Observations of stem water storage in trees of opposing hydraulic strategies

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Abstract.   Hydraulic capacitance and water storage form a critical buffer against cavitation and loss of conductivity within the xylem system. Withdrawal from water storage in leaves, branches, stems, and roots significantly impacts sap flow, stomatal conductance, and transpiration. Storage quantities differ based on soil water availability, tree size, wood anatomy and density, drought tolerance, and hydraulic strategy (anisohydric or isohydric). However, the majority of studies focus on the measurement of storage in conifers or tropical tree species. We demonstrate a novel methodology using frequency domain reflectometry (FDR) to make continuous, direct measurements of wood water content in two hardwood species in a forest in Michigan. We present results of a two month study comparing the water storage dynamics between a mature red oak and red maple, two species with differing wood densities, hydraulic architecture, and hydraulic strategy. We also include results pertaining to the use of different probe lengths to sample water content only within the active sapwood and over the entire conductive sapwood and the outer portion of heartwood in red oak. Both species studied exhibited diurnal cycles of storage that aligned well with the dynamics of sap flux. Red maple, a diffuse porous, relatively isohydric species showed a strong dependence on stored water during both wet and dry periods. Red oak, a ring porous relatively anisohydric species, was less reliant on storage, and did not demonstrate a dependence on soil water potential. Comparison between long and short FDR probes in the oak revealed that oaks may utilize water stored in the innermost layers of the xylem when soil moisture conditions are limiting. We found the FDR probes to be a reliable, functional means for continuous automated measurement of wood water content in hardwoods at a fast time scale. Application of FDR technology for the measurement of tree water storage will benefit forest ecologists as well as the modeling community as we improve our understanding and simulations of plant hydrodynamic processes on a large scale.

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INTRODUCTION

Water storage within the hydraulic systems of trees provides a buffer for the daily demands of transpiration (Cermak and Nadezhdina 2011, Scholz et al. 2011, Kocher et al. 2013). Stored

water within leaves, branches, stems, and roots plays an integral role in the regulation of xylem tension and cavitation avoidance (Waring and Running 1978). In tall trees, stem storage has been shown to have significant influence on sap flow and stomatal conductance (Andrade et al. 1998, Cermak et al. 2007). Various studies have demonstrated that 10–50% of daily transpiration may be provided by stem water stores (e.g., Phillips et al. 2003, Meinzer et al. 2004, Cermak et al. 2007, Kocher et al. 2013). The importance of water storage and hydraulic capacitance is well known, however, few studies have measured it. In most cases where water storage has been measured, the focus has been on tropical or coniferous species (e.g., Waring and Running 1978, Andrade et al. 1998, Domec and Gartner 2001, Meinzer et al. 2006, Cermak et al. 2007), rather than temperate hardwood species (Cermak et al. 1982, Wullschleger et al. 1996, Hernandez-Santana and Martinez-Fernandez 2008, Kocher et al. 2013).

Tree use of stem-stored water has been recognized as a critical component for the estimation of transpiration from stem sap flow data (Schäfer et al. 2000, Burgess and Dawson 2008, Kumagai et al. 2009, Phillips et al. 2009). The effects of storage on calculations of transpiration are typically accounted for using a lag coefficient, as the first portion of transpiration each day is typically withdrawn from storage reserves before sap flow begins (Schäfer et al. 2000). Yet, the volume of stored water and the reliance upon such stores is known to vary with tree size and species-specific hydraulic properties including wood anatomy, density, drought tolerance, and stomatal hydraulic strategy (anisohydric or isohydric; Kocher et al. 2013). Furthermore, the percent of storage able to be replenished by nightly recharge is dependent on water availability to roots.

Land-surface models produce errors in intra-daily simulations of transpiration. These errors are consistent with an inability to accurately simulate the fast dynamics of transpiration (Matheny et al. 2014a). The hysteretic nature of the relationship between transpiration and vapor pressure deficit (VPD) is one feature of the intra-daily transpiration dynamics that is not well resolved by models, and has been linked to hydrodynamic limitations of stomatal conduc-

tance (Unsworth et al. 2004), and response to soil moisture conditions (Wullschleger et al. 1998). It follows that the role of storage in both the hydraulic limitation of stomatal aperture as well as the response to soil conditions is nontrivial. These complexities make storage a critical, dynamic and challenging variable to estimate (Burgess and Dawson 2008, Phillips et al. 2009).

