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Rapid tree water transport and residence times in a Pennsylvania catchment

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ABSTRACT

Trees are responsible for the majority of precipitation recycling over land and can affect soil water storage, stream flow, and ground water recharge. Historically, water has not often been limiting in eastern U.S. forests. As a result, little work has been done to understand the timing of water use by vegetation in these systems. We used deuterium tracer, sap flux, and anatomical techniques to study tree water transport on a forested ridge top in central Pennsylvania. Three trees of each of the dominant ring-porous species, *Carya tomentosa* (mockernut hickory), *Quercus prinus* (chestnut oak), and *Quercus rubra* (red oak), and the diffuse-porous *Acer saccharum* (sugar maple), were studied. We hypothesized that tracer velocity would be higher in the ring-porous species because of their greater vessel diameters and water transport efficiency, but that tracer residence time would be largely dependent on tree size. The tracer travelled at velocities of 1 to 18 $\mathrm{m\,d^{-1}}$ with maximum deuterium concentration in the crowns of the study trees being reached between 1 and 12 days after injection. Tracer residence time ranged from about 5 to 22 days with no evidence of longer residence times in larger trees. There was also no evidence of a relationship between tracer velocity and calculated xylem specific conductivity, which varied by nearly an order of magnitude between species. However, the soil-to-leaf driving force for water transport may be a strong determinant of tracer velocity across species, and shows promise as a proxy for sap velocity in hydrologic modelling applications. Copyright © 2016 John Wiley & Sons, Ltd.

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KEY WORDS sap flux; ecophysiology; tree water use; stable isotopes; tracer; critical zone observatory; hydraulic conductance; xylem anatomy

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INTRODUCTION

How trees use water over various timescales can influence the dynamics of water uptake and retention, and can affect ground water recharge, stream flow, and the transport of signalling compounds through trees. Given that water has not often been limiting in Eastern U.S. forests historically, very little work has been done to understand the basics of timing of water use by vegetation in these systems.

The importance of vegetation to ecosystem water cycles has been well established. It is estimated that, globally, vegetation recycles more than half of precipitation that falls on land each year (Jackson *et al.,* 2000). However, hydrologists have often sought to study stream flow and ground water dynamics without studying vegetation directly. Early studies on watersheds demonstrated that forests regulate stream flow, prevent erosion, and control nutrient cycling (Bosch and Hewlett, 1982; Whitehead and Robinson, 1993). More recently, water age, or residence time of water, has been an important focus of exploration, but often limited to ground water, stream water, or soil water (Kazemi *et al.,* 2006; Cornaton and Perrochet, 2007; Duffy, 2010; Bhatt, 2012; Peters *et al.,* 2013). The age of water within vegetation is also an important component of understanding the water budget of a catchment beyond simply estimating evapotranspiration, and can be approached by studying two main factors: velocity of water transport and water residence time.

Tree water transport velocity ($\mathrm{m\ d^{-1}}$) is the distance water travels from roots to leaves divided by the elapsed time and is broadly controlled by the water potential difference between the soil and leaf, which provides the

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driving force, and by plant hydraulic conductance. The diameter of xylem conduit lumens, the packing density of conduits, and the sapwood area combine to influence plant hydraulic conductance and therefore the capacity for water transport in the trunk and branches of an individual tree (Tyree and Ewers, 1991; McCulloh *et al.,* 2010). Although velocity can be calculated from sap flux, none of the available sap flux techniques provide a true measure of velocity, as sap flux is an instantaneous measurement over a short vertical distance of sapwood on a sapwood area basis. However, the sapwood area includes not just conducting xylem vessels (or tracheids) but also non-conducting xylem parenchyma and cell walls (Meinzer *et al.,* 2006) and as a result, sap flux measurements underestimate true sap velocity.

Residence time is defined the amount of time a water molecule spends in a tree, from its entrance into the roots to its disappearance by the transpiration stream as vapour passing through the stomatal pores. If water remains in a tree for longer than the rate of transpiration would imply, we can assume that storage of water in tree tissues has occurred. In this sense, the tracer age can be a coarse measure of tree water storage, or mixing of older and newer water. In this study we use the concept of residence time to define the time for the tracer to enter and leave the tree and age to be the average age of molecules stored within the tree. Water storage dynamics operate at multiple time scales; residence times within a catchment typically range from a couple of days to several weeks for tree water (James *et al.,* 2003; Meinzer *et al.,* 2006), two weeks to a year for soil water, and from months, to years, to thousands of years for ground water (Kazemi *et al.,* 2006). Residence times of tree water have been negatively correlated with wood density (Meinzer *et al.,* 2003), and both positively and negatively correlated with tree size (James *et al.,* 2003; Meinzer *et al.,* 2006). Water storage within a tree can take place within multiple pools, including elastic, inelastic, and capillary storage (Tyree and Ewers, 1991). In a humid ecosystem, residence time is likely more indicative of the degree to which internal exchange occurs within tree tissues (James *et al.,* 2003), rather than storage over longer periods of time. This may relate to the hydraulic capacitance of sapwood (Meinzer *et al.,* 2003; Meinzer *et al.,* 2006; Steppe and Lemeur, 2007). Capacitance can be defined as the change in water content per unit change in water potential as an extension of the Ohm's law electric circuit analogy (Whitehead and Jarvis, 1981), and is often related to wood density (Scholz *et al.,* 2007; Meinzer *et al.,* 2008). The capacitance of sapwood allows for exchange of water between sapwood tissues and xylem conduit lumens, and can affect apparent hydraulic conductance by buffering changes in the soil-to-leaf water potential gradient with changes in flow. Storage of water because of sapwood capacitance can make up a large portion of stem mass and provide hours to days worth of water for transpiration (Whitehead and Jarvis, 1981).

The objective of this study was to examine the effect of tree species and size on the transport velocity and residence time of water in four tree species in a central Pennsylvania catchment, so that we could gain insight into the ability of trees in this system to buffer xylem tension associated with daily discharge and recharge of water stored within trees. We also sought to determine which factors could be important for modelling the timing of tree water uptake, the utilization of water, and the scaling of water use parameters over larger areas. We chose common, co-occurring tree species with some variation in xylem anatomy: Diffuse-porous *Acer saccharum* Marsh. (sugar maple), and the ring-porous *Carya tomentosa* Nutt. (mockernut hickory), *Quercus prinus* L.(chestnut oak), and *Quercus rubra* L. (red oak). We hypothesized that (1) ring-porous *Quercus* and *Carya* species would have higher transport velocities than the diffuse-porous *A. saccharum* because of larger maximum conduit size in ring-porous species, and (2) tree size would be a determinant of residence time, with larger trees able to store more water in living and non-living tissues than smaller trees. We did not expect to observe differences in residence time between tree species because of their similar wood density.

