

Water uptake and hydraulic redistribution across large woody root systems to 20 m depth

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ABSTRACT

Deep water uptake and hydraulic redistribution (HR) are important processes in many forests, savannas and shrublands. We investigated HR in a semi-arid woodland above a unique cave system in central Texas to understand how deep root systems facilitate HR. Sap flow was measured in 9 trunks, 47 shallow roots and 12 deep roots of *Quercus*, *Bumelia* and *Prosopis* trees over 12 months. HR was extensive and continuous, involving every tree and 83% of roots, with the total daily volume of HR over a 1 month period estimated to be approximately 22% of daily transpiration. During drought, deep roots at 20 m depth redistributed water to shallow roots (hydraulic lift), while after rain, shallow roots at 0–0.5 m depth redistributed water among other shallow roots (lateral HR). The main driver of HR appeared to be patchy, dry soil near the surface, although water may also have been redistributed to mid-level depths via deeper lateral roots. Deep roots contributed up to five times more water to transpiration and HR than shallow roots during drought but dramatically reduced their contribution after rain. Our results suggest that deep-rooted plants are important drivers of water cycling in dry ecosystems and that HR can significantly influence landscape hydrology.

Key-words: caves; deep roots; ecohydrology; gum bumelia; Heat Ratio Method; live oak; mesquite; woody plant encroachment.

INTRODUCTION

Plant roots are well known to transport water within the soil profile via the process of hydraulic redistribution (HR), defined as the passive movement of water from wet soil to dry soil through roots, driven by gradients in soil water potential (Richards & Caldwell 1987; Burgess *et al.* 1998). The occurrence of HR depends on a suite of biological and physical variables, including root system size, soil texture, and the degree of root-to-soil contact (Jackson *et al.* 2007). It typically occurs at night when stomata are closed and plants become disconnected to the atmosphere, but it can

also occur during the day if the gradient in water potential is greater to dry soil than to the atmosphere. HR is a global phenomenon that occurs in a wide range of species across many different biomes, from deserts to tropical rainforests (Caldwell, Dawson & Richards 1998; Jackson, Sperry & Dawson 2000).

There is mounting evidence that HR has significant potential to alter soil hydrology and provide ecological benefits to at least some plants. The amount of water involved in HR is often small, but large trees and shrubs can move relatively large amounts of water representing a considerable percentage of total daily water use (Ryel *et al.* 2002; Brooks *et al.* 2006). Studies have shown that the water from HR may delay the onset of soil drying during drought (Brooks *et al.* 2002; Hawkins *et al.* 2009), limit cavitation in fine roots (Domec *et al.* 2004), and moisten soil at the surface or at depth to facilitate processes such as root or mycorrhizal growth (Huang 1999; Querejeta, Egerton-Warburton & Allen 2003), decomposition (Aanderud & Richards 2009) and nutrient acquisition (McCulley *et al.* 2004). At large scales, HR may play an important role in ecosystem water, carbon and nutrient cycling (Jackson *et al.* 2000), and it may also affect the energy balance and climate of densely vegetated ecosystems (Lee *et al.* 2005). HR is likely increasing globally as the abundance of deep-rooted woody plants increases through woody plant encroachment, afforestation and other processes (Van Auken 2000; Engel *et al.* 2005; Jackson, Jobbagy & Noretto 2009). Studies are clearly needed to predict the possible ecohydrological consequences of HR, particularly in water-limited environments where deep-rooted plants can potentially tap and redistribute isolated water resources (Schulze *et al.* 1998; Seyfried *et al.* 2005; Scott *et al.* 2006; Lubczynski 2009).

Plants with large, expansive woody root systems tend to be the most effective redistributors of soil water. Large, deep root systems are advantageous for HR because they can connect multiple soil compartments and allow water to move in virtually any direction dictated by soil water potential gradients, including upwards (e.g. Burgess *et al.* 1998; Moreira *et al.* 2003), downwards (e.g. Smith *et al.* 1999; Burgess *et al.* 2001c) and laterally (e.g. Smart *et al.* 2005; Burgess & Bleby 2006). Deep roots in particular can allow access to deep water sources many tens of metres underground (Schenk & Jackson 2002), and they can play a

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critical role in facilitating both hydraulic lift (e.g. Penuelas & Filella 2003) and downward HR (e.g. Hultine *et al.* 2003a) in arid and semi-arid environments.

There is strong evidence that woody roots are well designed to facilitate water transport driven by HR. Water flow through woody root xylem is generally unrestricted in both directions (Schulte 2006), and HR-induced sap flow in intact lateral roots can be equal to or greater than sap flow induced by transpiration (Burgess & Bleby 2006). Recent work also suggests that deep roots are naturally well adapted for water transport over long distances against the force of gravity, in part due to their unique structural characteristics that promote high hydraulic efficiency, including large xylem diameters (McElrone *et al.* 2004). Less well understood is how large woody root systems function as an integrated whole in space and time to facilitate HR.

Understanding HR across large woody root systems requires knowledge of key attributes, including the role of roots of varying size and location in the root system (e.g. distal roots versus proximal roots), the behaviour of roots connected to ephemeral and perennial soil water sources and sinks (e.g. shallow roots versus deep roots), the occurrence of different types of HR (e.g. vertical HR versus lateral HR), and the occurrence of HR under different environmental conditions (e.g. during drought versus after rain). These attributes are best studied using techniques that can provide continuous data on the direction and quantity of water movement at specific locations. When roots are accessible, sap flow techniques are arguably the most powerful tool for studying HR, and a number of studies show that the best results are achieved when synchronous measurements of sap flow are obtained from as many roots, spanning as much of the root system, as possible (e.g. Hultine *et al.* 2004; Nadezhkina *et al.* 2006; Scholz *et al.* 2008; Scott, Cable & Hultine 2008).

In this paper, we focus on the role of woody roots in HR and the seasonal dynamics of HR in a water-limited savannah populated by deep-rooted trees. We monitored stem and root sap flow using the Heat Ratio Method (HRM; Burgess *et al.* 2001b) to determine whole-plant water use, seasonal patterns of HR, and the water transport characteristics of deep and shallow woody roots of Texas live oak (*Quercus fusiformis* Small), gum bumelia (*Bumelia lanuginosa* Michx.), and honey mesquite (*Prosopis glandulosa* Torr.) in a semi-arid, karst system in central Texas, USA. These species have strongly dimorphic, deep root systems spanning water sources and sinks likely to drive HR: lateral roots in this system are restricted to shallow calcareous soils (<0.5 m depth), whereas deep roots >10 m below ground are known to penetrate fractured limestone to access deeper water sources (McElrone *et al.* 2007). Substantial evidence from the literature also suggests that *Quercus* and *Prosopis* spp. are good facilitators of HR in dry environments under the right conditions (Querejeta *et al.* 2003; Hultine *et al.* 2004; Zou *et al.* 2005; Nadezhkina *et al.* 2008; Scott *et al.* 2008).

Deep roots are rarely studied *in situ* without extensive excavation and disturbance. In most cases, the

contribution of deep roots to HR is determined indirectly by monitoring sap flow in the upper portions of apparent tap or sinker roots (e.g. Hultine *et al.* 2003b; Oliveira *et al.* 2005), or by identifying lifted water in surface soil using stable isotopes (e.g. Penuelas & Filella 2003). While these approaches provide important information about the dynamics of HR and the approximate location of deep roots and water sources, they give little or no information about specific depths or locations of water uptake or actual rates of sap flow in deep roots. To overcome this limitation, we used a novel cave system to access woody roots directly at 20 m depth. We targeted roots that had been previously identified to parent trees above ground using DNA sequence variation (Jackson *et al.* 1999, 2002; McElrone *et al.* 2007), which allowed us to monitor water transport in the stem and in deep and shallow roots of the same plant.

Our objectives were threefold: (1) to describe the occurrence and frequency of HR for dominant evergreen and deciduous tree species in this ecosystem and how it changes in response to environmental conditions; (2) to determine the number of woody roots involved in HR and assess the degree of involvement of roots of varying size and depth; and (3) to determine the specific contribution of deep roots to HR, including their responses to surface soil moisture conditions and their coordination with shallow roots to supply water for transpiration and HR.

MATERIALS AND METHODS

Field site and study species

This study was conducted in the Edwards Plateau region of central Texas, USA. The region has karst geology characterized by shallow, calcareous soils (frequently <20 cm depth) overlying fractured Cretaceous limestone. The vegetation of the region is mainly savannah and woodland. We investigated three dominant tree species: the evergreen *Quercus fusiformis* (Texas live oak), the deciduous *Bumelia lanuginosa* (gum bumelia) and *Prosopis glandulosa* (honey mesquite). These species are found throughout the Edwards Plateau and are considered relatively slow growing and drought tolerant (Auken *et al.* 1980).

The study site was located near Menard, TX (30°55' N, 99°54' W, elevation 600 m above s/l), with a climate classified as subtropical and sub-humid that is characterized by hot summers and dry winters. MAP is approximately 630 mm, and monthly mean temperature ranges from 8 °C in January to 27 °C in July. Precipitation is evenly distributed throughout the year, supplied by irregular small rainfall events and occasional large thunderstorms. Microclimate data were acquired from our weather station at the site, including half-hourly measurements of rainfall (TR525I tipping bucket rain gauge; Texas Electronics, Dallas, Texas, USA), air temperature and relative humidity (HMP45C probe; Campbell Scientific, Logan, Utah, USA), and photosynthetically active radiation (LI-190 sensor; LI-COR, Lincoln, Nebraska, USA), all logged using a

CR10X datalogger (Campbell Scientific). Temperature and humidity measurements were used to derive vapour pressure deficit.

Soil moisture

We measured the volumetric water content of surface soil near two *Q. fusiformis* trees (used for sap flow measurements) using water content reflectometers (CS615 probes; Campbell Scientific) interfaced with a CR10X datalogger. Four reflectometers were installed in undisturbed soil approximately 3 m away from the trunks but beneath the canopy of the trees, and a further two reflectometers were installed in bare soil approximately 15 m away from the trunks of the trees. Reflectometers were installed at a 45° angle to a depth of 30 cm, taking care not to displace sensor rods in the shallow, gravelly soil. Reflectometers were installed primarily to observe major changes in soil moisture in the general vicinity of study trees over the course of the experiment.

