Interspecific variation in the timing and magnitude of hydraulic redistribution in a forest with distinct water sources

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Abstract

Aims Trees regulate water availability among their rooting strata through a nocturnal, passive transfer of water known as hydraulic redistribution (HR). This study investigates differences in HR and groundwater use among common canopy species in longleaf pine (Pinus palustris Mill., Pinaceae) woodlands and explores environmental factors influencing HR.

Methods HR was estimated by sap flux of lateral roots and main stems of three mature canopy species (P. palustris, Quercus laevis Walter., Fagaceae and Quercus margarettae Ashe., Fagaceae). We used δ18O and δD of xylem water, soil water, and groundwater to determine water source. Finally, we related HR to environmental factors (Temperature, VWC, VPD) to better understand controls of HR dynamics.

Results Pinus palustris had higher water use than either Quercus species, and also redistributed significantly more water as a nocturnal subsidy. HR fluxes were inversely related with mean nightly temperature and independent of shallow soil moisture. Stable isotope mixing models, based on δ18O and δD, indicated that all species have access to groundwater, but utilized shallow soil water in differing amounts when available.

Conclusions In systems with strong water potential gradients among soil strata, any species with access to a groundwater source is likely capable of HR; however, the magnitude of HR varies significantly by species, even among closely related taxa.

Keywords Hydraulic lift · δ18O · δD · Drought resistance · Root profile · Soil water content · Hydrologic niche · Groundwater use

Introduction

Hydraulic redistribution (HR) is a biophysical process wherein water is transferred across the soil profile through a plant’s roots (Caldwell et al. 1998). HR occurs primarily at night, when stomata are closed and the water potential gradient among soil layers...
is greater than that between soil and the atmosphere (Oliveira et al. 2005). HR has been observed and quantified in a variety of ecosystems worldwide and has been demonstrated as an important process in many forests (Neumann and Cardon 2012). Species with access to deeper groundwater may exhibit increased drought resistance, and HR likely provides other physiological advantages such as improved nutrient uptake and carbon assimilation (Domec et al. 2010, Nadezhdna et al. 2010, Armas et al. 2012, Neumann and Cardon 2012, Prieto et al. 2012, Cardon et al. 2013, David et al. 2013). Water availability from HR increases the lifespan of shallow fine roots and increases nutrient diffusion, both of which facilitate nutrient uptake during drought and optimizes use of rainfall pulses following drought (Nippert and Knapp 2007, Scott et al. 2008, Bauerle et al. 2008, Cardon et al. 2013, Prieto and Ryel 2014, Priyadarshini et al. 2016). Despite the importance of HR in forest ecosystems, relatively little is understood about interspecific variation in the timing and magnitude of HR in forests with distinct water sources.

Measurements of nocturnal sap flux among co-occurring tree species suggest that HR is influenced by both rooting profile and water transport capacity (Scholz et al. 2008, Neumann and Cardon 2012). Rooting profile, as used here, is a multi-dimensional term referring to a tree’s gross rooting depth, root distribution, and root morphology. There is a great deal of evidence for environmentally controlled plasticity in rooting profile, but broad differences remain among distantly related taxa (Callaway, 1990; Canadell, J., et al. 1996; Jackson et al. 1996; Hipondoka & Versfeld, 2006). Morphological differences in pine and oak rooting systems are especially apparent in many forests (Comas et al. 2002; Curt et al. 2005; Konôpka et al. 2005). When tree species with distinct rooting profiles co-occur, the ability to transport water via HR will differ among them. Tree species that rely exclusively on either shallow or deeper soil water have a poor capacity for HR in contrast to those that bridge across multiple soil strata (Scholz et al. 2008). In the coastal plain sandhills of the southeastern US, Pinus and Quercus species are known to redistribute groundwater, but the reported magnitudes of redistribution are inconsistent (Espeleta et al. 2004, Domec et al. 2010). These reported inconsistencies in magnitude may result from differences in measurement techniques among studies, such as psychrometry and sap flux, or due to differences in site-specific hydrology. Despite this, HR has been observed more frequently in Pinus species in the southeastern US, potentially due to higher plasticity in their rooting profile (Espeleta et al. 2004). Interspecific variations in root profile become especially important when estimating the effects of HR on ecosystem water budgets since redistributed water can represent a significant subsidy to shallow soil water available for transpiration (Domec et al. 2010).