STUDY SITE AND METHODS

Study site

The Shale Hills Critical Zone Observatory (Shale Hills) (Lat. 40°39′N, Long. 77°54′W, elev. 256–310 m) was chosen as a study site because of co-located meteorological and soil moisture observations. Shale Hills is a 7.9-hectare catchment within the Pennsylvania State University's Stone Valley Forest (Figure 1). For additional geographic context for study site, see Dere *et al.* (2013). The catchment is v-shaped with north- and south-facing slopes. The valley floor serves as a floodplain for the stream that runs east to west. The stream is a first-order headwater of Shavers Creek, which is a tributary of the Susquehanna River. The forest was last harvested for timber in the 1930s and has been used for research purposes since the 1970s (Naithani *et al.,* 2013). Forest composition on a basal area basis was predominantly composed of *Quercus*, *Carya*, *Acer*, *Tsuga*, and *Pinus* genera. This area receives about 1050 mm of precipitation annually, with mean annual air temperature of 9.5 °C, and the highest air temperatures occur in July (monthly mean of 19.0 °C) (SSHCZO, 2015).

Within the Shale Hills catchment, a small site was chosen on the south-facing ridge for a detailed tree water use study (Figure 1). This area was chosen for its uniform soils and topography, and co-occurring hardwood tree species including *Quercus* spp., *C. tomentosa*, and *A.*

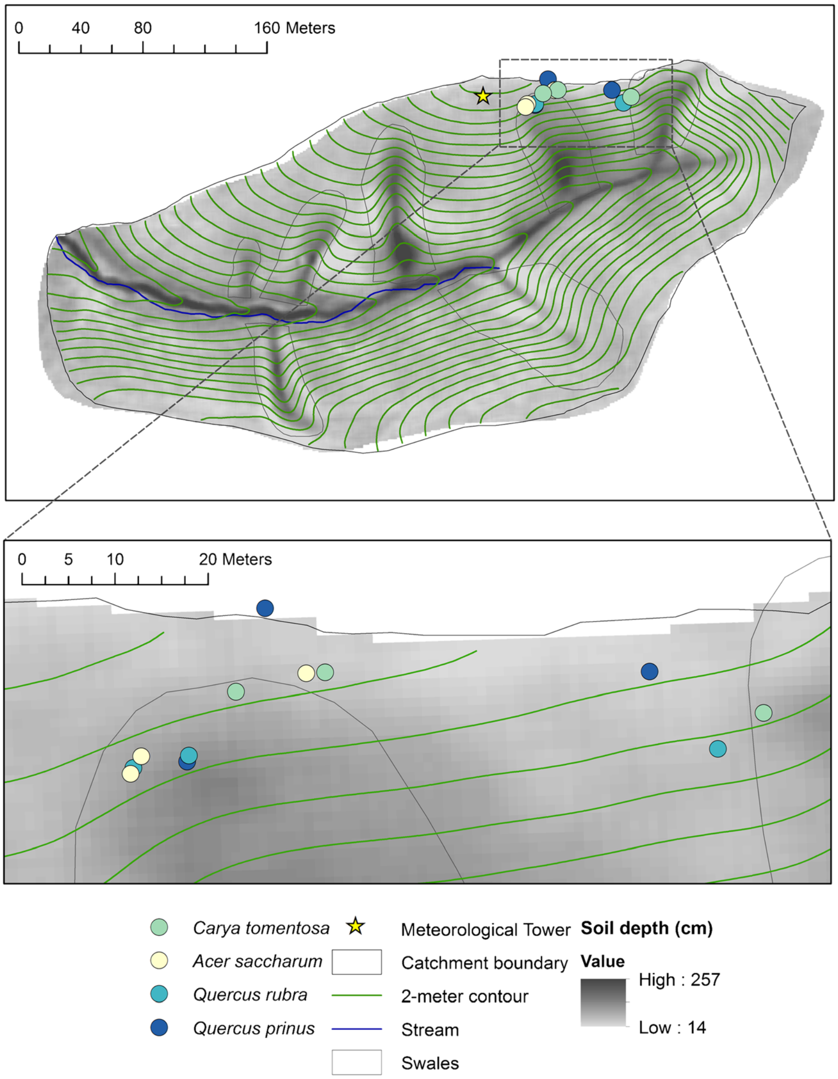

Figure 1. Map of study area at the Susquehanna Shale Hills Critical Zone Observatory (Lat. 40°39′N, Long. 77°54′ W, elev. 256–310 m) in the Stone Valley Research Forest in central Pennsylvania. Points show individual trees studied with colours representing tree species. Points overlay raster image of soil depth courtesy of Henry Lin.

saccharum. The soil at this site was in the Weikert series, which was well-drained and shallow, reaching depths of 20–30 cm with a high proportion of sand and low water-holding capacity (Baldwin, 2011; Thomas *et al.*, 2013).

Methods

Three individuals of each of four species, *A. saccharum*, *C. tomentosa*, *Q. prinus*, and *Q. rubra*, were selected on a south-facing ridge (Figure 1) based on their proximity to one another, minimum size (diameter at breast height, DBH > 0.18 m), and lack of obvious structural defects that would be likely to affect xylem water transport (Table I). In order to access the crown of each tree, three scaffolding towers with built-in ladders were constructed to a height of between 13 and 15 m.

Tree characteristics

A number of properties of the study trees were characterized that could be expected to affect their water transport and storage (Table I). Diameter at breast height (1.3 m) was measured with a diameter tape, and tree height was measured with a laser rangefinder (TruPulse 360, Laser Technology, Inc., Colorado, USA). Canopy class gives an indication of relative tree height in a stand and degree exposure of canopy branches to direct sunlight with dominant trees (D) tending to be the tallest and most exposed to sunlight and intermediate trees (I) shorter and less exposed to sunlight. Co-dominant trees (CD) were generally at about the height of most surrounding trees with fairly exposed crown branches.