Root system architecture

The woody root systems of *Q. fusiformis*, *B. lanuginosa* and *P. glandulosa* were strongly dimorphic. All species had shallow lateral roots near the surface and deep tap roots extending to at least 18–20 m depth. Numerous deep roots (diameter >1 cm) were observed growing through the roof and in sediment-laden side walls of a cave directly below the trees (see McElrone *et al.* 2004), and some of these roots tapped directly into a perennial underground stream. Lateral roots were observed after excavating surface soil to ~0.3 m depth around the base of each tree within a 1–2 m radius. Lateral roots of a range of sizes were distributed more or less evenly around the base of each tree. Roots within the excavated radius were classified into three different size groups based on diameter: 'large' roots >60 mm, 'medium' roots 40–60 mm, and 'small' roots <40 mm. Roots from each group were selected for sap flow measurement as described below. For this study, all roots in the shallow topsoil layer were considered as 'laterals'.

Several randomly selected lateral roots were excavated to a distance of 5 m from the tree base to assess root architecture in more detail. Most of these roots were found to terminate in shallow soil, and roots commonly changed direction and angle of descent to grow under and around chunks of fractured limestone. A small number of larger lateral roots appeared to descend into deeper epikarst layers of the profile, but it was not practical to excavate roots through meters of rock. Root branching patterns were complex and difficult to map, but in general, large structural roots near the base of the tree tended to branch into progressively smaller lateral roots, such that root size could be used as a proxy for location within the root system. It was generally assumed that distance to fine roots involved in the uptake and efflux of water increased with increasing root size such that small roots could be regarded as being distally

located and medium and large lateral roots could be regarded as being proximally located.

Sap flow measurements

Sap flow in stems and woody roots was measured using the HRM, as outlined in Burgess *et al.* (2001a,b). The HRM is well suited for measurements of sap flow in woody plants, and it is a preferred method for studying HR because of its ability to measure low, zero and reverse rates of sap flow (Burgess, Adams & Bleby 2000). We used a combination of custom-built HRM sensors constructed at the University of Western Australia (see Bleby, Burgess & Adams 2004) and commercially acquired ICT HRM-30 sensors (ICT International, Armidale, NSW, Australia). For stems and roots >20 mm diameter, we used 38 mm length probes with two thermocouple pairs located 7.5 and 22.5 mm from the needle tip. For roots <20 mm diameter, we used shorter 20 mm length probes with a single thermocouple pair located 5 mm from the needle tip. ICT HRM-30 sensors were connected to an ICT datalogger (SL5 Smart Logger; ICT International). All other HRM sensors were connected to CR10X dataloggers via AM16/32 or AM25T multiplexers (Campbell Scientific).

We deployed a total of 73 sap flow sensor sets in nine trunks, 47 lateral roots and 12 deep roots across nine individual trees (5 × *Q. fusiformis*, 2 × *B. lanuginosa*, and 2 × *P. glandulosa*) from May 2006 until April 2007. Our study was carefully designed to include trees that accessed underground stream water via the cave (above-stream) and those that did not (off-stream). Seven out of the nine trees were located directly above the cave within a rectangular 50 × 10 m plot, and the remaining two trees (2 × *Q. fusiformis*) were deliberately located several hundred meters outside this plot, far from the known permanent water source within the cave. Off-stream trees were measured similarly to on-stream trees, except that deep roots of off-stream trees were inaccessible and could not be measured.

Sap flow sensors were installed in three to nine shallow lateral roots of every tree except for one *Q. fusiformis* tree that had few lateral roots above 1 m depth. At least one root from each of the three size groups was measured for each tree, and the total number of roots measured in each size group was similar and fairly evenly distributed across all species (15 × large, 13 × medium, 19 × small). Sap flow sensors were installed in roots at least 0.5 m away from the trunk of the tree, and instrumented roots were further excavated to at least 2 m distance from the trunk to make sure that they were likely to terminate in shallow soil. Rhizomatous tissues and roots attached to clonal stems were carefully avoided. For several branched roots in *Q. fusiformis* and *B. lanuginosa*, we installed pairs of sensor sets in the proximal segment and attached distal segments of root branches to measure water exchange among directly connected roots.

In the cave, soil on the cave walls and along the banks of the underground stream was excavated to expose deep woody roots large enough (>10 mm diameter) for the

installation of sap flow sensors. Sap flow sensors were then installed in a total of 12 deep roots ($8 \times Q. fusiformis$, $4 \times B. lanuginosa$). All deep roots measured in the cave were small in size (<40 mm diameter).

Sap flow sensors were installed in a standard fashion in all trees for determining sap velocity and volumetric water flux through trunks or roots. Overlying bark was shaved where necessary and a steel drill guide was used to ensure accurate probe spacing (5 mm). In trunks, sensors were installed along the main axis at ~1.3 m height and positioned so that thermocouple pairs adequately covered the depth of sapwood. For smaller trees <0.15 m diameter at breast height (DBH), a single sensor set was installed on the trunk, facing north. For larger trees >0.15 m DBH, two replicate sensor sets were installed on the trunk, facing north and south, except for one large individual of *Q. fusiformis* with three co-dominant trunks where we installed single sensor sets in each of the two largest trunks, facing north. In roots, sap flow sensors were installed along the main axis, usually on the upper surface, with sensors positioned to adequately cover the cross-sectional area of sapwood. Sensors were firmly secured to stems and roots using cable ties, and those above ground were covered with reflective insulation to shield them from direct sunlight. Raw measurements of heat pulse velocity (V_h) were logged every 30 min.

Established protocols from Burgess *et al.* (2001b) and Bleby *et al.* (2004) were applied to correct raw measurements of V_h for probe misalignment and wounding, then to convert V_h to sap velocity (V_s), and then to convert sap velocity to a volumetric flow rate (Q). To correct for probe misalignment, $V_h = 0$ baselines were established over 12–24 h at the end of the experiment following the severing of xylem tissue surrounding each sensor. Xylem tissue was completely severed to halt sap flow in small roots, whereas deep notches were cut into the sapwood above and below sensors to halt sap flow in stems and large roots.

Wounding around each sap flow sensor was monitored *in situ* every 3 months by measuring the width of discolored xylem tissue around drill holes to within 0.1 mm using a magnifying glass and digital calipers. Microscope work in the laboratory on selected samples of each tissue type (shallow and deep roots and stems) of each species confirmed that there was a strong correlation between the width of discolored xylem tissue around drill holes and the actual wound width measured from blocked and damaged xylem vessels. Initial wound diameters were 2.0 mm for 1.4 mm diameter drill holes, while end wound diameters typically ranged from 2.0 to 3.0 mm after 9 months. On the rare occasions when it was determined from monitoring that wound diameters were >3 mm, sensors were immediately reinstalled. To account for gradual wound development, data were corrected for wounding on a daily basis using the daily rate of increase in wound diameter, assuming a linear increase over time.

Heat pulse velocity data were converted to sap velocity using equations supplied in Burgess *et al.* (2001b). Measurements of fresh weight, dry weight and fresh volume of

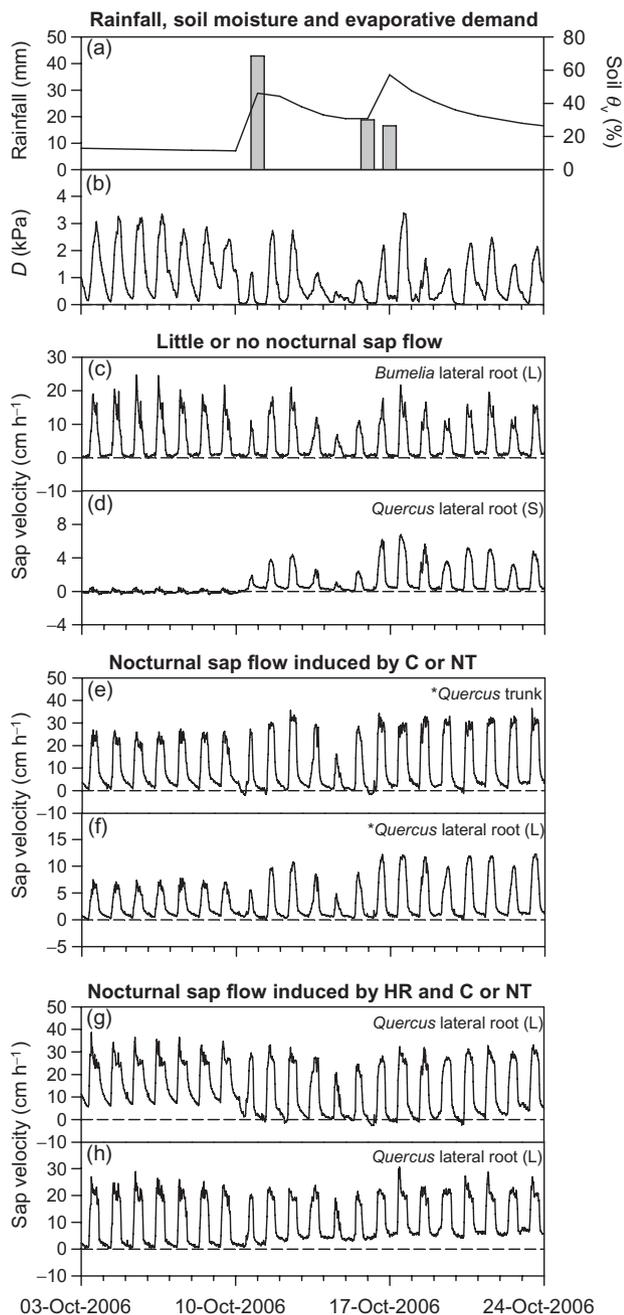
sapwood required for the conversion were obtained from excised discs of sapwood or cores extracted using a 5 mm diameter increment borer (Haglöf, Sweden). Half-hourly measurements of V_s were averaged to give hourly V_s for each sensor set, and replicate measurements of V_s from the same trunk or root were averaged as required. Average daytime sap velocities between 0600 and 1800 h ($V_{s \text{ day}}$) and average night-time sap velocities between 0100 and 0500 h ($V_{s \text{ night}}$) were calculated as required. The period of 0100–0500 h was chosen for the calculation of $V_{s \text{ night}}$ to limit any confounding effects of night-time sap flow driven by factors other than HR, such as the rehydration of xylem tissue and/or transpiration after dusk on warm nights, or the start of transpiration at the break of dawn.