It is also necessary to understand the degree to which different tree species can acquire deeper groundwater. (Ehleringer and Dawson 1992). Water from different soil strata can be used as a source for both HR and transpiration demand (Scott et al. 2008). HR of deep groundwater has been observed up to a depth of 20 m across arid regions of central Texas (Bleby et al. 2010). If a species does not have access to deeper groundwater, it may show a reduced HR capacity, or it may transfer water laterally from wetter soils to drier soils, rather than mixing soil water between strata (Scholz et al. 2008) and HR can still occur across non-saturated soil layers (Oliveira et al. 2005). Thus, HR may only be limited by the heterogeneity of water availability across a plant’s rooting profile, rather than depth to saturated soils (Kembel and Cahill 2005).

Understanding how environmental factors influence HR could facilitate a mechanistic understanding of HR and improve HR predictions from commonly measured variables (Richards and Caldwell 1987, Burgess et al. 1998). Assuming soil water potential gradients are the primary driver of HR, and not the water potential gradient across soil, plant, and atmosphere, it is predicted that the highest rates of HR occur during periods of low shallow soil moisture, (Emerman and Dawson 1996). However, it has also been hypothesized that extremely low soil moisture may hinder HR capacity due fine root mortality (Wang et al. 2011). High nocturnal VPD, which may depress HR capacity as the atmosphere competes as a strong driver for water loss through stomata, has also been linked to nocturnal transpiration in many plant species (Dawson et al. 2007). To eliminate the confounding effect of nocturnal transpiration on HR, VPD must consistently reach zero at night, reducing the competition between atmosphere and soil water gradients (Dawson et al. 2007).
We explored the capacity, interspecific variation, and water source of HR among dominant overstory in a xeric longleaf pine (Family-Pinaceae, *Pinus palustris* Mill.) woodland focusing on, *P. palustris* and two co-occurring hardwood species (*Quercus laevis* Walter and *Q. margarettae* Ashe; Fagaceae). Together, these species comprised 86% of the total woody basal area in our site. *P. palustris* is an evergreen conifer while *Q. margarettae* is commonly found as solitary trees within sandy, well-drained sites, and *Q. laevis* is found growing in small groves within more mesic habitats (Hacke, 2015; Coder, 2019).

Our first objective was to quantify the rate and volume of water movement through the stem and roots during transpiration and nocturnal HR for each of our study species. For this study, we constrain our use of HR and related terminology to the movement of water solely within plant tissues, not across the root-to-soil interface. We expected *P. palustris* to have a higher capacity for HR per unit sapwood area than either *Quercus* species, due to its heavy investment in belowground rooting biomass (Burns and Honkala 1990). The second objective was to identify accessible water sources. Longleaf pine woodlands receive high annual precipitation and experience high mid-day VPD and consistently low nocturnal VPD (Ford et al. 2008). The xeric woodland where this study occurred has deep, sandy, excessively well-drained soils resting atop a shallow karst-limestone aquifer (Bosch et al. 2003, Williams and Kuniansky 2016). We predicted that species using a higher proportion of ground water will show a lower correlation between shallow soil water availability and total water uptake. The final objective was to determine if environmental factors explained variations in HR. We related the magnitude of observed HR for both lateral roots and stem to temperature, daytime VPD, and shallow soil moisture.

**Methods**

**Site description**

We conducted this study at the Jones Center at Ichawaynochaway Creek, a privately-owned research site of 11,400 ha in the Dougherty Plain physiological district of southwest Georgia, USA. The climate is classified as humid subtropical, with ~1,310 mm mean annual precipitation and 19 °C mean annual temperature. This region sits atop the Upper Floridan Aquifer (UFA) at one of its closest points to the surface with a minimal confining unit. The UFA is an open, water-filled karst cavern system, which feeds directly into many of the surrounding river and stream systems and relies on soil infiltration for recharge (Williams and Kuniansky 2016).