Sapwood depth (mm) was measured at two sides of the tree at 50 cm from the base of the trunk using a 5-mm

Table I. Tree characteristics and tracer results. Species means and standard errors, in parentheses, shown for tracer dynamics. Canopy class – dominant (D), co-dominant (CD), intermediate (I). Asterisk (*) indicates trees for which injection was incomplete.

Tree species and ID	DBH (m)	Tree height (m)	Canopy class	Sapwood depth (mm)	Sapwood area (m^2)	D_2O injected (g)	Crown arrival time (d)	Time to reach maximum δ^2H (d)	Tracer velocity (m d^{-1})	Residence time (d)
ACSA 2068*	0.23	14.3	I	43.7	0.026	36.7	NA	NA	NA	NA
ACSA 2070	0.18	12.4	I	53.2	0.021	28.1	6.0	7.0	1.7	9.8
ACSA 689*	0.33	16.7	CD	56.2	0.048	51.4	2.1	12.0	1.3	16.8
						ACSA mean	*4.0 (2.0)*	*9.5 (2.5)*	*1.5 (0.2)*	*13.3 (3.5)*
CATO 2073*	0.23	19.7	CD	27.4	0.018	36.9	4.9	5.0	3.8	12.0
CATO 2076	0.45	20.2	D	22.9	0.031	70.2	1.1	1.1	18.0	9.3
CATO 688	0.31	19.7	D	29.1	0.025	48.3	1.0	5.0	3.85	11.7
						CATO mean	*2.4 (1.3)*	*3.7 (1.3)*	*8.6 (4.7)*	*11.0 (0.9)*
QUPR 2071	0.27	16.9	CD	16.7	0.013	42.7	1.0	2.0	8.0	21.6
QUPR 2074	0.35	18.2	D	17.1	0.018	54.3	4.0	6.0	2.9	5.9
QUPR 690	0.48	19.7	D	33.3	0.047	75.8	5.0	5.0	3.9	5.2
						QUPR mean	*3.3 (1.2)*	*4.3 (0.9)*	*4.9 (1.6)*	*10.9 (5.3)*
QURU 2069	0.29	14.6	CD	22.6	0.019	45.4	2.0	2.0	6.9	19.8
QURU 2072	0.46	16.7	D	26.4	0.036	72.6	7.0	7.0	2.3	11.6
QURU 2075	0.47	19.8	D	19.4	0.028	74.2	1.6	2.1	9.0	20.7
						QURU mean	*3.5 (1.7)*	*3.7 (1.6)*	*6.1 (2.0)*	*17.4 (2.9)*

increment borer (Haglof Inc., Madison, Mississippi) and calipers. Sapwood area (m^2) was calculated using DBH and the formula for the area of an annulus. The transition between sapwood and heartwood was identified by the colour change between the two.

At the branch level, additional measurements were collected to evaluate the role of vessel anatomy on the rate of water transport. Wood samples for these measurements were obtained from archived samples collected 6 August 2012 from one individual of each of the study species, with multiple cross sections analysed. Although this sampling was limited in scope, these properties were expected to be species specific and not affected to a large extent by variation within or among individuals of the same species. One branch segment between 3.9 and 5 mm in diameter was selected for each species. Samples were soaked overnight in distilled water for softening. Transverse hand sections were stained with 0.1% safranin-O for 1 min, soaked in distilled water overnight, rinsed with distilled water, and mounted with glycerin. A light microscope (Model, Olympus, Center Valley, Pennsylvania) and cellSens software (Version 1.9, Olympus, Center Valley, Pennsylvania) were used to examine and photograph each cross section. Vessel diameters were measured using ImageJ software (Version 1.49 h, National Institutes of Health, Bethesda, Maryland). Measurements of two axes for each vessel were used to calculate the diameter of an elliptical column (Lewis, 1988). Vessel mean hydraulic diameter, $(\Sigma d^4/n)^{1/4}$, and vessel packing density (number of conduits per wood area, mm^{-2}) were calculated using the diameter data (McCulloh *et al.,* 2010). Theoretical maximum hydraulic conductivity (kg m MPa^{-1} s^{-1}) was calculated with the Hagen–Poiseuille equation (Tyree and Ewers, 1991) then divided by the image area to determine specific conductivity (kg m^{-1} MPa^{-1} s^{-1}).

Environmental monitoring

Environmental conditions were monitored continuously at the study site during the deuterated water injection and sampling period in order to relate tree water transport and tracer dynamics to environmental variables for future modelling purposes. For example, precipitation (mm), air temperature (°C), relative humidity (%), and photosynthetically active radiation (PAR) (μmol m^{-2} s^{-1}) were measured at the meteorological tower site in a clearing on the north ridge (Figure 1) (Davis and Shi, 2013; Duffy, 2013; Thomas, 2013). Temperature and relative humidity were used to calculate vapour pressure deficit (VPD) using Teten's formula (Buck, 1981) expressed as daily maximum values. Soil volumetric water content was measured using soil moisture probes at a site close to the trees that were sampled. Soil moisture readings were collected each minute at 5, 15, and 25-cm depths, and averages were calculated every 10 min (Lin and Zhou, 2007; Lin, 2013a).

In order to calculate the difference between soil and plant water potential to estimate the driving force for water transport, soil matric potential (MPa), and midday leaf water potential (MPa) data were collected at the study site. The sampling for midday leaf water potential was able to be conducted once during the study period and therefore represents an estimate for this site and time of year. Soil water potential was measured at 20-cm depth at a location central to the towers on 24 July 2012 (Lin, 2013b). Midday leaf water potential was measured with a pressure chamber (PMS, Albany, Oregon) on 17 July 2012 in a subset of the tower trees, using three to four excised branches 20 cm long for one tree of each species, with the exception of *Q. rubra*, which was not sampled. Because of this missing value, an average value from literature sources for midday water potential in *Q. rubra* was chosen to reflect a representative value for this species (−2.42 MPa – Kubiske and Abrams, 1992; −2.62 MPa – Parker *et al.,* 1982; −2.74 MPa – Bahari *et al.,* 1985). Recent work suggests that the driving force for water movement may be similar within tree and shrub species over a large range of sizes (Smith and Sperry, 2014).