To calculate volumetric sap flow rates (Q) in trunks and roots, we multiplied V_s by the cross-sectional area of conducting sapwood (A_s). Conducting sapwood was determined from 5 mm diameter cores and wood discs, which were examined under a dissecting microscope to determine sapwood–heartwood boundaries and sapwood widths. Sapwood areas of trunks and roots were then determined from measurements of outer-bark diameter, bark thickness, and sapwood width. Estimates of Q for roots with small sapwood areas measured using short-length probes were determined from a single point measurement of V_s (sapwood widths typically <20 mm), whereas estimates of Q for trunks and roots with larger sapwood areas measured using standard-length probes were determined from point measurements of V_s at two depths (sapwood widths typically 20–40 mm). For two-point determinations of Q , we divided total sapwood area into a pair of concentric bands delimited by the mid-point between the measurement depths, and calculated Q based on the addition of sap flows from bands associated with inner and outer point measurements of V_s . Hourly measurements of Q ($L \text{ hr}^{-1}$) were then summed over 12 or 24 h periods to give daytime, night-time, or total daily values ($L \text{ day}^{-1}$) as required.

Identification of HR

Diurnal sap flow traces from all roots were carefully examined to determine the occurrence of HR based on the night-time pattern of flow. This was a multi-step process. Firstly, we identified when ‘significant’ night-time sap flow had occurred in roots; that is, when $V_{s \text{ night}}$ was $>+2 \text{ cm h}^{-1}$ (significant positive flow) or $<-2 \text{ cm h}^{-1}$ (significant negative flow) over a period of at least five consecutive days. This range lies well outside the zero flow ($V_s = 0$) error range of our measurement technique, which was conservatively estimated to be $\pm 1 \text{ cm h}^{-1}$ (see Bleby *et al.* 2004).

Next, root sap flow data were carefully examined alongside meteorological data, soil moisture data, and sap flow data from trunks of parent trees and neighbouring roots to determine when night-time sap flow (specifically positive flow) was due to HR and not some other phenomenon. In general, surface soil beneath and away from the



canopies of trees was dry during drought (θ_v ~10%), but it wetted rapidly after rain (θ_v ~60%) and gradually dried out thereafter (as shown in Figs 1a, 2a & 4a,b). Of note, diurnal trends in vapour pressure deficit (D) were characterized by a gradual decline to near zero just before dawn on warm, dry days, but on cool, wet days, D declined shortly after dusk and remained near zero for most of the night (as shown in Fig. 1b).

Apart from HR, the most likely drivers of night-time flow in this system were considered to be capacitance (C) and nocturnal transpiration (NT). Night-time flow due to C and/or NT was differentiated from HR based on a distinctive pattern of flow characterized by a gradual decrease in

Figure 1. Diurnal sap velocity traces and environmental data illustrating the presence and absence of night-time sap flow in woody roots and trunks of selected measurement trees (*Quercus fusiformis* and *Bumelia lanuginosa*). Measurements are from a representative 3 week period in October 2006 (autumn) when surface soil was initially dry and then wet. Daily rainfall and volumetric soil moisture content (θ_v) at 0–0.3 m depth are shown in panel (a), and vapour pressure deficit (D) is shown in panel (b). Panels (c) and (d) show examples of little or no night-time sap flow in lateral roots. Panels (e) and (f) show examples of night-time sap flow in trunks and lateral roots related either to rehydration of xylem tissue as determined by capacitance (C) and/or nocturnal transpiration (NT) driven by D at night. Panels (g) and (h) show examples of night-time sap flow driven by hydraulic redistribution (HR) including the effects of C and/or NT. Lateral roots were measured in shallow soil at 0–0.5 m depth. Small roots (S) were <40 mm and large roots (L) were >60 mm in diameter. Asterisks (*) denote measurements from the same plant.

sap velocity after transpiration from dusk to dawn. This pattern was consistent with the gradual rehydration of xylem tissue determined by C, and at times (e.g. warm, dry nights), it was also consistent with the gradual release of water to the atmosphere as a result of NT driven by evaporative demand, in line with the diurnal pattern of D as described above.

Although it was not possible to identify C and NT exactly or separate their effects on sap flow (e.g. using dendrometry, monitoring nocturnal stomatal conductance, etc.), we observed that non-HR-related flow occurred more commonly in the trunks of larger trees (*Quercus*) than the trunks of smaller trees (*Bumelia* and *Prosopis*), and more commonly in large structural roots directly attached to the trunk than in smaller distal roots, suggesting that flow may have been dominated by C rather than NT. Nevertheless, the effects of C and/or NT on the pattern of night-time sap flow were clearly different from that of HR, even when C and/or NT occurred at the same time as HR (as shown in Fig. 1g,h). In general, the effects of C and/or NT were more easily identified during times of drought than after rain, possibly because there was less need to recharge trunk xylem under wetter conditions (McElrone, unpublished data).

Once HR was identified, roots were then classified as being involved in either HR uptake or HR efflux, in line with the physical principles governing the occurrence and direction of HR. These principles assert that that woody roots involved in water uptake are connected to parts of the root system that absorb water from moist soil, whereas woody roots involved in water efflux are connected to parts of the root system that efflux water into dry soil. Thus, night-time water movement in a positive direction towards the stem indicated HR uptake, whereas movement in a negative direction towards the soil indicated HR efflux. We then classified root involvement in HR in relation to environmental conditions, specifically whether HR occurred in response to drought (drought-induced HR), rainfall (rainfall-induced HR) or both.

Finally, each root involved in HR was assessed individually and compared with other roots to map the timing and direction of HR in individual trees. This allowed us to identify the occurrence of different types of HR, specifically vertical HR or lateral HR. In this study, we defined lateral HR as the sideways movement of water in any direction in the horizontal plane within a certain depth range, in this case surface soil to around 0.5 m depth. Group assessments from all trees were combined to develop conceptual (schematic) models of water movement across whole root systems during HR for the ecosystem, highlighting the roles of different types of roots with respect to size (small, medium and large), location (distal and proximal) and depth (shallow and deep).

Quantification of HR

The degree of root involvement in HR was quantified using a proportional sap flow index (HRI), defined as the ratio of average sap velocity at night to average sap velocity during the day ($V_{s \text{ night}}/V_{s \text{ day}}$). Ratios were based on scalar values of velocity irrespective of the direction of flow. HRI values for individual roots indicated the degree of sap flow activity during HR and the amount of water transported for HR as a proportion of that transported for transpiration.

To estimate the contribution of HR to tree water balance, we compared the total volume of water transported at night (for HR) by all measured roots with that transported during the day (for transpiration) by the same roots over a representative period of 28 d that encompassed both wet (vertical HR) and dry (lateral HR) conditions in equal amounts (14 d before and 14 d after the major rainfall event on 11 Oct shown in Figs 1 & 2). For this estimate, the flow of water through each root during HR (in a positive or negative direction) was conceptually assumed to be a discrete occurrence unconnected to flow in any other root, such that the same water was not 'counted twice', and it was also assumed that all flow eventually terminated in dry soil. Also, any data that showed obvious signs of C and/or NT were excluded from the estimate.

RESULTS

Numbers of trees and roots involved in HR

HR was observed in every measured tree, and it involved 49 of the 59 measured woody roots (83%). All deep roots and approximately 80% of all shallow lateral roots displayed evidence of HR (Table 1). The remaining 20% of lateral roots displayed very little, if any, sap flow at night at any time, indicating little or no HR.

There was no evidence from trunk or lateral-root measurements that off-stream *Quercus* trees behaved differently from above-stream *Quercus* trees with respect to HR. The range of sap velocities measured in off-stream trees during HR was the same as that measured in on-stream trees, and there was no statistical difference in

Table 1. Summary data showing the number of measured shallow lateral roots and deep roots involved in hydraulic redistribution (HR)

	Lateral roots (<0.5 m depth)	Deep roots (~20 m depth)
Total number roots measured	47	12
Number of roots involved in HR	37 (79%)	12 (100%)
Number of roots involved in HR:		
Only during drought	9 (24%)	9 (75%)
Only after rain	10 (27%)	–
During drought and after rain	18 (49%)	3 (25%)
Number of roots involved in HR that displayed:		
Positive flow only (uptake)	13 (35%)	12 (100%)
Negative flow only (efflux)	9 (24%)	–
Positive and negative flow at different times	15 (41%)	–
Positive flow during drought	17 (46%)	12 (100%)
Negative flow during drought	20 (54%)	–
Positive flow after rain	27 (73%)	3 (25%)
Negative flow after rain	10 (27%)	–

Roots were considered to have been involved in HR if they displayed 'significant' night-time sap velocity (V_s) at some point during the 10 month study period, defined as average night-time (0100–0500 h) $V_s > 2 \text{ cm h}^{-1}$ or $< -2 \text{ cm h}^{-1}$ for ≥ 5 consecutive days. Also shown are the number of roots involved in specific types of HR behaviour associated with the direction and timing of night-time sap flow. Data were pooled from *Quercus*, *Bumelia* and *Prosopis* spp. Percentage values are shown in parentheses. Percentages for the number of roots involved in HR are with respect to the total number of roots measured. All other percentages are with respect to the number of roots involved in HR.

the number and type of roots involved in HR (data not shown). Daytime water uptake by off-stream trees was also similar to that of above-stream trees (Table 2).

Sap flow patterns attributed to HR

Night-time sap flow was absent in a minority of roots (e.g. Fig. 1c,d), but it was clearly present in the majority of roots and in the trunks of some trees (e.g. Figs 1e–h & 2b–h). We identified at least seven different types of HR behaviour in roots over the course of the study (Fig. 2b–h), each with its own distinct pattern of night-time sap flow. These patterns are described below within the context of the two dominant HR regimes that occurred in this system: drought-induced HR and rainfall-induced HR.