Our study site occupies a flat xeric plateau (Goebel et al. 1997), approximately 10 m above Ichawaynochaway Creek, with porous, excessively well-drained sandy soil that supports low volumetric water content, maximum VWC ~ 25% (Fig. 1). We selected four individuals from three dominant canopy tree species: *P. palustris* (mean DBH 32.15 cm), *Q. laevis* (mean DBH 28.01 cm), and *Q. margarettae* (mean DBH 27.75 cm), with *P. palustris* occurring across a broad range of soil types and the latter two species primarily associated with xeric sites. During the study period (June-November), 615 mm of rainfall were recorded at a nearby USGS rain gauge (USGS gauge #02355350). There was a period of low rainfall beginning in mid-September until the end of the study in November, less than 10% of the total recorded precipitation was observed in that time period. Mean daily temperature ranged from 8 °C - 28 °C, with a mean of 23.9 °C. We recorded soil moisture at 20 cm depth (EC-5 cm, METER, Pullman, Washington, USA) in 15-minute intervals throughout the duration of the study. These measurements were collected from a field devoid of large trees immediately adjacent (~150 m) to the sap flux study site.

**Sap flux**

We constructed heat ratio method (HRM) sap flux sensors following the Burgess et al. (2001) methodology. The HRM utilizes an upstream and downstream thermocouple with a central heat pulse to allow for bi-directional sap flux measurements. The accuracy of these sensors excels at low to medium flow conditions (Steppe et al. 2010). These two properties make the HRM ideal for capturing flow during nocturnal negative outflow and contrasting against diurnal water uptake, which we considered transpiration. For each tree, we installed two HRM sensors in opposing lateral roots 30 cm from the stem base and an additional sensor in each primary stem at a height of 1.3 m to estimate total tree transpiration. Aluminum templates were used to install HRM sensors in a -1 cm, 0 cm, 1 cm
configuration for both root and main stem sensors (Burgess et al. 2001).

Dataloggers (CR1000, Campbell Scientific, Logan, Utah, USA) recorded thermocouple temperature for 80 s after a 6 s heat pulse, every 30 min. To determine sap velocity \( V_s \) \( \text{cm sec}^{-1} \), we first calculated heat pulse velocity \( V_h \) \( \text{cm sec}^{-1} \) from thermocouples and applied to Eq. 2 from Burgess et al. 2001:

\[
V_h = \left( \frac{k}{x} \right) \ln \left( \frac{v_1}{v_2} \right) \times 3600
\]

where \( k \) is the thermal diffusivity for each species \( (\text{cm}^2 \text{ s}^{-1}) \), \( x \) is distance between heating element and sensor, and \( v_1 \) and \( v_2 \) denote the thermocouple temperatures after the heat pulse (Burgess et al. 2001). To calculate \( k \), we weighed and oven dried sapwood samples from each species to obtain density \( (\rho) \) and water content for specific heat calculations \( (c) \). Thermal conductivity of green wood \( (K_{gw}) \) was obtained using species specific density, water content, and following steps outlined in Swanson & Whitfield, 1983. Species specific \( k \) was then calculated as outline in Eq. 8 from Burgess et al. 2001.

\[
k = \frac{K_{gw}}{\rho c} \times 10,000
\]

The distance \( x \) between heat pulse generation and thermocouple measurement is critical to calculating the heat pulse velocity, so error due to probe misalignment is a serious concern when using the HRM (Ren et al. 2017). To address this, we performed a two-week laboratory trial under zero flow conditions using four sensors in excised stem segments of each study species. We established these conditions by sealing both ends and the sensor installation points with silicone gel. The error due to probe misalignment during installation was calculated at less than 1% among all species. We applied this empirically derived error rate to the corrected heat pulse Eq. 4 from Burgess et al. (2001):

\[
V_c = \frac{4kt \ln\left(\frac{v_1}{v_2}\right) - (x_1^2 - x_2^2)}{2t(x_1 - x_2)} \times 3600
\]

From the corrected heat pulse velocity \( V_c \text{ cm sec}^{-1} \), \( V_s \) can be calculated once wounding effects are considered, based on sensor needle size and spacing. \( x_j \) is assumed to be the correctly aligned distance between the thermocouple and heat pulse, while \( x_2 \) is the incorrectly aligned distance based on the two-week laboratory trial. The \( t \) variable connotes the time \( \text{sec} \) between heat pulses. Afterwards, the final sap velocity was calculated using the corrected heat pulse value Eq. 7 from Burgess et al. 2001:

\[
V_s = \frac{V_c \rho_b(c_w + m_c c_s)}{\rho c_s}
\]

where \( \rho_b \) (g cm\(^{-3}\)) denotes the density of wood, \( c_w \) and \( c_s \) (J g\(^{-1}\) °C) denote the specific heat capacity of the wood and sap respectively, \( m_c \) denotes the water
content of sapwood (ml g⁻¹), and \( \rho_s \) (g cm⁻³) denotes the density of water (Burgess et al. 2001). The coefficients calculated for each species can be found in Table 1. Positive sap velocity indicated uptake due to transpiration, while negative sap velocity indicated reverse sap flux, which we attribute to nocturnal HR transport out of lateral roots.