Deuterated water study

Deuterium oxide (D_2O) tracer (99.999 ‰, Sigma-Aldrich Corp, St. Louis, Missouri) was injected into the study trees to estimate the rate of xylem sap flow to the upper branches. Each tree's dose was calculated at 0.05 g per centimetre of trunk circumference (Table I) and injected with transfer pipettes into 2-cm-deep holes drilled at a 30° angle from vertical, downward into the sapwood, at a height of 50 cm from the base of each tree (James *et al.,* 2003). Six trees were injected on 11 July 2012, and the remaining six trees were injected on the following day. Because of slow tracer uptake, injection took place over the course of 6 h, from 0900 to 1500 h. For three individual trees with the slowest uptake, a small amount of the dose remained unapplied (Table I).

Stem samples were collected to determine baseline natural abundance of stable isotopes for oxygen ($\delta^{18}O$) and hydrogen (δ^2H) before tracer injections on 10 and 11 July 2012. Using samples cut from the trees, small segments of fully suberized, small branches 3–5 mm in diameter were cut and quickly sealed in glass vials with polyseal caps and parafilm to prevent water loss. These samples were frozen prior to extracting water by cryogenic vacuum distillation at a later date (Shimabuku, 2001). The extracted water was analysed by stable isotope mass spectrometry using the equilibration method at the Center for Stable Isotope Biogeochemistry at the University of California at Berkeley. This method had a long-term external precision of ± 0.80‰ for δ^2H and ± 0.12‰ for $\delta^{18}O$ (CSIB, 2014).

Leaves were collected the day following injection to determine the concentration of deuterium present in leaf water, with 14 additional samples over the next 35 days. Sampling frequency was daily for week 1 of the study, three times during week 2, twice during week 3, and once per week for weeks 4, 5, and 6. Two to three sun-exposed, canopy-height branches of approximately 30 cm in length were collected from different parts of the crown by climbing the scaffolding towers or tree climbing. Leaves were placed in plastic zipper storage bags, transported back to the lab, and allowed to transpire under greenhouse lamps for about 2–4 h. About 1 to 5 ml of condensate was collected from each of the bags later the same day using a transfer pipette. The water was then stored in vials wrapped in Parafilm in a cool, dark area prior to laboratory analysis. Condensate water collected from leaves was analysed with a liquid water stable isotope analyser (DLT-100, Los Gatos Research, Mountain View, California) to estimate the δ^2H composition of the samples. Samples were analysed following IAEA Standard Operating Procedure (Newman *et al.,* 2008). The analytical precision of the instrument was 0.8‰ for deuterium (Lis *et al.,* 2008). Sample concentrations were reported as percentage of maximum over the baseline natural abundance concentration for each individual tree. Although tree leaf water was sampled for up to 35 days past injection, because of instrument technical difficulties from exposure to high concentrations of deuterium in some of the samples, sample analysis was ended after completing samples for 19 days past injection. This is the point at which it was observed in preliminary results that leaf water deuterium concentration had returned to baseline levels in the individual trees being sampled.

Sap flux and tracer calculations

Fixed depth (2 cm) heat dissipation sap flow probes (Granier, 1985) were installed in study trees. Sap flux density ($g\,m^{-2}\,s^{-1}$) was calculated using the temperature difference between heated and unheated sensors in the probes relative to the maximum temperature difference at zero flow (ΔT_{max}). To account for nighttime flux, a regression technique was used to estimate ΔT_{max} when the slope of the temperature difference (ΔT) versus VPD for the early morning hours (midnight to 5 am) was significantly different from 0 ($P < 0.05$) (Meinzer *et al.,* 2013). In all other cases, the ΔT_{max} observed on a given day was used. Data were cleaned to remove observations from probes that appeared to have failed or otherwise provided anomalous readings, such as unrealistically high values, or those that were negative or very close to zero. Sap flux density values were weighted in order to account for zero flow occurring in inactive xylem that was in contact with the probe in trees with shallow sapwood, defined as sapwood depth less than 20 mm (Clearwater *et al.,* 1999). To this end, sap flux density values were multiplied by the proportion of sapwood out of the total sap flux probe length (20 mm).

Tracer arrival time was defined as the time it took for the tracer to reach 10% of the maximum tracer concentration in the leaves sampled (Meinzer *et al.,* 2006). Velocity was calculated as tracer path length (tree height minus injection height), divided by the arrival time (Meinzer *et al.,* 2006). The duration to achieve the maximum tracer concentration in leaves of each tree was also calculated. Residence time was defined as the time needed to return to within 5% of the baseline deuterium concentration. The date and time at which that point was reached for each tree were estimated by fitting an exponential model through the deuterium concentrations for the last three or four sample dates (Dye *et al.,* 1992).

In order to determine whether sap flux could be used as a proxy for tracer velocity, sap flux density measurements were integrated daily for the first week of the study and converted to velocity units by expressing daily sap flux as a volume per unit sapwood area ($m^3\,m^{-2}\,d^{-1}$) which was compatible with velocity units ($m\,d^{-1}$). The estimated sap-flux velocity was an 'apparent velocity,' and was expected to underestimate true velocity because of probe contact with non-conducting tissues (Meinzer *et al.,* 2006).

Statistical analyses

One-way analyses of variance were conducted to test the effect of species and wood type on tracer velocity, time to achieve maximum tracer concentration, and residence time. Simple linear regression was used to test for linear effects of (1) VPD on sap flux density, (2) VPD on δ^2H concentration, (3) PAR on δ^2H concentration, (4) tree size (DBH) on tree water residence time, and (5) tree height on water residence time. Potential predictors of tracer velocity were also examined. These included soil-to-leaf driving force, theoretical maximum hydraulic conductivity, theoretical maximum specific conductivity, maximum vessel diameter by species, and vessel mean hydraulic diameter. The relationship of these potential predictors with tracer velocity was examined using simple linear regression. Because of the occurrence of precipitation during the study, the relationship of precipitation with the timing of tracer arrival was qualitatively assessed. Pearson's product–moment correlation was used to compare the relationship between tracer velocity and sap flux velocity. Tukey's Honest Significant Difference (HSD) post-hoc test was used to assess pair-wise differences in genus, wood type, and species groups. All statistical analyses were performed using R base packages (R Core Team, 2014). Colour scheme for colour figures was chosen with ColorBrewer 2.0 (Brewer, 2013).

RESULTS

Tree characteristics

The study trees ranged in size from a DBH of 0.18 (*A. saccharum*) to 0.48 m (*Q. prinus*) with height ranging from 14.3 m (*A. saccharum*) to 20.2 m (*C. tomentosa*) (Table I). Individuals belonging to the genera *Carya* and *Quercus* had either dominant or co-dominant crowns, while the *Acer* individuals were either co-dominant or intermediate. Sapwood depth ranged from an average of 23 ± 3 mm in *Quercus* to 51 ± 4 mm in *Acer*.