Drought-induced HR was characterized by the simultaneous uptake and efflux of water by different roots prior to rain when surface soil was dry. Under this regime, some roots were involved only in uptake (Fig. 2b) while other roots were involved only in efflux (Fig. 2c). Measurements of uptake by deep roots with permanent access to water and efflux by shallow lateral roots of the same plant (Fig. 2b,c) suggested that the type of HR that dominated during drought was vertical HR (hydraulic lift). In contrast, rainfall-induced HR was characterized by the simultaneous uptake (Fig. 2d) and efflux (Fig. 2e) of water by different roots after rain. The dominant type of HR that occurred after rain was determined to be lateral HR, as evidenced by

Species	Tree ID	Date measured	A_s (cm ²)	E (L day ⁻¹)	D (kPa)	E_n (L day ⁻¹ m ⁻² kPa ⁻¹)
<i>Q. fusiformis</i>	O1	14-Aug	749	124	1.6	1035
	O2	15-Aug	2056	365	2.5	710
	O3	18-Aug	278	40	2.9	496
	O4	7-Oct	875	167	1.4	1363
	O5	7-Oct	697	115	1.4	1178
<i>B. lanuginosa</i>	B1	21-Aug	179	31	2.6	666
	B2	21-Aug	92	8	2.6	334
<i>P. glandulosa</i>	M1	15-Aug	43	5	2.5	465
	M2	15-Aug	71	8	2.5	451

Table 2. Whole-tree water use parameters for each of the nine measured trees

Parameters include species, tree ID, trunk sapwood area at breast height (A_s), whole-tree transpiration (E), average daytime vapour pressure deficit (D , calculated between 0600 and 1800 h), and normalized whole-tree transpiration (E_n). Normalized transpiration values, defined as $E_n = E/A_s/D$, are included for comparative purposes to account for the fact that not all trees were the same size, and complete data sets from all trees were not available on exactly the same day for technical reasons (heater failure in some sap flow sensors). All trees were located 'above-stream' except for trees O4 and O5, which were 'off-stream', and measurements are from representative warm, sunny days at the end of summer 2006. Average $E_n \pm$ SE was 957 ± 157 for evergreen *Quercus fusiformis*, and 479 ± 68 for deciduous *Bumelia lanuginosa* and *Prosopis glandulosa*.

measurements of uptake and efflux by opposing shallow lateral roots of the same plant (Fig. 2d,e) and by the general observation that very little water was supplied for HR by deep roots after rain (Fig. 2b).

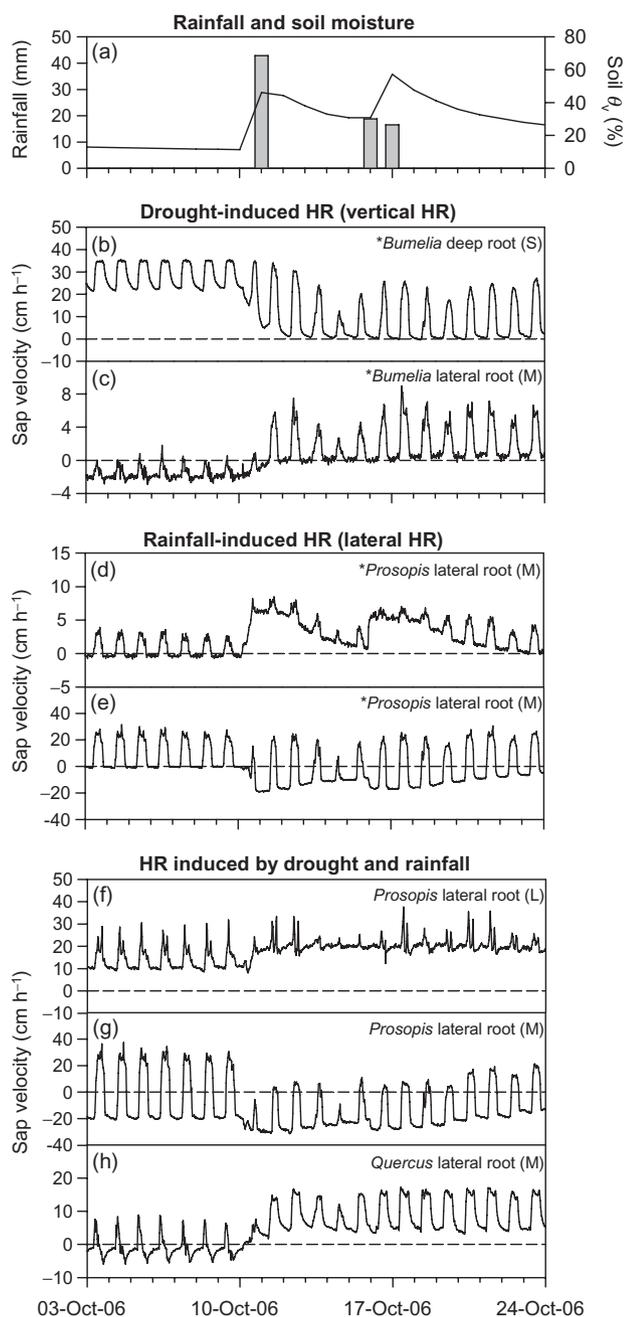
Approximately one quarter of lateral roots were involved in HR only during drought, while one quarter were involved in HR only after rain (Table 1). The remaining half of all lateral roots were constantly involved in HR during drought and after rain (Table 1); some roots were involved only in constant uptake (Fig. 2f) while others were involved only in constant efflux (Fig. 2g), and some roots were capable of switching from efflux during drought to uptake after rain or vice versa under the combined regime (Fig. 2h). The occurrence of switching was somewhat predictable in some roots following observations of responses to repeated cycles of drought and rainfall, but the direction of switching (from uptake to efflux or vice versa) was generally not predictable for any given root. Notably, rainfall tended to have an additive effect on baseline levels of HR established during drought (Fig. 2f,g). Across all regimes (i.e. drought-induced HR, rainfall-induced HR, and drought and rainfall-induced HR), ~40% of lateral roots switched between uptake and efflux at different points in time compared with 35% that were involved only in uptake and ~25% that were involved only in efflux (Table 1). During drought, the number of HR roots that displayed uptake (46%) was approximately the same as the number that displayed efflux (54%); but after rain, the number of HR roots that displayed uptake (73%) was three times the number of roots that displayed efflux (27%).

Compared with the wide range of HR behaviours observed in lateral roots, the behaviour of deep roots was relatively uniform. All deep roots were involved in water

uptake at night during drought, but this reduced dramatically after rain (Table 1 and Fig. 2b). Downward transport of water (efflux) did not occur in deep roots at any time (Table 1). Rates of night-time sap flow in deep roots during drought were the highest measured values during HR for all roots ($V_s > 20$ cm h⁻¹), commonly higher than maximum daytime velocities measured in many shallow roots during the day (e.g. Figs 1c,d,f & 2c,d,h).

Daytime sap flow in deep roots was consistently high during drought ($V_s > 30$ cm h⁻¹), but it decreased markedly in response to large rainfall events >10 mm (Fig. 2b). Daytime sap flow in lateral roots varied from root to root and was difficult to predict with respect to soil water availability or the presence or absence of HR. In response to rain, daytime sap flow increased in some roots (e.g. Figs 1d,f & 2c,d,h), decreased in others (Fig. 2g) or did not substantially change (Figs 1c,g,h & 2e,f). Some lateral roots lay completely dormant during drought and then became highly active after rain (Fig. 1d). Other roots were affected by competing demands for water during the day from both transpiration and HR, leading to only small positive rates or negative rates of sap flow during the day (Fig. 2c,g,h). The most predictable daytime patterns of sap flow were measured in large proximal roots directly attached to the trunk, which tended to mimic patterns measured in the trunk (Fig. 1e,f).

In winter, leafless species continued to facilitate rainfall-induced HR and drought-induced HR (Fig. 3). In some cases, deep roots continued to take up water at substantial sap velocities of around 20 cm h⁻¹ in the absence of rain (Fig. 3a) at the same time as small amounts of water were released by shallow lateral roots (Fig. 3b), indicating the occurrence of vertical HR (hydraulic lift). In other cases, opposing lateral roots that were dormant during drought



became involved in uptake (Fig. 3c) and efflux (Fig. 3d) after large rainfall events, indicating the occurrence of lateral HR. In general, water appeared to move steadily through the root systems of dormant-deciduous trees in the absence of transpiration according to prevailing soil water potential gradients regardless of the time of day. The exact reason for the large fluctuation in efflux shown in Fig. 3b could not be determined, but it clearly shows that HR patterns are not always regular or predictable in individual roots connected to large, expansive root systems through which the flow of water is integrated and affected by spatially complex gradients in soil water potential.

Figure 2. Diurnal sap velocity traces illustrating the range of sap flow behaviours measured in woody roots as a result of hydraulic redistribution (HR). Examples are drawn from all species (*Quercus fusiformis*, *Bumelia lanuginosa* and *Prosopis glandulosa*) and measurements are from the same period as shown in Fig. 1. Daily rainfall and volumetric soil moisture content (θ_v) at 0–0.3 m depth are shown in panel (a). Panels (b–h) show examples of ‘positive’ night-time sap flow (towards the base of the tree) and ‘negative’ night-time sap flow (towards the soil) during HR. Panels (b) and (c) show uptake by a deep root and efflux by a shallow lateral during drought, indicative of vertical HR (hydraulic lift). Panels (d) and (e) show uptake and efflux by opposing shallow roots after rain, indicative of lateral HR. Panels (f) and (g) show examples of constant uptake and efflux in lateral roots during drought and after rain, and panel (h) shows an example of a lateral root that switched from efflux during drought to uptake after rain. Lateral roots were measured in shallow soil at 0–0.5 m depth, while deep roots were measured in a cave at ~20 m depth. Small roots (S) were <40 mm, medium roots (M) were 40–60 mm, and large roots (L) were >60 mm in diameter. Asterisks (*) denote measurements from the same plant.

Seasonal patterns of HR

HR was continuous in space and time, as evidenced by the continual flow of water in roots at night (Fig. 4). Drought-induced HR (vertical HR) dominated in the absence of rain, while rainfall-induced HR (lateral HR) dominated immediately after large rainfall events, and there tended to be a blend of these two regimes while surface soil gradually dried out after rain. Drought-induced HR occurred at a steady pace over long periods up to 2 months in the absence of rain when surface soil was dry (θ_v ~5–10%), until interrupted by rainfall (Fig. 4). Rainfall caused rapid changes in night-time root water uptake and efflux, and a switch in HR behaviour. Switches were clearly identified by a dramatic 80–90% decrease in water uptake by deep roots that coincided with a rapid uptake and efflux by lateral roots following rain (Fig. 4). In general, the magnitude of efflux by lateral roots tended to be greater after rain than during drought (Fig. 4).