Conductive sapwood area

For each study species, we estimated conductive sapwood area (CSA) via active staining of stem and root tissues (Reyes-García et al. 2012). Before peak transpiration (~9 am), a 1-cm diameter hole was drilled into each tree at a height of 1.3 m, or at 30 cm from the tree base for root samples. We drilled these holes either to a depth of half the stem diameter or 15 cm (whichever was lower), and gravity-fed crystal violet dye into the drill hole. We sampled from trees adjacent to the sample flow site with a DBH range for P. palustris (n = 17) between 5.3 and 28.2 cm, Q. laevis (n = 13) between 4.8 and 31.4 cm, and Q. margarettae (n = 10) between 4.0 and 35.5 cm. After 24 h, wood bore samples 3 cm above the drilled hole, and the length of stained tissue were measured. We calculated conductive sapwood area from the stained tissue via:

\[
A_{sw} = \pi \left( \left( \frac{D_i}{2} \right)^2 - \left( \frac{D_i}{2} - L_{sw} - L_b \right)^2 \right)
\]

where \( A_{sw} \) is the CSA, \( D_i \) is the total diameter, \( L_b \) is the bark depth, and \( L_{sw} \) is the measured sapwood depth from the crystal violet stain (Reyes-García et al. 2012).

Table 1 Sap velocity coefficients calculated for each study species

|                | P. palustris | Q. margarettae | Q. laevis |
|----------------|-------------|----------------|----------|
| \( k \) (W m⁻¹ · cm⁻² · s⁻¹) | 0.081       | 0.059          | 0.048    |
| \( \rho_b \) (g cm⁻³)      | 0.42        | 0.77           | 0.71     |
| \( m_w \) (ml g⁻¹)         | 0.38        | 0.31           | 0.29     |
| \( c_w \) (J g⁻¹ · °C⁻¹)   | 4.65        | 3.60           | 3.47     |

(\( \text{cm}^2 \text{sec}^{-1} \) = thermal diffusivity (W(m·K)⁻¹), \( \rho_b \) = density of wood, \( m_w \) = water content of sapwood (ml g⁻¹), \( c_w \) = specific heat capacity of wood (J g⁻¹ °C⁻¹))

Stable isotope analysis

We sampled precipitation water, soil water, and water from plant xylem for analysis of \( \delta^{18} \)O and \( \delta D \) isotope ratios in August and October to capture a period of low vs. high VWC (19.3% and 23.6% respectively; Fig. 1). We obtained soil water samples from 20 to 100 cm depths, and wood samples from the three study tree species (n = 10 per species). Deep soil pits were infeasible due to the risk of collapse in sandy soil, but a closed spigot from a well water pump was available close to the site to collect deeper samples from > 10 m underground (n = 10). Plant water samples were taken from the terminal ends of the lowest branches. After collection, we wrapped sample vials in paraffin wax to prevent evaporation and immediately put them on ice for transport to the laboratory.

We cryogenically extracted plant and soil water from each sample at 155 °C for 25 min, verified to be within 99% of water extracted (Werner and Brand 2001). We then sent the samples to a stable isotope mass spectrometry lab, the UGA Center for Applied Isotope Studies, to obtain \( \delta^{18} \)O and \( \delta D \) ratios. \( \delta^{18} \)O and \( \delta D \) were analyzed by sources (20 cm soil, 100 cm soil, and ground water) and mixtures (P. palustris, Q. laevis, and Q. margarettae).