High frequency (half-hourly) measurements of storage made across a wide spectrum of woody tree species will help to evaluate hydrodynamic models and lag parameters in simpler empirical models and improve the estimation of transpiration on the basis of stem and crown sap flow measurements. A growing number of advanced tree-level hydrodynamic models resolve the movement of sap within the tree system, and with it the water mass-budget inside trees including the xylem capacitance and storage (Bohrer et al. 2005, Steppe and Lemeur 2007, Janott et al. 2011, Bittner et al. 2012a). While these model predictions were successfully validated with regards to stomatal conductance and sap flow, to date, they have not been directly evaluated using in situ observations of storage. Direct measurement of storage would provide data for estimation of lag parameters used by classical transpiration models while providing another axis of evaluation for physical mechanistic models.

Presently, storage is most commonly measured using a combination of electronic dendrometers and sap flow data at the base of the stem and at multiple locations along transpiring branches (Phillips et al. 2009). Scholz et al. (2007) demonstrated the use of thermocouple psychrometers for the measurement of sapwood water potential. Wullschleger et al. (1996) introduced the use of time domain reflectometry (TDR) to monitor wood water content at a monthly time scale in hardwoods, where little change in stem diameter was detected. Here, we propose the use of frequency domain reflectometry (FDR), with sensors located at the top and bottom of the storage compartment for the direct, continuous measurement of wood volumetric water content. These probes are low cost, low power and high durability, making them ideal for continuous field-based, automated data collection.

In this work, we explore the feasibility of

deploying FDR probes to measure wood volumetric water content and test hypotheses regarding trunk water storage. Sensors were installed in two hardwood tree species, one diffuse porous and the other ring porous. Our study primarily focuses on the use of a novel method for in situ measurement of trunk water storage in mature trees, with less emphasis on species-specific storage dynamics. We hypothesized that storage dynamics for both species would be dependent on soil water availability on a daily-weekly time scale and would fluctuate with sap flux at a half-hourly time step. We also hypothesized that storage would play a more important role in daily transpiration in the diffuse porous species when compared to the ring porous species.

METHODS

Site description

This study was conducted from 10 July to 14 September, 2014 at the University of Michigan Biological Station (UMBS) located in northern, Lower Michigan, USA (45°33′35″ N, 84°42′48″ W, elev. 236 m). The site is described in depth in Matheny et al. (2014b). The site receives 805 mm of mean annual precipitation and has an annual average temperature of 6.8°C. Soils consist of well drained Haplorthods of the Rubicon, Blue Lake, or Cheboygan series that are 92.2% sand, 6.5% silt and 0.6% clay (Nave et al. 2011). We conducted our study in a forest plot within the footprint of the US-UMB Ameriflux-affiliated eddy covariance flux station (http://ameriflux.lbl.gov/; Site ID US-UMB; Gough et al. 2013), which provides measurements of plot-level meteorological conditions as well as carbon and water vapor fluxes. The study area is dominated (~30% of leaf area and 59.6% of stem area) by early successional bigtooth aspen (*Populus grandidentata*) and paper birch (*Betula papyrifera*). Later successional species such as red oak (*Quercus rubra*), red maple (*Acer rubrum*), white pine (*Pinus strobus*), American beech (*Fagus grandifolia*), and sugar maple (*Acer saccharum*) are increasing in their relative portion of the stand basal area (Gough et al. 2013). Mean canopy height is approximately 25 m, average tree age of canopy dominant trees is 90 years, mean peak growing season LAI is ~3.9 m^2/m^2, and average stem density is ~750 trees/ha (for trees with diameter at breast height ≥8 cm). We focused our study on the most dominant mid-late successional species: red maple (23.3% LAI, 19.2% stem area) and red oak (24.1% LAI, 12.1% stem area) because these two species will likely become dominant in the near future, after the senescence of the early successional species, and because we have previous observations of different aspects of these trees' hydrodynamics (Thomsen et al. 2013, Matheny et al. 2014b). We use a combination of meteorological, sap flux, and wood water content measurements to test the effectiveness of FDR sensors for measuring tree water storage and water use dynamics in one red maple and one red oak tree of similar size, height, canopy position and proximity to one another.