Switches from drought-induced HR to rainfall-induced HR tended to be triggered by large rainfall events (>20 mm) that increased surface soil water content above 20% (e.g. early September and mid October, Fig. 4a,b). Small rainfall events (<10 mm) not preceded by a large rainfall event had only a minor impact on soil water content and tended not to trigger a major switch away from drought-induced HR (e.g. early and late July, Fig. 4a,b). The magnitude and duration of rainfall-induced HR tended to scale with the amount of rain, and the largest response was observed following 78 mm of rainfall over 1 week in mid-October 2006, which increased θ_v from 15% to 60% (Fig. 4a,b). During this event, night-time sap velocities in roots ranged from –10 to +20 cm h⁻¹ and rainfall-induced HR dominated for nearly a month (Fig. 4c,d), after which there was a gradual reversion back to drought-induced HR.

In general, deep roots displayed very consistent behaviour during drought periods before and after rainfall events (Fig. 4c,d). It was also striking that night-time sap velocity in

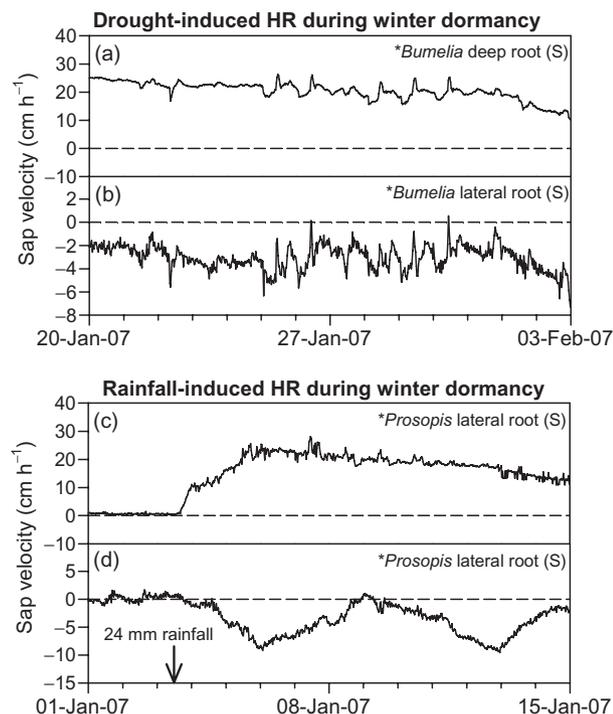


Figure 3. Examples of hydraulic redistribution (HR) activity in leafless deciduous trees in winter. The upper panels show simultaneous water uptake in a deep root (a) and efflux in a shallow lateral root (b) of *Bumelia lanuginosa* during drought, indicative of vertical HR (hydraulic lift). The lower panels show simultaneous uptake (c) and efflux (d) at times in opposing shallow lateral roots of *Prosopis glandulosa* following rain, indicative of lateral HR. Lateral roots were measured in shallow soil at 0–0.5 m depth, while deep roots were measured in a cave at ~20 m depth. Small roots (S) were <40 mm in diameter. Asterisks (*) denote measurements from the same plant.

deep roots was up to 5 times greater than that in lateral roots during drought in *Quercus* (Fig. 4c) and up to 20 times greater in *Bumelia* (Fig. 4d).

Role of individual roots in HR with respect to size and location

The general direction of water movement during HR and the roles of different types of roots with respect to size and location within the root system were determined from group assessments of sap flow patterns similar to those shown in Fig. 4. Although it was not known exactly how individual roots were connected to other roots, it was clear that the basic pathway of water transport during HR was from distal small roots close to the source of uptake to distal small roots close to the site of efflux, via medium and large proximal roots, as depicted in Fig. 5. During drought-induced HR (vertical HR), water was transported from distal roots at depth to distal roots near the surface (e.g. Figs 2b,c & 4c,d July–August, represented in Fig. 5a), whereas during rainfall-induced HR (lateral HR), water was transported both to and from distal roots near the

surface (e.g. Figs 2d,e & 4c,d October, represented in Fig. 5b). Although not measured, it is possible that water may have also been transported to distal roots at mid-level depths under both regimes (Fig. 5a,b).

Similar numbers (30–50%) of distal and proximal lateral roots were involved in HR during drought, and numbers increased slightly (50–60%) after rain (Fig. 6a). All deep roots were involved in HR during drought, but only a few (25%) remained involved after rain (Fig. 6a). In general, distal roots were more dynamically involved in water uptake for transpiration and HR than proximal roots, as indicated by significantly larger changes in sap velocity in deep and shallow distal roots in response to drought and rain (Fig. 6b,c), and the fact that HRI values decreased significantly with increasing root size (and thus distance from fine roots), both during drought and after rain (Fig. 6d).

HRI values also indicated differences among roots in the amount of water transported for HR as a proportion of that transported for transpiration (Fig. 6d). In deep roots, the proportion of uptake for HR was 60% when uptake for transpiration was relatively high ($V_s \sim 30 \text{ cm h}^{-1}$) during drought, but only 10% when uptake for transpiration was reduced by half after rain (Fig. 6b,d). Distal lateral roots transported roughly the same amount of water for HR as for transpiration when uptake for transpiration was relatively low ($V_s \sim 5 \text{ cm h}^{-1}$) during drought, and 50% of that for transpiration for HR when uptake doubled during the day after rain (Fig. 6b,d). Medium-sized proximal lateral roots behaved similarly to distal lateral roots, but HRI values for larger proximal lateral roots were consistently low at 15–20% during drought and after rain (Fig. 6b,d).

Examination of sap flow pathways across Y-junctions of shallow lateral root branches showed that distal small roots did not always require the involvement of larger proximal roots to facilitate HR (Fig. 7, and see Fig. 5b). In the example shown, night-time sap flow occurred in the smaller distal segment of the Y-junction (Fig. 7a), but not in the larger proximal segment (Fig. 7b), indicating that water was redistributed from one small distal root to another, completely bypassing the larger proximal root (Fig. 7c).

Contribution of HR to tree water balance

The total volume of water transported at night by roots involved in HR over the selected 28 d period was 1081 L, compared with 4076 L during the day for transpiration (night-time = 27% of daytime). Assuming that 83% of all roots were involved in HR (i.e. 49 out of the 59 measured roots, Table 1) and that the same roots contributed a proportionate 83% of whole-tree water uptake during the day, it follows that the volume of HR equated to 22% of total transpired water (i.e. 27% of 83%). This approximate value may be considered an upper bound if it assumed that all water transported at night was for HR.

The contributions of individual roots to whole-tree transpiration and HR were strongly dependent on both root size and the size of the root system to which they were connected.

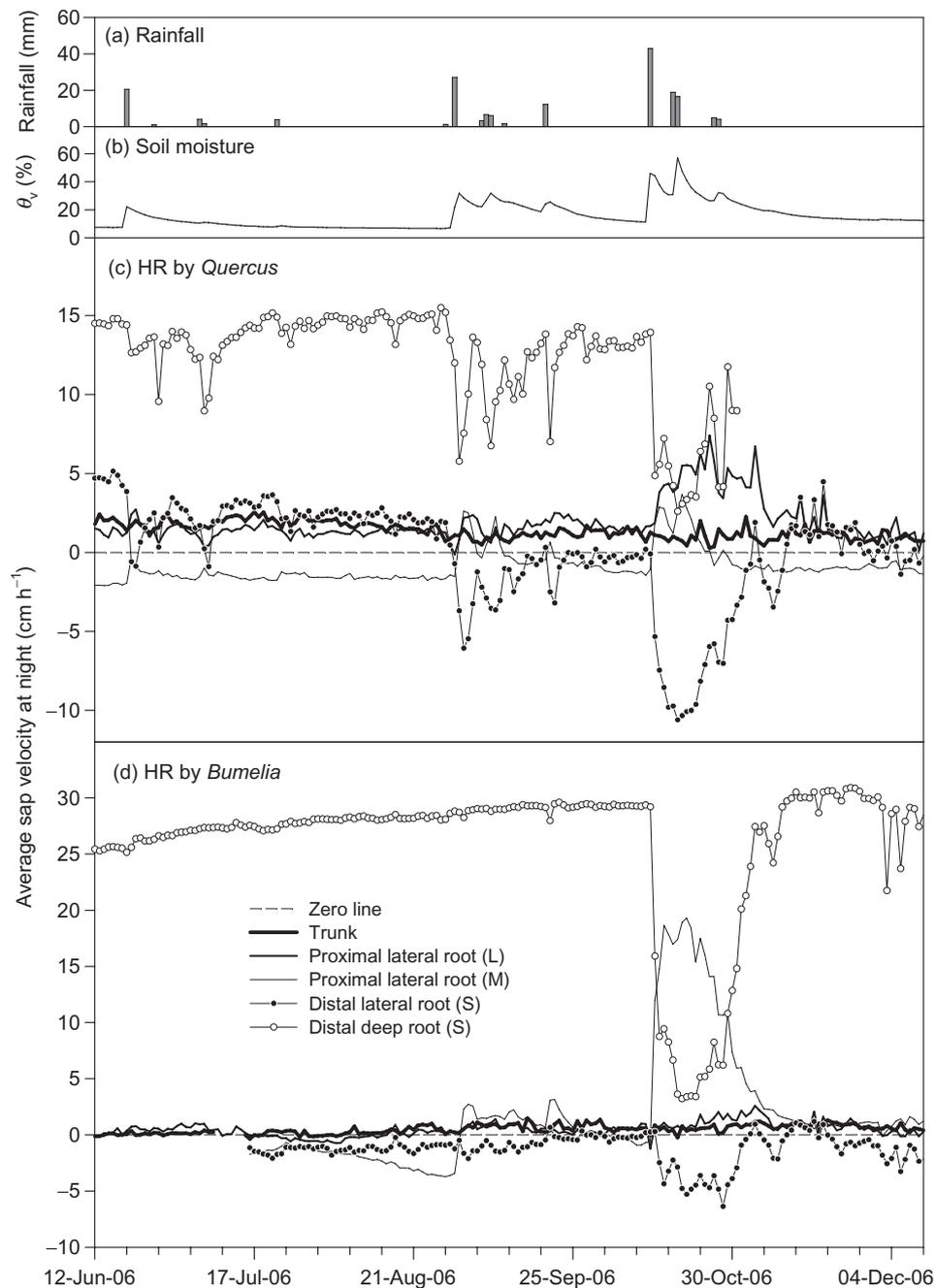


Figure 4. Seasonal patterns of hydraulic redistribution (HR) across whole root systems from summer (June) through to winter (December). Daily rainfall (a) and volumetric soil moisture content (θ_v) at 0–0.3 m depth (b) are shown, followed by average night-time sap velocity (0100–0500 h) in trunks and roots from representative individuals of *Quercus fusiformis* (c) and *Bumelia lanuginosa* (d). Lateral roots were measured in shallow soil at 0–0.5 m depth, while deep roots were measured in a cave at ~20 m depth. Small roots (S) were <40 mm, medium roots (M) were 40–60 mm, and large roots (L) were >60 mm in diameter. Root size was considered a proxy for relative location within the root system, whereby distal small roots were assumed to be closer to fine roots involved in water uptake or efflux than larger proximal roots. For clarity, data are provided for only one root from each size and depth class. Incomplete data sets are due to heater burnout in some sap flow sensors.