Environmental drivers of HR

To examine the relationship between stem and root sap flux and environmental factors, we obtained data from an array of environmental variables recorded within our study site using a HOBO weather station (ONSET, Bourne, Massachusetts). Our measured variables were 20 cm soil volumetric water content (VWC), mean daily vapor pressure deficit (VPD), maximum daily VPD, daytime solar radiation (PAR), and mean nightly air temperature (°C) (Fig. 1). Temperature and VPD have a strong co-variation and are typically not used as separate factors when assessing relationships with transpiration. Nighttime temperature at our site was variable, while nighttime VPD reached zero for 87% of the nights during this study. Due to this lack of variation in VPD, correlations were impossible to draw to nocturnal sap outflow. Instead, we chose to analysis nighttime temperature and mean/maximum daily VPD as separate factors due to weak correlation between them.
We correlated CSA to DBH and created species-specific allometric equations for P. palustris (\(y = 1.22 \times 10^{-0.044x}; R^2 = 0.89\)), Q. laevis (\(y = 1.403 \times 10^{-0.073x}; R^2 = 0.97\)), and Q. margarettae (\(y = 1.0874 \times 10^{-0.052x}; R^2 = 0.97\)). These equations were applied to a standard diameter for the lateral roots (5 cm) and main stem (25 cm) to obtain CSA estimates for each species. Flow volumes were calculated using the hourly velocity obtained at each HRM sensor. We summed diurnal and nocturnal flow velocities separately and multiplied by the species-specific CSA to calculate hourly sap volumes to test for the effect of species on mean uptake (diurnal sap flux) and HR (nocturnal sap flux) over the course of this study. We used these data in a mixed-effects repeated measures ANOVA with species as a fixed effect, time as the fixed repeated factor, and individual tree as the random effect.

We imposed stepwise regression based on minimum AIC to determine the environmental variables which explained a significant portion of HR variation. We analyzed the factors chosen above and their interactions against mean cumulative diurnal uptake and mean cumulative nocturnal HR for each species in a multivariate ANOVA. We plotted the predicted relationship from these tests against the observed data to determine how well these two factors could predict HR outflow.

The \(\delta^{18}O\) and \(\delta D\) ratios from soil sources and plant mixtures were plotted against the local meteoric water line (LMWL) for southwest GA but were fractionated along the \(\delta^{18}O\) axis (Fig. 4). Many of the soil water \(\delta^{18}O\) ratios lay outside the boundary of the LWML, indicating potential \(^{18}O\) fractionation caused by evaporative demand within the sandy soil. To draw inferences from these potentially fractionated sources, we analyzed the source \(\delta^{18}O\) and \(\delta D\) contributions to the plant mixture ratios using a Bayesian stable isotope mixing model in R (SIMMR package; Parnell et al. 2013). We ran the model for 200,000 iterations with a burn rate of 20,000, using statistical mean and standard deviation (Parnell et al. 2013). Sources for this model were defined as shallow soil water (20 cm), deep soil water (100 cm) and groundwater (~10 m). This method is preferred for high variance data rather than the simple mass balance approach (Eddy, 2004; Jian Wang and Bojie 2019). The predicted means and variance from our SIMMR should be taken as reasonable estimates rather than concrete values to avoid misrepresentation (Phillips et al. 2014).

**Results**

**Lateral root sap movement**

*P. palustris* had the highest mean nocturnal outflow in lateral roots (\(p < 0.001\)) when compared to either *Quercus* species (Fig. 2). Over the course of the study, mean (±SE) diurnal uptake for *P. palustris* (6.2 cm mean diameter) was 407.2 ± 21.8 ml day\(^{-1}\) (Fig. 3). Less than 20% of uptake occurred during the latter half of the study, between September and November (Fig. 2). The opposite trend was found for *P. palustris*’ mean nocturnal root outflow, estimated at 198.1 ± 18.1 ml day\(^{-1}\), 48% of diurnal root uptake. Over 50% of nocturnal outflow in lateral roots among all species occurred during the last two months of the study, between October and November (Fig. 2).

*Q. margarettae* showed significantly higher mean nocturnal outflow than *Q. laevis* within the lateral roots (\(p = 0.003\)). Mean diurnal uptake for *Q. margarettae* (6.1 cm mean diameter) was 141.5 ± 5.68 ml day\(^{-1}\) (Fig. 3) with a nocturnal root outflow of 89.1 ± 9.7 ml day\(^{-1}\), 53% of diurnal uptake. Mean diurnal uptake for *Q. laevis* (6.1 cm mean diameter) was 81.6 ± 2.656 ml day\(^{-1}\) (Fig. 3) with a nocturnal root outflow of 17.2 ± 1.72 ml day\(^{-1}\), a fifth of mean diurnal uptake (Fig. 4).