Sap flux measurement

Additional details on the methods of sap flow measurements we used at this site are listed in Matheny et al. (2014b). The study trees were instrumented with Granier-style thermal dissipation sensors (Granier 1987) to continuously measure sap flux densities. Data were recorded every minute and averaged to half hourly time steps. Pairs of 20 mm long, custom-manufactured sap flux sensors were inserted into the sapwood at breast height (1.37 m) on the north-facing side of each tree. Sap flux sensors were installed with a vertical separation of ~10 cm. Sap flux data were processed using a daily maximum temperature baseline procedure (Oishi et al. 2008). No radial scaling information was available for our plots (Phillips et al. 1996). We therefore assumed that our sap flux measurements represented an average sap flux density through the entire conductive area. Sap flux measurements used in this study were collected as part of an on-going, large-scale experiment in which plot scaled sap flux data is compared with respect to eddy covariance measured latent heat flux. For 2011–2014, plot level sap flux comprised 76.3%, 93.3%, 86.4% and 82.7% of latent heat flux for growing season respectively. Conductive sapwood area (A_s) was approximated using species-specific allometric Eqs. 1 and 2 relating diameter at breast height (DBH) to sapwood area. These allometric relationships were developed for our site by Matheny et al. (2014b) and Bovard et al. (2005). Measurements of oak sapwood depth were verified by two independent

researchers along three axes of comparison: visually, using a tetrazolium chloride staining assay (see Bovard et al. 2005), and under a stereoscopic microscope. We assumed that A_s can be calculated at any location on a tree bole using the diameter at that location in place of DBH. Sap flow (g/s) was calculated by multiplying sap flux ($g \cdot m^{-2}_{sapwood} \cdot s^{-1}$) by A_s (cm^2). Eq. 1 shows red maple (Bovard et al. 2005), and Eq. 2 shows red oak (Matheny et al. 2014*b*).

$$A_s = 17.04 \text{DBH} - 110.66 \qquad (1)$$

$$A_s = 0.21 \text{DBH}^{2.1838} \qquad (2)$$

GS-3 sensor deployment

Six ruggedized soil moisture sensors (model GS-3; Decagon Devices, Pullman, Washington, USA) were installed in our two study trees. Sensors were installed at two locations in each tree: at the base of the trunk (0.5 m above the ground), and just below the first branching split (~5.5 m from the ground). Conductive tissue depth was estimated at each sensor location using the measured diameter at that location in place of DBH with Eqs. 1 and 2. Given the depth of the active xylem in the different species, the 5 cm long probes on the GS-3 sensors extended past the active xylem at both the top and bottom positions on the oak tree, but not the maple. Therefore, the probes in one pair of GS-3 sensors were cut to a length of 2 cm to ensure that they did not penetrate the oak heartwood. One full sized, 'long' sensor and one cut, 'short' sensor, were inserted at different circumferential locations at both the top and bottom of the oak. The long and short sensors were separated horizontally by ~10 cm. Holes were pre-drilled to a diameter just smaller than that of the sensor probes using a custom made template. Sensor probes were cleaned with rubbing alcohol and hammered into place using a dead-blow hammer. Once the sensors were fully inserted, silicon sealant was used to ensure that no stem flow could penetrate the sensor. Sap flux and GS-3 sensors were covered with reflective insulation to protect the sensors from inclement weather and external heating.

GS-3 sensor calibration

Prior to installation, long and short sensors were calibrated to the density of oak and maple wood. One large branch (10–12 cm diameter) from a separate tree of each species was harvested and segmented into 10–15 cm pieces (total $n = 33$). Segments were pre-drilled for sensor placement, and either soaked in water or dehydrated for varying lengths of time. After drying or soaking, segments were weighed, wrapped in plastic to prevent additional moisture loss, and measured using both a long and short sensor. Following measurement, segments were dehydrated for four weeks at 30°C. After desiccation, segments were reweighed and the volumetric water content (VWC) calculated for each segment. Calibration curves were fitted to the dielectric potential sensor output and the measured VWC for each species and each probe length. The resulting calibration equations for the volumetric water content ($m^3_{water}/m^{-3}_{wood}$) are