In *Quercus*, individual roots contributed a relatively small percentage to whole-tree water uptake (e.g. 0.1% for small lateral roots, up to 4% for large lateral roots, Fig. 8a), which reflected the large root system of this species, probably in the order of hundreds of roots. In contrast, individual roots of

Bumelia and *Prosopis* contributed much larger percentages to whole-tree water uptake (e.g. 1–5% for small lateral roots, up to 60% for large lateral roots, Fig. 8b), which reflected the comparatively smaller root systems of these species, more likely in the order of tens of roots.

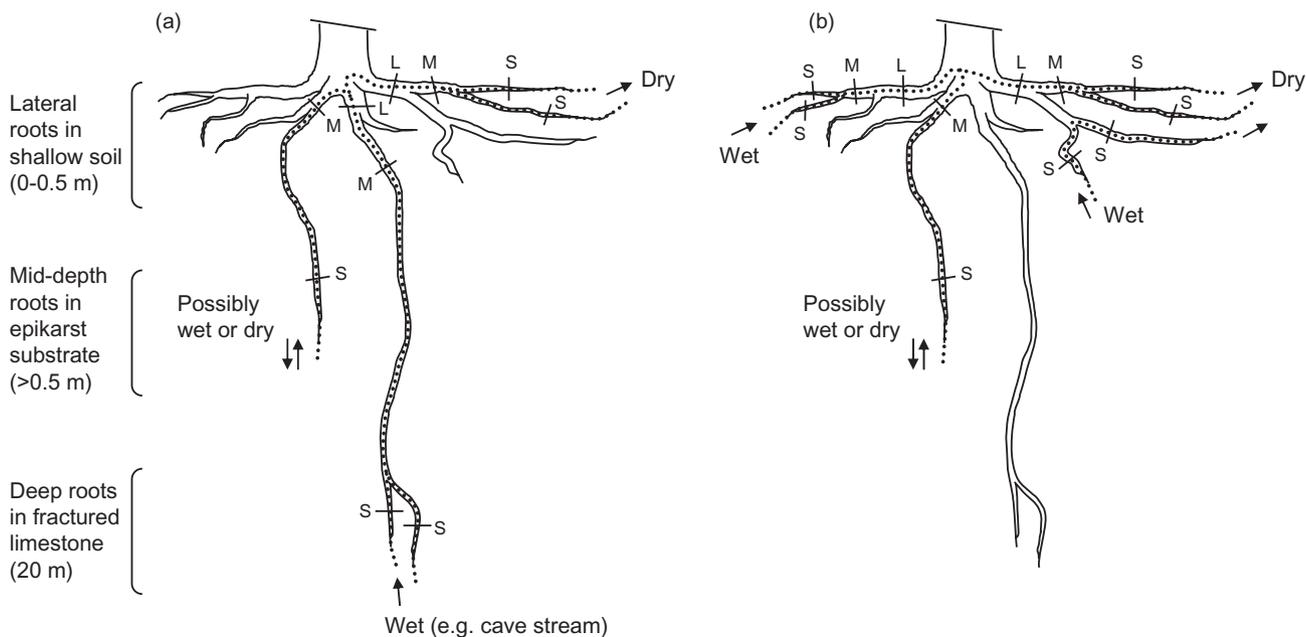


Figure 5. Schematic diagrams of hydraulic redistribution (HR) by deep-rooted trees in a karst savannah ecosystem. Diagrams show the general pathway (dotted lines) and direction (arrows) of water movement and the proposed involvement of roots of varying size, depth and location within the root system during drought-induced HR (a) and rainfall-induced HR (b). Models are consistent with sap flow patterns measured in roots of varying size and depth (Figs 1–4 & 7) measured in this study and basic knowledge of the soil profile and root system architecture at the study site. Lateral roots in shallow soil and deep roots in fractured limestone are shown to be the major facilitators of HR. Roots at mid-level depths (not measured in this study) are included to depict the possibility that epikarst portions of the profile (the transition zone between soil and bedrock) may act as additional sources or sinks of water for HR. Root size is indicated by the labels S, M and L, where S = small roots <40 mm, M = medium roots 40–60 mm, and L = large roots >60 mm in diameter. Root size also indicates the relative location within the root system, whereby distal small roots are located closer to fine roots involved in water uptake or efflux than larger proximal roots.

For all species, the contribution of larger lateral roots to daily whole-tree water uptake remained steady during drought and after rain, but smaller roots dynamically altered their contribution in response to rain (Fig. 8a,b). Notably, uptake by small lateral roots doubled after rain at the same time as uptake by deep roots decreased by roughly a third (Fig. 8a,b). In *Quercus*, deep roots contributed significantly more to transpiration than small lateral roots during drought ($P < 0.05$), but similar amounts to small lateral roots after rain (Fig. 8a). In *Bumelia*, deep roots and small lateral roots contributed similar amounts to transpiration during drought, but deep roots contributed significantly less than small lateral roots after rain ($P < 0.05$) as a result of the dramatic increase in uptake by small lateral roots (Fig. 8b).

Most roots of *Bumelia* and *Prosopis* contributed roughly the same amount of water at night for HR as they did for transpiration (Fig. 8b), while most roots of *Quercus* contributed less than half the amount for HR as they did for transpiration (Fig. 8a). However, the amount of water transported for HR by large lateral roots of all species was on average only about one quarter of that transported for transpiration (Fig. 8a,b), and the contribution of deep roots to HR reduced dramatically to near zero after rain (Fig. 8a,b).

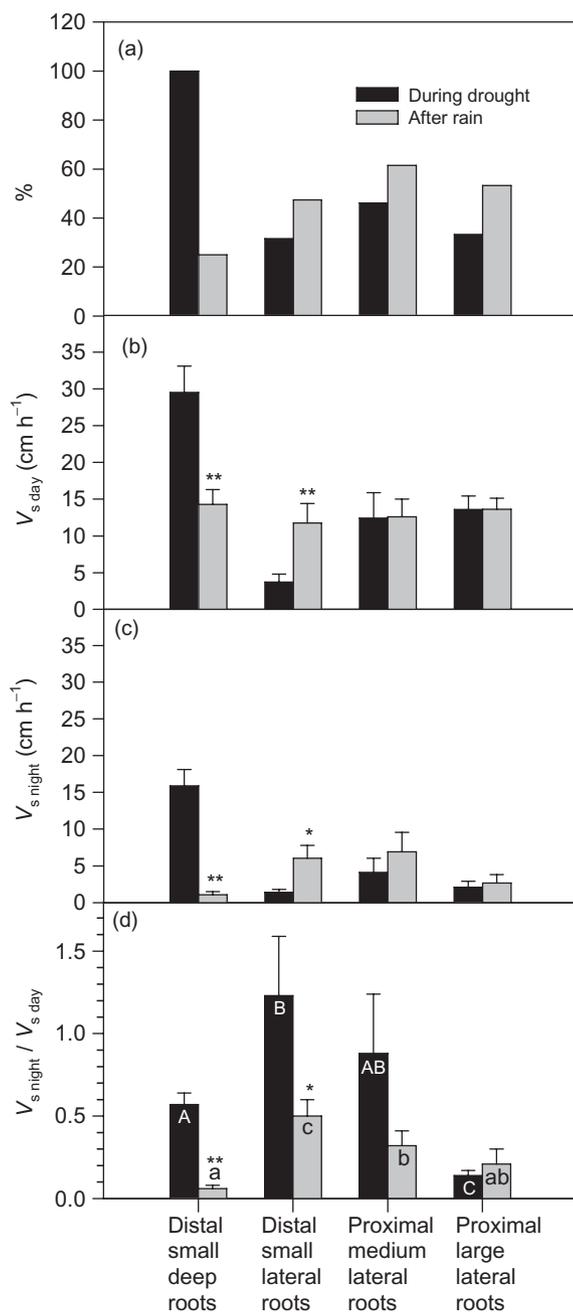
Deep roots were the most active contributors to HR in *Quercus*, particularly during drought when they transported

up to six times more water than small lateral roots at night (Fig. 8a). In contrast, small lateral roots were the most active contributors to HR in *Bumelia* and *Prosopis*, particularly after rain when they transported approximately three times more water at night than they transported at night during drought, in line with increased daytime uptake after rain (Fig. 8b).

DISCUSSION

HR is a well-known and widely reported phenomenon (see Dawson 1993; Jackson *et al.* 2000; Ryel 2004), but the eco-hydrological significance of HR generally remains poorly understood (Seyfried *et al.* 2005; Lubczynski 2009). Here, we provide a comprehensive view of the spatial and temporal extent of this phenomenon in a semi-arid ecosystem broadly representative of large areas of wooded land across the southern USA and globally. Our unique data set provides a wealth of information about key environmental and biological drivers of HR in dry environments, including the role of woody roots, root size and depth, soil water sources and sinks, rainfall, drought, species, and season.

The most striking feature of this study was the sheer abundance of HR that occurred at this site. At the stand level, HR occurred in every measured tree irrespective of species, evergreen or deciduous habit, or above-stream or



off-stream position in the landscape. At the scale of individual trees, HR occurred across entire root systems and involved the vast majority of all woody roots (83%), from large structural roots near the trunk to smaller shallow and deep lateral roots to 20 m depth. In fact, we observed HR in a surprising 80% of measured surface roots and in every deep root.