**Main stem sap movement**

*P. palustris* exhibited consistent fluctuations in stem uptake over the 158-day study. Mean diurnal uptake for the mean stem diameter (32.15 cm) was 15.9 ± 0.459 L day\(^{-1}\), significantly higher than either *Quercus* species (\(p < 0.001\)). Mean nocturnal negative flow was 10.2 ± 0.680 L day\(^{-1}\), 64% of uptake (Fig. 3). More than 60% of negative flow in the main stem occurred between October and November (Fig. 2). *Q. laevis* exhibited a lower mean nocturnal negative flow in the main stem than the other species (\(p < 0.001\)). Mean diurnal uptake for the main stem (mean diameter = 28.75 cm) was 8.09 ± 0.301 L day\(^{-1}\). Mean nocturnal negative flow was 1.99 ± 0.219 L day\(^{-1}\), or 25% of uptake (Fig. 2). *Q. margarettae* had significantly greater mean nocturnal negative flow than *Q. laevis* (\(p < 0.001\),
but significantly lower nocturnal negative flow than \textit{P. palustris} ($p < 0.001$). \textit{Quercus laevis} exhibited an increased diurnal uptake during the last two months, October through November, which accounted for over 40% of total water use during the study (Fig. 2). Mean diurnal uptake for the main stem (mean diameter 27.40 cm) was 5.53 ± 0.395 L day$^{-1}$. Nocturnal negative flow within the main stem was less consistent and accounted for a smaller proportion of daily uptake than was observed in lateral roots. Mean nocturnal negative flow was 2.17 ± 0.223 L day$^{-1}$, 39% of uptake (Fig. 3).

As with \textit{Q. laevis}, the majority of nocturnal negative flow (>60%) within the main stem occurred between October through November (Fig. 2).

**Stable isotope analysis**

In August, we estimated (Mean ± SE) that \textit{P. palustris} sourced a majority of water uptake, 88.3 ± 2.59%, from groundwater. Comparatively, the SIMMR predicted only 4.75 ± 1.24% of water was sourced from 20 cm soil layer, and 6.95 ± 2.05% of water from the
100 cm deep soil layer (Fig. 5). These proportions were closely matched by *Q. laevis* (5.61 ± 1.41%, 7.67 ± 2.10%, and 86.7 ± 2.71% respectively) and *Q. margarettae* in August (5.92 ± 1.23%, 6.85 ± 1.53%, and 87.2 ± 1.91%, respectively) (Fig. 5).

The October samples show different water sources within all three study species. *P. palustris* was estimated to source 32.4 ± 6.0% of xylem water from 20 cm soil layer, 38.8 ± 7.22% of xylem water from the 100 cm deep soil layer, and 28.8 ± 5.38% of xylem water from groundwater in October (Fig. 5). These proportions were similar in *Q. laevis* (35.2 ± 6.41%, 40.7 ± 7.5%, and 24.1 ± 4.87% respectively), but differed substantially in *Q. margarettae* (68.8 ± 6.42%, 20.4 ± 5.69%, and 10.8 ± 2.76%, respectively) (Fig. 5).

Environmental drivers of HR

For all species, mean diurnal uptake in the main stem had a moderate to strong positive relationship with mean daily VPD when correlated by a simple linear regression (mean *P. palustris* $R^2 = 0.56$; *Q. laevis* $R^2 = 0.73$; *Q. margarettae* $R^2 = 0.49$). When relating HR to environmental factors, all three species showed a moderate to strong relationship between HR and the combination of nightly air temperature, mean daily VPD (kPa), and their interactive effects (*P. palustris* $R^2 = 0.71$; *Q. laevis* $R^2 = 0.85$; *Q. margarettae* $R^2 = 0.90$; Table 2). Mean nightly temperature (°C) explained 64% of the variation in HR for *P. palustris*, 68% for *Q. laevis*, and 78% for *Q. margarettae* (Table 2). This was an inverse relationship between nocturnal negative flow and mean nightly temperature. By contrast, mean daily VPD (kPa) only explained 2 – 14% of the daily variation in HR among all three species (Table 2). Daily VPD (kPa) had a positive relationship with HR. Most surprisingly, hourly 20 cm soil VWC did not explain enough variation in mean nocturnal HR to be included in any regression models.