Vessel mean hydraulic diameters ranged from 22 μm in one individual of *A. saccharum* to 46 μm for *Q. rubra* (Table II). The distribution of vessel diameters varied by wood type (Figure 2); the maximum vessel diameter in *C. tomentosa* (74 μm) and *Quercus spp.* (QUPR = 106 μm, QURU = 87 μm) were two to three times the diameter of the largest *A. saccharum* vessel measured (38 μm, Table I). Although *A. saccharum* had the highest packing density of the individuals we examined, *Quercus spp.* and *C. tomentosa* had much larger maximum theoretical specific hydraulic conductivities because of their larger mean vessel hydraulic diameters and the effect of raising vessel diameter to the 4th power in the Hagen–Poiseuille equation (Table II).

Environmental conditions

Climatic conditions for July 2012 were within the average range for central Pennsylvania (NOAA, 2014). The average maximum daily air temperature during the study period was 27.9 °C with similar weather conditions on the two injection days (maximum air temperature of 29.1 °C) for 11 July (DOY 193) and 29.6 °C for 12 July (DOY 194) (Figure 3) (Davis and Shi, 2013). VPD ranged from a daily maximum of 3.6 kPa on a warm, dry day early in the study (8 July 2012, DOY 190), to 0.3 kPa for a rainy day (21 July 2012, DOY 203) (Figure 3). There was a small amount of

Table II. Vessel diameter and hydraulic conductivity results. Results represent averages among multiple cross sections for a branch from each species.

Species	Packing density (mm^{-2})	Maximum vessel diameter (μm)	Vessel mean hydraulic diameter (μm)	Theoretical maximum specific hydraulic conductivity ($kg\,m^{-1}\,MPa^{-1}\,s^{-1}$)
Acer saccharum	194	38	22	1.0
Carya tomentosa	65	74	41	4.3
Quercus prinus	87	106	44	7.7
Quercus rubra	90	87	46	9.4

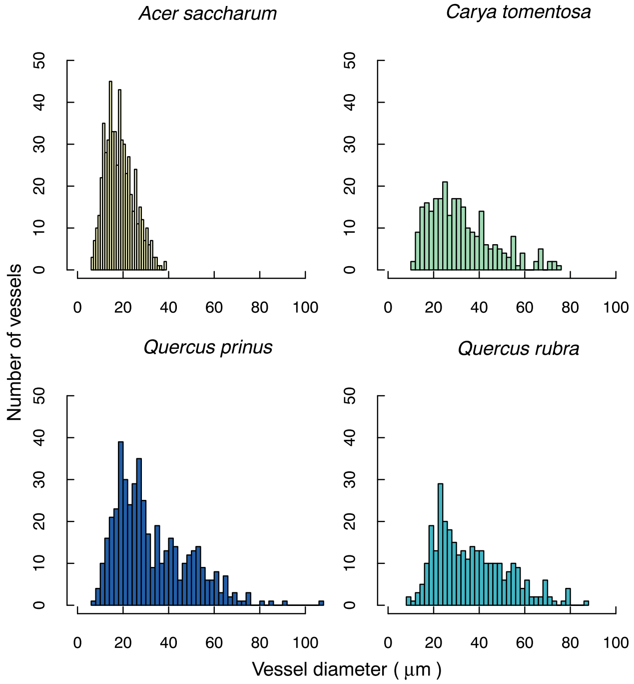

Figure 2. Vessel size distribution for one branch sample from each tree species with counts of vessels in each size category. Between five and nine cross sections were analysed per branch. Total number of vessels analysed: QUPR, $n = 463$; QURU, $n = 315$; CATO, $n = 268$, ACSA, $n = 573$.

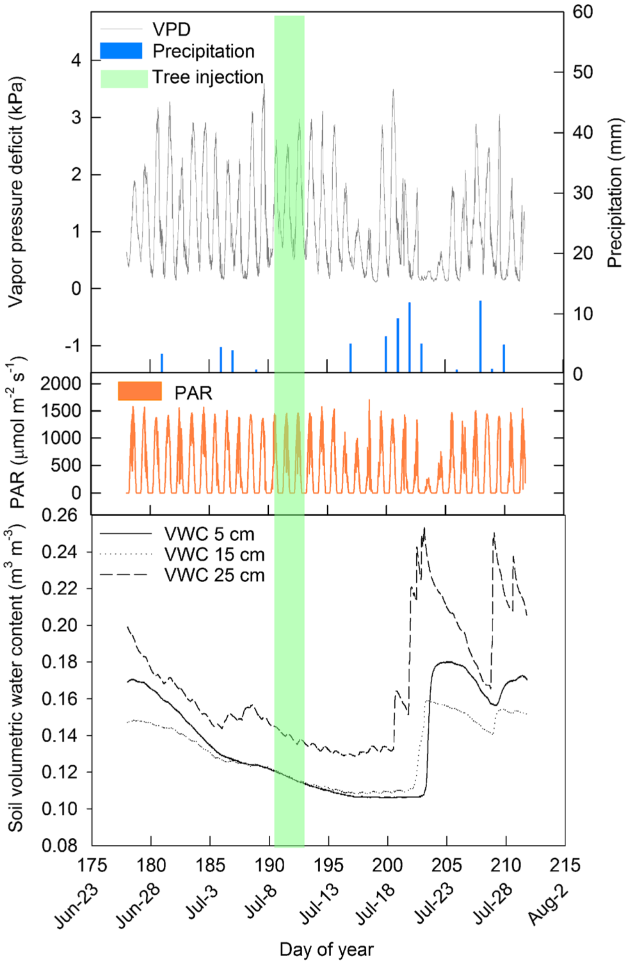

Figure 3. Environmental conditions during the study and two weeks prior. Top panel: vapour pressure deficit and precipitation, with a bar indicating days the trees were injected with deuterium. Middle panel: photosynthetically active radiation. Bottom panel: volumetric water content at 25, 15, and 5-cm soil depths showing drying and rewetting of soil.

rain in the weeks prior to the study (9.4 mm of rain between 1 July and 12 July, arriving in two small storms). However, soil moisture between 5 and 25 cm deep had declined in the weeks leading up to the experiment (Lin, 2013a; Figure 3). The first rain event after tracer injection occurred on 15–16 July (5.3 mm), and there was a larger storm 18–21 July (32.6 mm) (Duffy, 2013; Figure 3).