HR occurred continuously throughout the year in one form or another, and changes in behaviour were rapid and dynamic, often involving an increase or decrease in night-time sap velocity by an order of magnitude within 12–48 h. Night-time rates of sap flow during HR varied from very low rates close to zero to very high rates that often equalled or exceeded that which occurred during the day for

Figure 6. The percentage of roots involved in hydraulic redistribution (HR) (a), average daytime sap velocity ($V_{s \text{ day}}$) during transpiration (b), average night-time sap velocity ($V_{s \text{ night}}$) during HR (c), and proportional sap flow during HR (d) for roots of varying size and location within the root system. Proportional sap flow [referred to as the HR index (HRI)] is the ratio of $V_{s \text{ night}}$ to $V_{s \text{ day}}$ using scalar velocities. Larger HRI values indicate a relatively greater degree of sap flow activity in roots during HR, and a greater amount of water transported for HR as a proportion of that transported for transpiration. Mean \pm SE values of sap velocity and HRI are shown for $n = 12$ deep roots, $n = 13$ small lateral roots, $n = 11$ medium lateral roots, and $n = 13$ large lateral roots pooled from *Quercus fusiformis*, *Bumelia lanuginosa* and *Prosopis glandulosa*. Small roots were <40 mm, medium roots were 40–60 mm, and large roots were >60 mm in diameter. Lateral roots were measured in shallow soil at 0–0.5 m depth, while deep roots were measured in a cave at ~20 m depth. Distal small roots were assumed to be closer to fine roots involved in uptake or efflux than larger proximal roots. Measurements were acquired in the week before and the week after a 40 mm rainfall event on 12 October – 2006 when daytime conditions of light, temperature and evaporative demand were similar. Significant differences between measurements during drought and after rain within root classes are denoted by asterisks (* $P < 0.05$, ** $P < 0.01$, Student's t -test). In panel (d), bars labelled with the same letter of the same case are not significantly different, whereas bars with different letters of the same case are significantly different at the $P < 0.05$ level (Student's t -test). Capital letters are used for measurements during drought. Lower case letters are used for measurements after rain.

transpiration. We also observed water efflux during the day in some roots, indicating that the soil water potential gradients across a large root system may still result in HR during the day, even in the presence of a transpiring canopy (Hultine *et al.* 2003a). Our data also show that HR occurred in roots of leafless trees in winter, adding to the growing number of reports that root systems of deciduous plants can continue to transport water while the canopy is dormant (Leffler *et al.* 2005; Scott *et al.* 2008).

Another striking feature was the complexity of responses in individual roots. We identified at least seven distinct patterns of night-time sap flow spanning the full range of involvement in HR. Some roots only exhibited daytime sap flow towards the transpiring crown, indicating no involvement in HR, but most roots exhibited night-time sap flow associated with water uptake, efflux or both (at different times), in roughly similar proportions. Similarly, roots displayed a full range of responses to environmental conditions, from those involved in HR only during drought or only after rain to those involved in HR both during drought and after rain, also in roughly similar proportions. Roots were randomly selected around each tree without knowledge of how roots were interconnected or where they terminated in the profile, and not surprisingly, we found the specific response of individual roots was similarly random. However, we did find that many roots displayed consistent behaviour over time with respect to the direction and timing of HR, indicating that such roots were connected to parts of the soil profile that were consistently wet or dry.

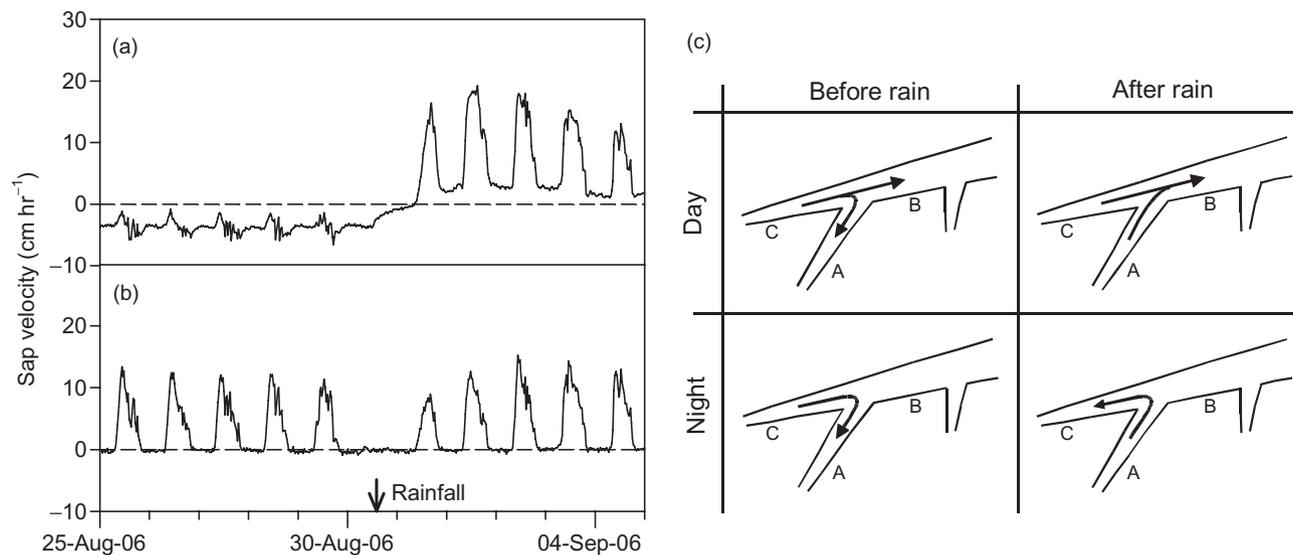


Figure 7. Diurnal sap velocity traces showing the involvement of distal (a) and proximal (b) segments of a lateral root ‘Y-junction’ of a *Bumelia lanuginosa* root during hydraulic redistribution (HR). Measurements were obtained over a 2 week period during a switch from drought-induced HR to rainfall-induced HR after a 25 mm rainfall event on Aug – 30. Two sap flow sensors were installed 0.5 m apart across the junction: one in the smaller of the two distal segments (segment A, diameter = 20 mm) and the other in the larger proximal segment (segment B, diameter = 50 mm). Distal small root segments were assumed to be closer to fine roots involved in uptake or efflux than the larger proximal segment (see Fig. 5). Schematic diagrams (c) are provided to show the direction of sap flow across the junction during the day and at night before and after rain. The direction of sap flow in segment C was inferred from measurements obtained from segments A and B.

Two major types of HR were observed in this system: hydraulic lift during drought (HL) and redistribution by lateral roots after rain (lateral HR). During drought, HL was facilitated by deep roots that tapped permanent deep water sources at 18–20 m and by lateral roots located in dry soil layers (water sinks) closer to the surface. HL is the most common type of HR reported in the literature, and it is known to occur in many deep-rooted tree species growing in semi-arid and arid environments (e.g. Yoder & Nowak 1999; Moreira *et al.* 2003; Espeleta, West & Donovan 2004; Scholz *et al.* 2008). After rain, the contribution of water from deep roots to support HL decreased to near zero, and complex patterns of night-time uptake and efflux in shallow lateral roots indicated the presence of lateral HR instead.

In this system, the major driver of both types of HR appeared to be dry surface soil. We suspect that a large fraction of the total amount of water redistributed via HL and lateral HR was deposited in this upper layer based on a reasonable assumption that the majority of lateral roots were located close to the surface in soil that was known to be shallow and prone to quick drying during drought. However, it is also possible that some water may have been redistributed downward to dry layers at intermediate depths via mid-depth lateral roots or branched tap roots. Recent work by Schwinning (2008) indicates that karst savannah tree species in this region including *Quercus* may tap into the epikarst layer (the transition zone between soil and bedrock), and other studies in dry environments have shown that hydraulic descent of water via deep laterals or taproots may play an important role in maintaining root

growth in deeper soil layers that are not regularly recharged by rainfall (Burgess *et al.* 2001c; Hultine *et al.* 2003a).

Long-term monitoring provided valuable insights into the timing, extent and duration of HR in this system, and the regularity of switching between HL and lateral HR. During drought, HL persisted for several months at a more or less constant rate until interrupted by rainfall. HL was affected but not eliminated by small rain pulses, indicating the presence of dry soil not wetted by rain or efflux from neighbouring lateral roots participating in HL. Only the largest storms were able to reduce night-time sap flow in deep roots close to zero, signalling a total reduction of HL. At the same time, however, large rain pulses triggered lateral HR events lasting many days to weeks, while small pulses sometimes did not trigger lateral HR at all. Rainfall was clearly the major driver of lateral HR, and the magnitude and duration of lateral HR was closely related to the magnitude of individual rainfall events, plus the accumulation of rainfall over time (see Fig. 4). These results are consistent with other studies in dry environments that report rapid switches in HR behaviour following major rainfall events (e.g. Hultine *et al.* 2003b, 2004; Nadezhkina *et al.* 2008) and suggest that climatic changes to rainfall patterns – if they were to occur – would in turn alter patterns of HR in this system.

The phenomenon of HR was common in trees across the site, but the distribution of HR within and around a tree was patchy in space and time. This is consistent with the shallow soil environment and the likelihood that shallower soil layer may dry out more quickly during drought and

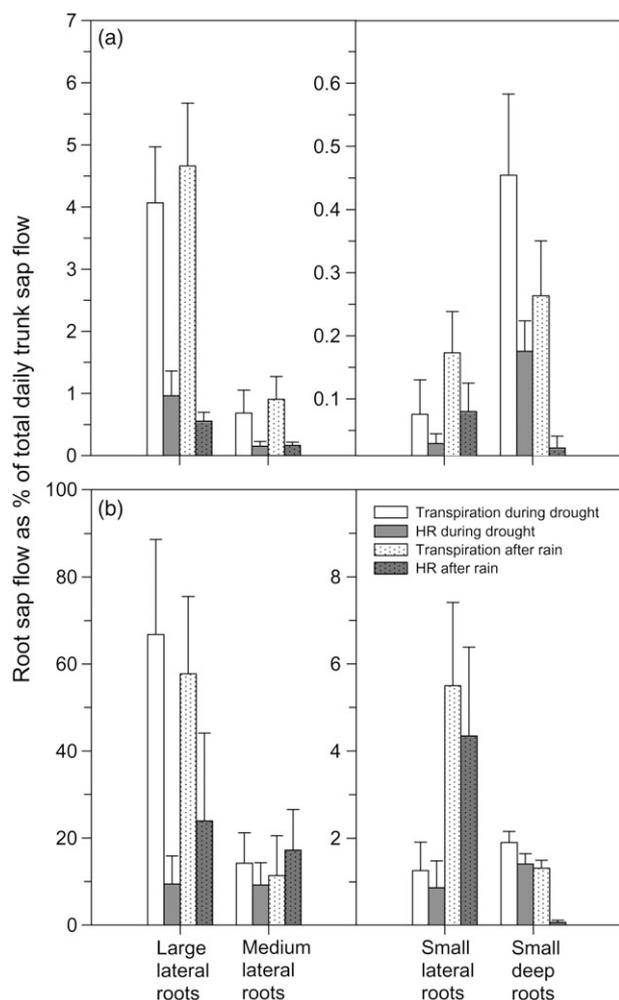


Figure 8. The average volume of sap flow in individual roots during transpiration and hydraulic redistribution (HR) measured during drought and after rain, expressed as a percentage of total daily sap flow (transpiration) in the trunk of the parent tree. Data from evergreen *Quercus fusiformis* (a) and deciduous *Bumelia lanuginosa* and *Prosopis glandulosa* (b) are shown for a representative warm, sunny day in the week before and the week after a 40 mm rainfall event on 12 October 2006. Daytime sap flow (transpiration) was totalled between 0600 and 1800 h, and night-time sap flow (HR) was totalled between 1800 and 0600 h. For *Quercus*, data are mean \pm SE for eight large lateral roots, seven medium lateral roots, eight small lateral roots and six small deep roots. Combined data for *Bumelia* and *Prosopis* are mean \pm SE for five large lateral roots, four medium lateral roots, five small lateral roots, and four small deep roots (BL only). See methods for exact details of root size and depth, and see Table 2 for whole-tree transpiration estimates for each species.