Discussion

Differences in HR by species

Based on our estimates, HR in the lateral roots for *P. palustris* equaled almost half of the volume measured
during diurnal uptake. *P. palustris* exhibited higher volumes of HR through lateral roots and main stem than either of the *Quercus* species, despite similarities in numbers of lateral roots and sap velocities (Dupuy et al. 2005a). The higher CSA in *P. palustris* contributed to greater water use and HR as compared to either *Quercus* species. This was seen primarily in the main stem, which had more than double the mean daily transpiration of either *Quercus* species. The lateral roots of *Q. margarettae* had significantly higher water use than *Q. laevis*, suggesting it may be more reliant on its lateral root system for water acquisition than the main tap root. If this is the case, their lateral roots appear to explore the soil vertically between strata. This is supported by the change in water source estimates between August and October 2017, when *Q. margarettae* switch from shallow soil use to deeper soil strata. *Q. laevis* by contrast had significantly lower mean daily water uptake within the lateral roots, but a higher overall uptake in the main stem than *Q. margarettae*. This suggests *Q. laevis* is more reliant on its tap root, exploiting water sources from deeper soil strata. This agrees with our isotope data, indicating that *Q. laevis* relied less on shallow soil water than *Q. margarettae* during periods of higher shallow soil moisture availability.

The large proportion of negative flow events recorded in the main stem of all three species lends evidence to the stem-mediated HR hypothesis (Bleby et al. 2010). Because these three species all have a tap root with a pattern of access to deeper soil strata, it is likely that water transported via HR must first travel within the main stem before exiting through the lateral roots. Stem-mediated HR, as observed as

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**Fig. 4** $\delta^{18}O$ and $\delta D$ isotope ratios for source and xylem water samples plotted against the local meteoric water line for Dougherty Plains, GA (LMWL). Data are separated by sample date (color) and sample type (shape). Soil water samples were collected at 0.2 and 1 m depths, well water was collected at 10 m depth, while trees samples were taken from xylem water in the terminal branches of each species. Error bars represent standard deviation from the mean. The $\delta^{18}O$ ratio is extremely variable, especially among xylem water, indicating potential fractionation occurring either at the time of sample or during analysis. All samples were verified to have extracted at least 99% of water within the sample.
negative sap flux in the main stem, is useful in relating total daily transpiration to HR but could only be used as a conservative estimate if lateral root data were not available. As has been shown in other studies, roots provide the most accurate estimates of HR, as stem-mediated HR is only a portion of total tree HR and the magnitude is very sensitive to changes in both sensor height and azimuth (Burgess and Bleby 2006, Nadezhdina et al. 2009). Our stem-mediated HR estimates match well with the magnitude of HR in the lateral roots, averaging between three to seven times greater than major individual lateral roots. These numbers agree well with the number of major lateral roots estimated in these species by past research (Drexhage et al. 1999, Dupuy et al. 2005b).

**Table 2** Species models for the multiple regression analysis of mean daily HR

| Species          | AIC & Model Components | $R^2$   | Prob > F |
|------------------|------------------------|---------|----------|
| *P. palustris*   | Minimum AIC: 931.44    | $R^2 = 0.71$ | < 0.001  |
|                  | Nightly Temperature    | $R^2 = 0.64$ | < 0.001  |
|                  | Mean daily VPD         | $R^2 = 0.023$ | < 0.001  |
| *Q. laevis*      | Minimum AIC: 942.35    | $R^2 = 0.85$ | < 0.001  |
|                  | Nightly Temperature    | $R^2 = 0.64$ | < 0.001  |
|                  | Mean Daily VPD         | $R^2 = 0.13$ | < 0.001  |
|                  | Temperature * VPD     | $R^2 = 0.021$ | 0.004    |
| *Q. margarettae* | Minimum AIC: 758.49    | $R^2 = 0.90$ | < 0.001  |
|                  | Nightly Temperature    | $R^2 = 0.78$ | < 0.001  |
|                  | Mean Daily VPD         | $R^2 = 0.14$ | 0.0015   |

Factors were selected via a stepwise regression based on minimum AIC. $R^2$ values are shown for the model as well as the contributions for individual factors.
strata for water uptake, likely in response to changes in shallow soil water availability (Dawson and Pate 1996). The variation in estimated water source contributions suggests these tree species, like many other plants, utilize soil water from the source of highest water potential, or strongest passive gradient between soil and atmosphere. Of all species, *Q. margarettae* showed the heaviest use of shallow soil water in October, potentially indicating a higher investment in shallow root biomass than either *P. palustris* or *Q. laevis*. All three species preferentially uptake shallow soil water when available, but the isotope data suggest some portion of water is always sourced from groundwater.