Sap flux and tracer dynamics

The process of drilling into the sapwood and injecting deuterium oxide had no discernable effect on sap flux during the study. A visual inspection of plots of sap flux density before and after injection did not reveal any patterns that could be distinguished from typical daily variation (Figure S1). Maximum daily VPD was positively related to maximum daily sap flux density for the majority of trees we examined (Figure S2, $P < 0.01$, $R^2 = 0.6$ to 0.8). The two *C. tomentosa* individuals for which we had functional sap flux probes showed a positive, although non-linear, response of sap flux density to VPD (Figure S2).

The deuterium tracer was detected in the canopy leaves of 11 out of the 12 trees and arrived as one or multiple peaks (Figure 4). The tracer was detected in two out of the three *A. saccharum* trees. Many trees reached their maximum tracer concentration following a rain event about 4 days into the study, and all trees reached their maximum by 12 days after injection. The time to reach maximum tracer concentration did not differ significantly among species ($P = 0.14$), except when grouped by wood type, where diffuse-porous *Acer* took more than twice as many days as the ring-porous species ($P = 0.01$; Table I; Figure 5). The time to reach maximum δ^2H concentration was not consistently related to either VPD or PAR. Water transport velocities estimated from sap flux were on average nearly five times slower than tracer velocities (Figure S3), and not correlated with tracer velocities ($P = 0.52$, $r = 0.21$).

It is unclear whether precipitation may have had an effect on the arrival time of the tracer. Three *Quercus* trees reached their maximum composition of δ^2H before any precipitation occurred (QUPR 2071, QURU 2069, and QURU 2075), while seven *Quercus* and *C. tomentosa* individuals reached their maximum δ^2H by

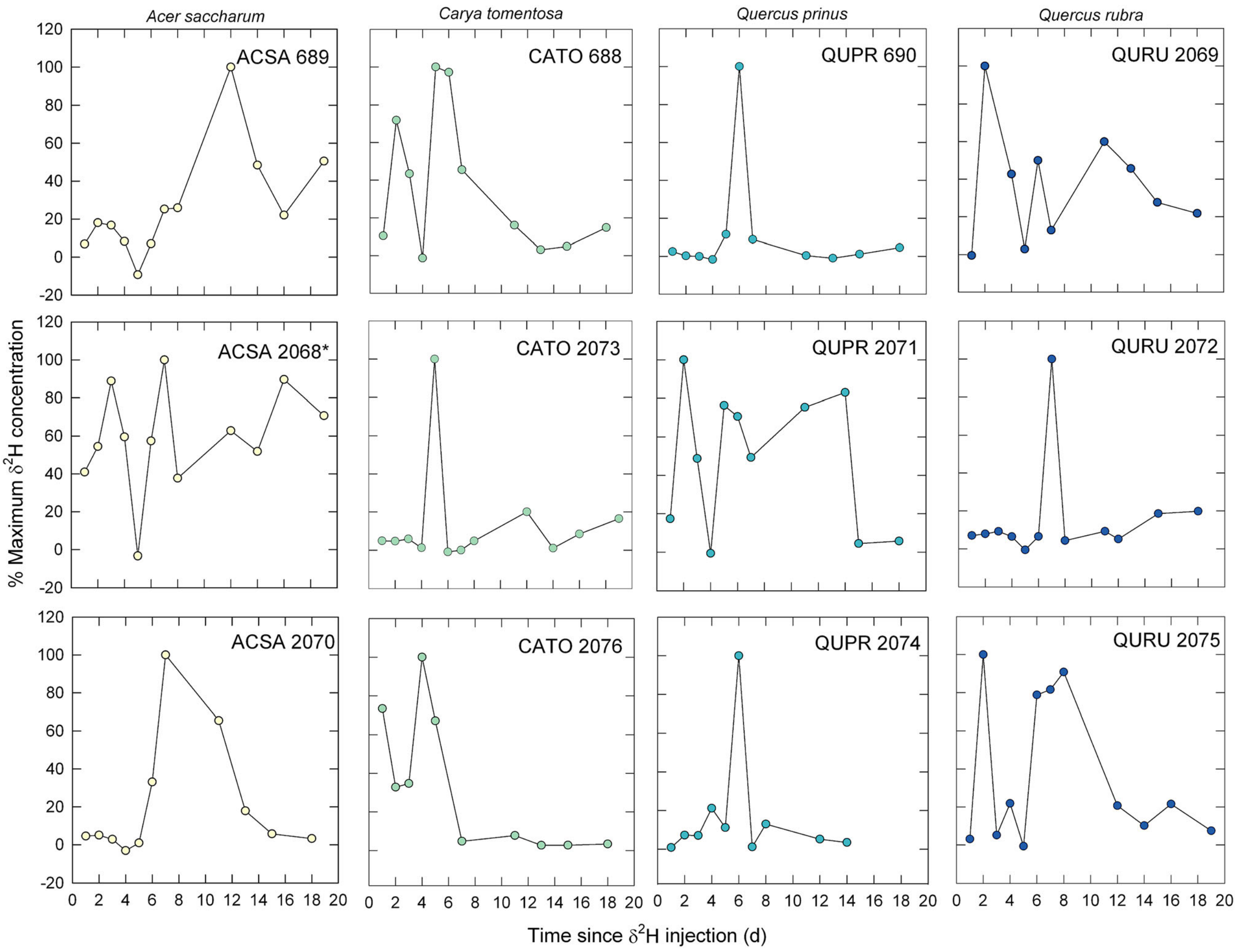

Figure 4. Tracer pulse dynamics for each tree in the study. δ^2H compositions in leaves were normalized by the percentage of maximum observed δ^2H above the baseline natural abundance levels. *Tracer did not appear in ACSA 2068 leaves.

the time 5 mm of rain had accumulated. Two *Acer* trees reached their maximum later, after 11 and 38 mm of precipitation (ACSA 2070 and ACSA 689, respectively).

Tracer velocity ranged from 1 to 18 m d^{-1} and tended to be most rapid in *C. tomentosa*, followed by *Q. rubra*, *Q. prinus*, and then *A. saccharum*, but it was quite variable among individual trees ($P = 0.52$ for species and $P = 0.20$ for wood type) (Table I). Tracer residence time ranged from 5 to 22 days across all 11 trees (Table I, Figure 6). Mean residence times among species and between wood types were not significantly different ($P = 0.54$ and $P = 0.96$, respectively, Figure 6). Contrary to our hypothesis, there was also no evidence of larger trees having longer residence times ($P = 0.61$ for DBH, Figure S4, $P = 0.52$ for tree height, data not shown).

