summer than in midsummer (Lin et al. 1996, Williams and Ehleringer 2000). In our study, mean maximum soil temperature at rooting depth (average of 10- and 30-cm depths) from July 2 to 11 was 30.1 °C (SE = 0.84), whereas from August 5 to 14, mean maximum soil temperature was 29.6 °C (SE = 0.52) (Tim Keefer, USDA-ARS, Southwest Watershed Research Center, personal communication). Thus, differences in soil temperature apparently do not explain the shifts in response to rain pulses between the two periods. Although unlikely, we cannot rule out the possibility that conditions between the two periods were near the threshold temperature at which _J._ _major_ develops and maintains functional roots.

An alternative explanation is that seasonal patterns of fine root production may be developmentally timed to match the most favorable “monsoon” period from August to September. Ehleringer and Dawson (1992) hypothesized that woody perennials allocate carbon below ground to portions of the rooting zone most likely to have access to water throughout the growing season. Preferential carbon allocation to rooting zones with stable water supply may be most common in plants that are highly susceptible to xylem cavitation, because the cost of building fine roots in marginally moist soils may exceed the benefit of water and nutrient acquisition (Williams and Snyder 2002). Riparian trees, such as _J._ _major_, are highly vulnerable to cavitation relative to upland desert species (Pockman and Sperry 2000). In southeastern Arizona, the summer rainy season typically does not commence until mid-July, and generally increases in intensity throughout August. Because precipitation is unpredictable during the early rainy season, it may not be beneficial for _J._ _major_ to invest carbon in shallow rooting zones until later in the rainy season, when soil water content is relatively stable.

### Probe spacing error corrections

We compared two methods for gauging probe spacing errors and determined that analysis of X-ray photographs provides a suitable replacement for in situ calibration of probe spacing. The new method can be used in cases where probes fail prior to in situ calibration. Alternative methods for gauging probe spacing errors have been reported, including the placement of over-length probes into drill holes and measuring the spacing and angle of the protruding probes (Hatton et al. 1995). X-ray analysis, however, may be more accurate than protruding probes because bending of the probes within the wood matrix can be accounted for with the X-ray images. Nevertheless, we note that X-ray analysis cannot detect errors that are independent of probe spacing, such as asymmetrical wood thermal properties (Burgess et al. 2001b) or errors in thermocouple placement within the probe (Becker 1998).

### Conclusions

_Juglans major_ transfers a measurable amount of water absorbed from shallow soils to deep soil layers after shallow soils are wetted by precipitation, although the timing of hydraulic descent may be limited to periods when rainfall is highly probable. We caution against making broad conclusions based on a single specimen. However, if the behavior of the studied _J._ _major_ tree is typical for individuals of this species under similar conditions, hydraulic descent could be an extremely important process affecting plant water balance and survival in habitats where groundwater is unavailable.

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### References