Because of the large morphological difference among *Pinus* and *Quercus*, we expected greater hydrological niche differentiation between genera (Nippert and Holdo 2015). We predicted that *P. palustris* would be better able to access ground water and thus, rely more heavily upon this resource than either *Quercus* species due to early-life taproot development and lower shallow root investment (Barnett, 2002). However, the inference from our water partitioning data suggests that all three of these species acquired water from similar sources. The largest discrepancy in water acquisition was between the two *Quercus* species, *Q. laevis* and *Q. margarettae* showed stronger differentiation among water sources during both August and October, indicating these more closely related species exhibit stronger hydrologic niche differentiation than *Pinus* and *Quercus* across genera. Shallow soil VWC (i.e., 20 cm) was never correlated with diurnal sap flux, supporting the de-coupling between shallow soil water and transpiration that occurs if a species has access to groundwater. In addition, shallow soil moisture dynamics are influenced by more than transpiration; soil evaporation, canopy interception, and local topography all may be negatively affecting the strength of correlation.

A factor potentially influencing the source contributions of water in our study was the effect of HR itself on the isotopic ratios of shallow soil water via mixing of distinct isotope end members. We hypothesize, due to the high volume of HR in this system, that there may be a dampening effect which artificially lowers the δ^{18}O and δD of shallow soil water. This would affect the baseline comparisons that were used in our model, causing less discrimination among soil strata, and appearing as a more “well mixed” system. Tree species would be observed to rely on more varied sources of soil water than in reality. Several previous studies have used labeled δD tracers to confirm the presence of HR in shallow soils across a variety of ecosystems (Brooks et al. 2002, Leffler et al. 2005, Priyadarshini et al. 2016). This methodology acknowledges the vertical mixing of soil water that occurs due to HR, made apparent by deuterated water’s extreme δD. It is unclear to what degree HR may confound the natural δ^{18}O and δD gradients that would otherwise be present. Future studies may need to rely on distinctly labeled water tracers, injected across the rooting profile, to determine tree water sources without the influence of HR mixing.

Environmental drivers of HR

The pattern of HR changed throughout the study with higher magnitudes during October and November. Nighttime temperature had the strongest impact on HR volumes, showing increased prevalence and magnitude of HR as nightly temperatures cooled during the months of October and November. In this system, both *Quercus* species begin the process of abscission in mid to late November, whereas *P. palustris* continues active transpiration throughout the winter (Burns and Honkala 1990; Coder 2019). This temperature effect was present in all three species despite the functional trait differences between deciduous and evergreens, suggesting an abiotic mechanism rather than a species dependent one. Mean daily VPD was a weak predictor of mean daily HR for each species, which agrees with our current understanding, since HR movement primarily occurs at night, when VPD is typically zero at our study site. Because we chose to compare mean daily VPD to HR we observed a weaker relationship than might be expected between these factors given HR’s strong correlation to mean nightly temperature.

Shallow soil moisture (VWC) was a poor predictor of HR within the lateral roots of all study species. The relationship between soil moisture and HR has been clearly documented in prior research, but this specific system does not show a strong link (Scott et al. 2008, Neumann and Cardon 2012). The wettest and driest shallow soil conditions observed in our study period differed by only 7% VWC. This difference may not be large enough to produce a significant effect on HR due to highly saturated deeper soils. The gradient
between shallow and deep soil water is generally very large within our study area due to excessively well-drained shallow soils sitting atop a water-filled karst topography (Bosch et al. 2003, Williams and Kuniansky 2016). According to the isotopic data, all three tree species appear to have access to deeper groundwater, which may have created the potential gradient to drive HR between shallow and deeper soils regardless of smaller fluctuations in shallow soil moisture over time (Gou and Miller 2014).

Conclusions

Our results suggests that a substantial amount of water is transported during nocturnal HR and sourced from deeper groundwater. This deeper stratum is more saturated than shallow soils and is linked by the rooting profile of all the three tree species studied here, with the highest magnitudes recorded in *P. palustris*. This connection allows the difference in soil moisture to drive HR upwards, redistributing both water and soil nutrients (Nadezhdina et al. 2010). This reasoning is often used to suggest that HR is able to act as a community level water subsidy for all taxa unable to otherwise access deeper groundwater (Muler et al. 2018). If this is the case, future studies should aim to quantify HR’s role in facilitating seedlings and understory plants and incorporated HR into our current view of ecosystem water dynamics.

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