Of the hydraulic parameters based on xylem anatomy that we considered (maximum vessel diameter, theoretical maximum hydraulic conductivity, theoretical maximum specific hydraulic conductivity, and vessel mean hydraulic diameter), none were strong linear predictors of tracer velocity (*P-values* ranged from 0.24 to 0.66). Tracer velocity scaled linearly with the soil-to-leaf driving force for water transport based on the difference between midday leaf water potential for each representative of each tree species in the study (ACSA = −1.2 MPa, CATO = −3.5 MPa, QUPR = −2.8 MPa, QURU = −2.4) and soil matric potential (−0.415 MPa) ($P = 0.04$, $R^2 = 0.88$; Figure 7).

DISCUSSION

Tracers have been used to study water use by vegetation for decades, beginning with the use of chemical tracers (Greenidge, 1955; Kozlowski and Winget, 1963), radioisotopes like tritium (Kline *et al.,* 1970; Waring and Roberts,

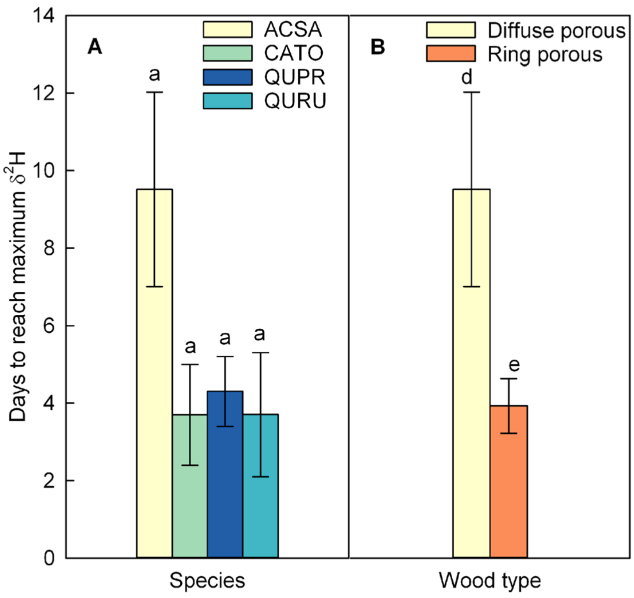

Figure 5. Time to reach maximum leaf tracer concentration by (A) tree species and (B) wood type. Error bars indicate mean standard error ($n = 3$, except ACSA, $n = 2$). Letters indicate significant differences. Differences between species were not significant ($P = 0.14$), except when grouped by wood type ($P = 0.01$).

1979), and later the stable isotope deuterium (Calder *et al.,* 1986; Dye *et al.,* 1992; Kalma *et al.,* 1998; Marc and Robinson, 2004). Few of these studies have taken place in the humid temperate forests of the eastern U.S.

The results of this study show tracer velocities and residence times in the same range as previous studies on angiosperm trees (Kline *et al.,* 1970; Meinzer *et al.,* 2003; Schwendenmann *et al.,* 2010). We observed the arrival of a deuterium tracer, used as a proxy for natural water, in the crown of 12 to 20-m-tall *Acer*, *Carya*, and *Quercus* trees from one day to one week after it was injected, moving at speeds of up to 18 m d^{-1}. The tracer persisted in the leaves for up to about 3 weeks afterward, indicating water exchange between the transpiration stream and storage compartments within the trees. In comparison, tracer velocities ranged from 2.4 m d^{-1} in old-growth *Tsuga heterophylla* (Meinzer *et al.,* 2006) to 26 m d^{-1} in the tropical angiosperm *Cordia alliodora* (Meinzer *et al.,* 2003). Tracer residence times ranged from 2 to 30 days in tropical ecosystems (Kline *et al.,* 1970; Meinzer *et al.,* 2003; Schwendenmann *et al.,* 2010), 10 to 35 days in arid ecosystems (Calder *et al.,* 1986; Dye *et al.,* 1992; Kalma *et al.,* 1998), and up to two months in old-growth conifers (Meinzer *et al.,* 2006).

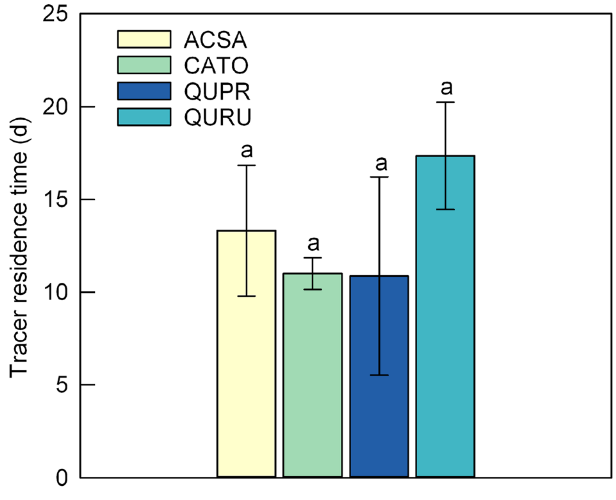

Figure 6. Residence time estimates for each tree species. Residence time was calculated by fitting an exponential decay model to the last three to four sample collection points, based on the return to baseline levels of δ^2H. The residence time shown is for a return to 5% of maximum δ^2H. As letters indicate, species differences were not significant ($P = 0.55$).

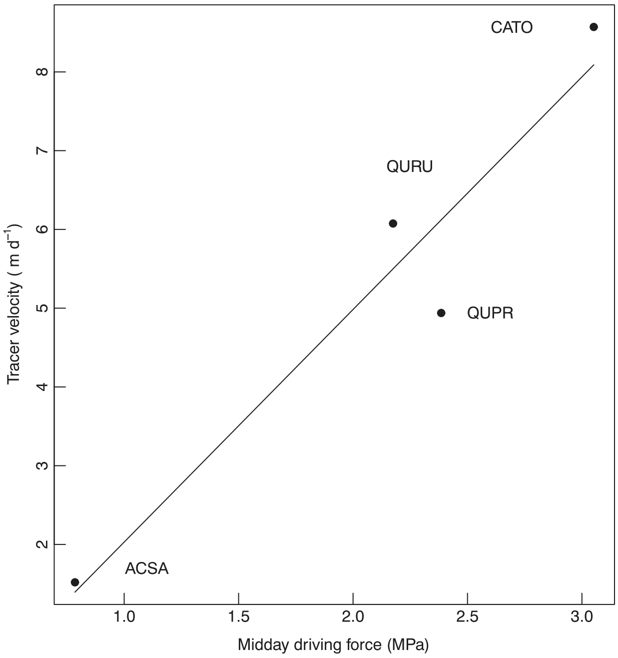

Figure 7. Average tracer velocity by species and the midday driving force for water transport, $P = 0.04$, $R^2 = 0.88$. Driving force is the difference between soil matric potential and midday leaf water potential, measured in July, 2012.