maple	$VWC = 0.0607E_b - 0.1584$
oak, long	$VWC = 0.4901\ln(E_b) - 0.6570$
oak, short	$VWC = 0.3334\ln(E_b) + 0.0426$

$$(3)$$

where E_b is the dielectric potential (unitless) reported by the GS-3 sensor. While the manufacturer does recommend calibrating the FDR sensors for materials of different density, they do not require temperature calibration for use in soil and are approved for temperatures ranging from −40° to 60°C, a range much larger than that experienced during the study period. We surmised that because the sensors do not require temperature calibration for use outdoors in soil that they would similarly not require temperature calibration for use outdoors in wood.

Calculation of storage and storage withdrawal

Dielectric potential was recorded every minute and averaged to half hourly time steps. Eq. 3 was used to convert dielectric potential to VWC and bole storage (kg) was calculated for each tree by integrating VWC over the conductive volume of the bole. Conductive volume of the bole was approximated based on the assumption that active xylem depth changed linearly between the 0.5 m and 5.5 m sensor heights. Conductive area was determined from linearly interpolated diameters every 10 cm along the bole segment

and integrated to conductive volume. ΔStorage (g/s) was calculated as the time derivative of storage at half-hourly increments. Storage withdrawal (kg) was calculated by subtracting the afternoon minimum storage from the peak morning storage for each day.

Soil water potential measurements

Soil moisture and temperature were recorded at four locations at depths of 5, 15, 30, and 60 cm, and at two locations at depths of 100, 200, and 300 cm (Hydra probe SDI-12; Stevens Water Monitoring Systems, Portland, Oregon, USA; He et al. 2013). Soil moisture values in each measurement depth were averaged (two to four measurements, depending on depth). 95% of fine root biomass within our site has been shown to lie within the top 80 cm of the soil column (He et al. 2013). However, because soil moisture at each depth was highly correlated with soil moisture at all other depths, we integrated soil moisture along the 3 m soil column. Soil moisture measurements were converted to soil water potential values (Ψ, MPa) using the Van Genuchten hydraulic parameterization (Van Genuchten 1980) with site specific parameters developed for our site by He et al. (2013) and (Matheny et al. 2014*b*).

Determination of ''wet'' and ''dry'' soil conditions

Days were categorized into "wet" and "dry" on the basis of daily minimum soil water potential. Values of soil water potential ranged from −0.06 to −1.5 MPa during the study period. We observed a strong discontinuity in the variation of water storage occurred when soil was drier than −0.2 MPa. Therefore, we consider days having a daily minimum $\Psi > -0.2$ MPa "wet," and those with $\Psi \leq -0.2$ MPa as "dry." All data processing and statistical analyses were conducted in Matlab (R2014a; MathWorks, Natick, Massachusetts, USA).

Results

Average daily dynamics of storage corresponded well with average daily dynamics of sap flux. Sap flux increased after dawn and peaked typically between 14:00 and 15:00, then declined in the evening (Fig. 1). Storage tended to peak shortly past dawn, between 06:00 and 08:00, with a sharp decline between 10:00 and 18:00, when sap flux was highest, then recharged in the early evening (Fig. 1). The maple tended to have narrower peaks in both sap flux and storage than the oak. Although the long probes in the oak did show a diurnal cycle, it was not as regular as the cycle measured by the shorter probes. Average daily storage withdrawal from the maple was 4.8 kg/day and from outer xylem of the oak (short probes) was 2.9 kg/day. Storage withdrawal as measured by the long probes in the oak tree averaged 1.1 kg/day. Maximum daily storage withdrawal during the study period was 13.4 kg/day for the maple, 11.15 kg/day as measured by the short oak probes, and 6.7 kg/day as measured by the long oak probes.