rehydrate more quickly after rain, leading to a mosaic of patchy dry soil. Importantly, measured long-term patterns of HR indicate that patchy dry soil is a constant feature of this system and that trees actively maintain roots in dry soil over long periods. Rather than die off in dry soil, roots responded quickly and dynamically to changes in soil water status, even during winter, and they continuously 'equalized' water availability by redistributing it more uniformly

across the rooting zone. Interestingly, our results also suggested that the same patches of dry soil remained dry time after time in between rainfall events and to roughly the same degree of dryness. This is evident from the large number of roots that displayed consistent HR behaviour from one drought period to the next.

A continuous supply of small amounts of water to dry soil from HR may play a role in maintaining viable fine roots in surface soil layers or deeper rocky substrate. Previous work has shown that water supplied by HR can help to keep fine roots hydrated (Domec *et al.* 2004), and it can delay the drying of surface soil layers (Brooks *et al.* 2002). There is also evidence that fine root hydraulic activity is highly responsive in trees of this ecosystem, and the rewetting provided by HR likely activates aquaporins in shallow roots in addition to re-establishing physical connections with the soil (McElrone *et al.* 2007). The persistence of roots in dry soil has obvious implications for whole-plant water use and growth in dry environments, allowing plants to respond very rapidly to rainfall to improve their water status (e.g. Fig. 4d), which in turn may allow them to increase transpiration and photosynthesis (Ryel *et al.* 2002).

Results from this study suggest that the potential for continuous HR may be strongest in arid or semi-arid systems where some component of the vegetation has access to a reliable supply of water, roots exist in a thick vadose zone, and rainfall occurs often enough to ensure that surface soil layers do not dry out completely to the point where fine roots may lose contact with the soil, desiccate or die. This contrasts with some examples from hyper-arid deserts, where plants have grown deep roots and gain access to deep water sources, but where extremely dry topsoil prevents the growth of shallow fine roots that could potentially redistribute water (Zeng *et al.* 2006).

The ability of trees to maintain roots and facilitate HR in patchy dry soil appears strongly linked to root system size and architecture. Here, we demonstrate that a clear benefit of having an expansive deep root system is that it can be used to establish good hydraulic linkages between wet and dry compartments of the profile across large distances. The effectiveness of these linkages was evidenced by the comprehensive span of HR behaviours and high degree of variation in sap flow rates and patterns measured in individual roots, particularly lateral roots in shallow topsoil. This complexity among lateral roots almost certainly reflects the large number of hydraulic linkages made by roots in the mosaic of dry surface soil. In contrast, the behaviour of deep roots was consistent and predictable, reflecting the permanent availability of water deep in the karst profile.

Water transport across large woody root systems is an inherently complex process, especially during HR. An important aim of this study was to gather information about the generalized hydraulic function of different size and depth classes of woody roots during transpiration and HR. In general, small roots were more dynamic than larger roots, particularly during HR, similar to recent findings of Nadezhdina *et al.* (2006). Small roots near the surface were

involved in the rapid uptake of water following rain and rapid efflux into dry soil both during drought and after rain, while small roots at depth rapidly took up water for HR during drought. This behaviour is consistent with small woody roots being closely connected to distal fine roots embedded in sources and sinks of water. Larger lateral roots were clearly necessary to facilitate HR across whole root systems, as indicated by their involvement in both positive and/or negative sap flow at night, but the degree to which they were involved tended to decrease with increasing size (Fig. 6), consistent with their more proximal location in the root system and increasing distance from fine roots (Fig. 5).

The degree of involvement in HR of different sectors of the root system depends on many factors, including the strength of the water potential gradient driving water flow and the pathway resistance through roots. The study of deep root systems provides a unique opportunity to explore the degree to which discrete roots and the root system as a whole can participate in HR. In theory, water is expected to flow from regions of high to low water potential through roots along the shortest pathway of least resistance. In individual roots (unbranched segments), resistance to flow is generally the same whether water moves forward or backward. However, resistance to flow in root systems is thought to be greater when water moves towards the soil compared with towards the trunk (Schulte 2006), owing to the fact that xylem conduits are naturally arranged to promote axial water transport towards the trunk rather than for water transfer among distal root branches. Sometimes these factors interact to localize the occurrence of HR within the root system (e.g. Brooks *et al.* 2002, 2006), while other times, they interact to involve the whole root system in HR, including large roots close to the base of the tree and even the stem (e.g. Burgess & Bleby 2006; Nadezhkina *et al.* 2009).

In this study, HR involved all parts of the root system including large roots at times, but there was also evidence to show that in places HR was confined to smaller roots. Soil water potential gradients in localized patches of soil were strong enough to drive radial water flow through sidewalls of xylem conduits at root junctions from one distal small root to another, completely bypassing larger roots. In other cases, however, large roots did become involved in HR, most likely because they were the only way to connect smaller roots located in wet and dry parts of the profile that were widely separated (e.g. stream water at 20 m depth versus shallow topsoil at 0.2 m depth). Again, these observations point to the patchy nature of HR. They also suggest that no parts of the root system obstruct HR and that any root may or may not participate in HR depending on the geometry of connections between individual roots and the strength of the water potential gradients involved.

Deep woody roots with permanent access to water were a major feature of this ecosystem, and our data provide a rare view of water uptake and transport from many tens of metres depth in combination with surface measurements. Deep roots displayed some of the fastest rates of sap flow,

and they transported up to five times more than shallow roots of the same size, consistent with recent findings from the same system that deep roots are structurally and functionally more efficient at transporting water than shallow roots or stems (McElrone *et al.* 2004). It was remarkable that during drought, water flowed constantly through deep roots at significant velocities ($>25 \text{ cm h}^{-1}$) 24 h a day. Deep roots contributed large amounts of water during drought but dramatically reduced their contribution following rain, opposite to the actions of shallow roots. Deep roots responded rapidly to hydraulic signals from above, and they coordinated tightly with shallow roots to supply water for transpiration and HR. Overall, these results clearly show that deep roots do not function in isolation. Rather, their behaviour is strongly linked to surface soil conditions.

We suggest that apparent 'coordination' between deep and shallow roots to supply water is a passive phenomenon related to root system hydraulic architecture. The anatomy, specific hydraulic conductivity and length of individual roots play major roles in determining the ease with which water flows across root-to-trunk (transpiration) or root-to-root (HR) pathways, and these factors are known to differ between deep and shallow roots in this system. Xylem vessels are larger and hydraulic resistance per unit length is lower in deep roots compared with shallow roots in these species (McElrone *et al.* 2004), but presumably, 20 m deep roots are much longer than most shallow roots. In this study, we found that water was taken up mostly from shallow soil in preference to stream water when water potential gradients associated with wet and dry patches of shallow soil approached those associated with permanent deep water sources and shallow dry soil after rain. This was a clear indication that shallow roots provided a shorter, less resistant pathway for water movement to leaves and dry soil than 20 m deep roots. Deep roots were inherently less resistant than shallow roots, but it appears that this was partially overridden by the cumulative resistance to flow over the entire path length, and perhaps also changes in resistance closer to the trunk due to other factors such as vessel tapering (Petit, Anfodillo & De Zan 2009). Of note, however, deep roots still maintained moderate sap velocities (up to 15 cm h^{-1}) under conditions of saturated topsoil, which gives an indication of their high conductive capacity and year-round importance to whole-plant water use.

Finally, this study identifies HR as a major ecohydrological process with significant potential to influence the water balance of semi-arid woodlands and ecosystems where woody plant encroachment is increasing. For the species studied here, the total volume of HR was estimated to be in the order of one-fifth of the volume of transpired water. One-fifth is a significant fraction of whole-plant water use, and from this it is reasonable to suggest that HR water played an important role in supporting the transpiration demands of plants during times of drought. From a hydrological perspective, this value represents a significant amount of water extracted from the soil profile that would not have otherwise been accessible to plants for transpiration. Our estimate of the magnitude of HR compares

favourably with work conducted by Brooks *et al.* (2002) in the Pacific Northwest USA where it was estimated that HR replenished 28 and 35% of total daily water utilization in dry ponderosa pine (*Pinus ponderosa*) and moist Douglas-fir (*Pseudotsuga menziesii*) ecosystems, respectively.

Live-oak woodlands like the one studied here and other savannah ecosystems are common across large areas of the southern USA and globally. If the majority of trees in such systems participate in HR, then the area of land subject to this phenomenon may be directly proportional to the coverage of deep-rooted woody plants (Schenk & Jackson 2005). Using total projected canopy cover measured from aerial photographs as a conservative index of the land area over which HR water is taken up and released by participating trees, we estimate that HR affects around 5% of land at our study site that has been heavily cleared for cattle grazing (approx. 4 stems ha⁻¹). However, we estimate that this value rises to at least 20% of land in an adjacent, more heavily wooded system not used for grazing (approx. 70 stems ha⁻¹). Woody plant encroachment, afforestation (growing trees in grasslands and shrublands), and clearing are additional land-cover changes that can alter the balance of water uptake and, based on results of studies like ours, HR. Understanding how such transformations alter the water balance and redistribution of water resources is a key component of global-change research today.

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