The multiple peaks that we observed in the δ^2H signal as the tracer arrived at the leaves in the transpiration stream have several possible methodological or physiological explanations. Methodological issues include spilling of tracer during injection (we think this was unlikely), incomplete mixing of deuterium in the crown (Kline *et al.,* 1970), or deuterium injection depth that exceeded the sapwood depth in some individuals; tracer injected into sapwood should have been transported directly to the crown, while deuterium in the heartwood may have been stored there for a short period of time before it diffused into the sapwood. Physiological explanations may include transient pulses in sap flow in response to fluctuating environmental conditions, or differences in velocity of water movement through vessels of different sizes. The latter may explain the occurrence of multiple peaks in many of the ring porous individuals if one portion of sap moved quickly through the largest, more conductive vessels and another portion of sap moved more slowly through smaller vessels.

While maximum daily VPD was a strong predictor of maximum daily sap flux density in most of the study trees, VPD alone did not explain the patterns of δ^2H arrival that we observed. We were also unable to assess whether precipitation was a driver of variations in the arrival of the δ^2H signal at the leaves. While many trees reached their maximum level of δ^2H after a small amount of rain, others peaked before any rain occurred, and two *Acer* individuals peaked only after additional precipitation. The soil-to-leaf driving force, calculated as the difference between soil matric potential and midday leaf water potential, was a better predictor of tracer velocity than any of the xylem anatomy-based hydraulic parameters that we examined. Perhaps with a larger sample size we may have been able to detect a stronger influence of hydraulic parameters on the tracer velocity. However, it is possible that the interspecific variation in xylem anatomy that we observed at the branch level may not have led to hydraulic differences at the whole-tree scale if there was allometric compensation through variation in leaf area to sapwood area. For example, if individuals with efficient water transport at the branch level also had higher leaf area per unit sapwood area, these individuals could have very similar whole-tree leaf area-specific hydraulic conductance to individuals with less efficient xylem, but lower leaf area. Our results may suggest a common relationship between soil-to-leaf driving force and sap velocity among co-occurring trees of different species and wood anatomy at this site. Although divergent, the species patterns appeared to be predictable. For example, *C. tomentosa* had a higher transport velocity as a result of its more negative midday leaf water potential and therefore a larger driving force, while *A. saccharum* had a lower transport velocity because of its less negative leaf water potential. The *Quercus spp.* individuals had intermediate levels of soil-to-leaf driving force and tracer velocity. The soil-to-leaf driving force may have potential for modelling purposes, with additional validation of this relationship in field settings, as it is easier to measure or estimate than hydraulic parameters, particularly if its relationship to transport velocity applies uniformly across species.

Differential effects of species and wood type on maximum hydraulic conductivity and specific conductivity were also evident from our calculations using the Hagen–Poiseuille equation (Tyree and Ewers, 1991). Despite lower packing densities, the larger-vesseled *Quercus spp.* and *C. tomentosa* had higher specific hydraulic conductivities than the diffuse porous *A. saccharum*. Similar results have been shown in other work (Steppe and Lemeur, 2007). Species and/or wood type could also be important for explaining differences in stem capacitance (Greenidge, 1955; Kline *et al.,* 1970; Meinzer *et al.,* 2003; Meinzer *et al.,* 2006;), which we would expect to influence tree water residence time and velocity. Capacitive exchange of water between storage tissues and the transpiration stream can buffer diurnal changes in xylem tension, which could slow water transport and increase water residences times (Meinzer *et al.,* 2006). Capacitance can also change carbon allocation patterns within trees; for example, there may be less investment in thick conduit cell walls if embolism were less likely because of high capacitance. This strategy could be particularly well-suited to humid forests, where severe water limitation is infrequent (Tyree and Ewers, 1991).

We did not observe the differences in tracer residence time with respect to tree size that we expected at the onset of the study. While whole-tree water use has been shown to scale with tree size (Kalma *et al.,* 1998; Meinzer *et al.,* 2003, 2005), water residence time may not (Kline *et al.,* 1970; Schwendenmann *et al.,* 2010) unless size differences are substantial (Meinzer *et al.,* 2006). This could have implications for hydrologic models that include vegetation water residence time; tree size may not be a key component of such models unless forests with highly variable tree sizes are part of the landscape.

Although tree size alone may not directly determine tracer dynamics, canopy class and relative position of sampling can be important sources of variation. Smaller, more suppressed crowns, and lower branches tend to have better mixing compared to higher branches and more dominant crowns (Kline *et al.,* 1970; Calder *et al.,* 1986) because of the differences in light interception and resulting driving forces for transpiration depending on light interception. In one of the less dominant *A. saccharum* individuals, the tracer was not detected over the course of the study. This could have been at least partially because of a more suppressed crown with less light exposure, or other factors like injury at the point of injection or decay within the xylem tissue without clear evidence on the exterior of the tree.

Water age and residence time are concepts that have been largely confined to hydrogeology and hydrology studies (Kazemi *et al.,* 2006; Duffy, 2010; Bhatt, 2012; Hrachowitz *et al.,* 2013), with little emphasis on vegetation, despite the history of tracer experiments in vegetation. Nevertheless, age of water in vegetation is an important concept that deserves consideration for hydrologic models because vegetation can serve as a major avenue for water loss and biogeochemical change in the hydrologic system. Current and future tree species distributions, particularly in relationship to wood type, could be important for shaping the forest water balance and carbon-water relations. Across the four species in this study, the soil-to-leaf driving force in particular appeared to be a strong control on tracer transport velocity, and holds promise for use as a proxy for transport velocity in modelling tree water uptake and use and scaling water use parameters over large areas.

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