Extended time series analysis for the entire 6-week experimental period showed that volumetric water content as observed by the GS-3 and the derived stem water storage dynamics correspond with soil moisture and precipitation, as well as with sap flow (Fig. 2). The half hourly change of storage (ΔStorage) in both the oak and the maple spiked in response to increases in soil water content after rainfall (Fig. 2A, D, E), although these spikes tend to be larger in oaks than in maples. Partial sensor wetting due to stem flow may influence the magnitude of these spikes. Future applications using broad deployment of FDR sensors may be able to disambiguate this behavior. In response to drying soil conditions (e.g., DOY 205–224; Figs. 2 and 3), the oak and maple demonstrated different patterns of VWC and ΔStorage. The maple showed larger variation of the daily mean VWC levels than oak during the inter-storm dry-down period (DOY 205–224; Figs. 2B, C and 3A, B). The oak tended to have smaller diurnal changes in ΔStorage when soil moisture was moderate (DOY 205–212) and larger diurnal changes in ΔStorage when soil moisture was very low (DOY 215–224), while maple tended to have large diurnal variation in ΔStorage when soil moisture declined (DOY 210–215) and relatively no change in ΔStorage when soil moisture was very low (DOY 215–224; Figs. 2D, E and 3C, D). Similarly, when comparing a period when soil was relatively wet (DOY 225–257), to a period when soil was relatively dry (DOY 191–224) distinct differences between the oak and the maple in the patterns of VWC and ΔStorage emerged (Fig. 2B–E). The oak tended to
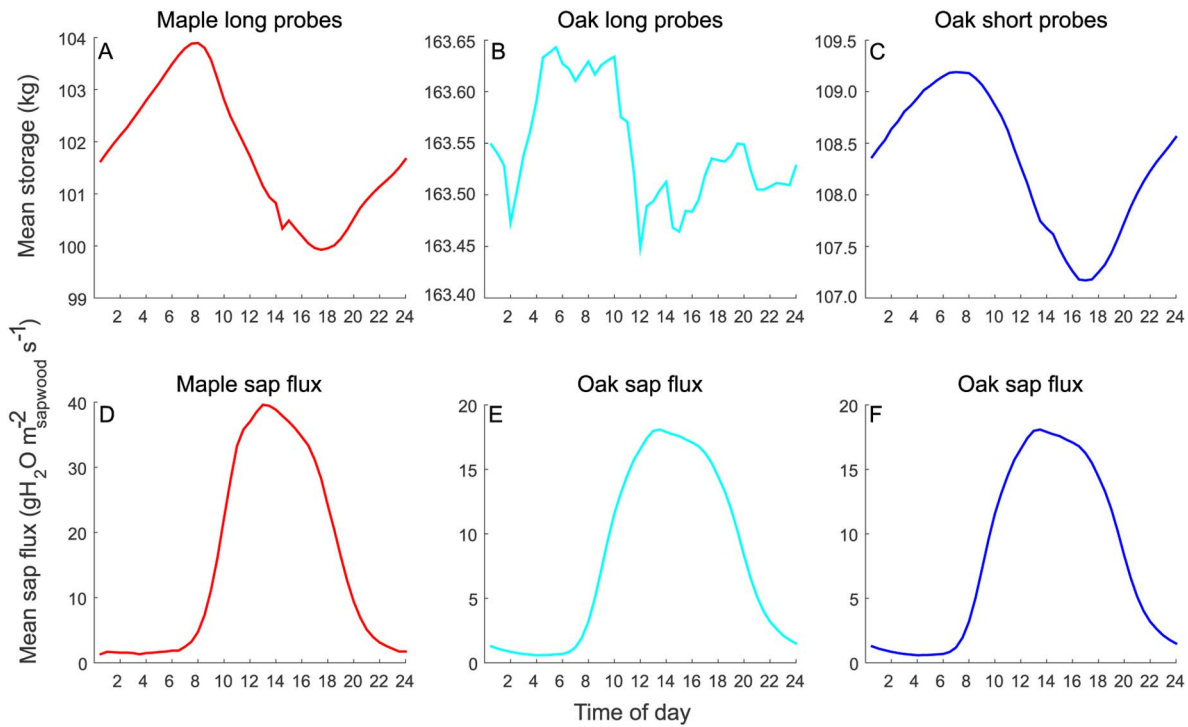
Fig. 1. Average diurnal cycles of sap flux (bottom panels) and storage (top panels) for maple (red), oak long probes (cyan), and oak short probes (blue). Diurnal patterns of water use between storage and sap flux were corroborative.
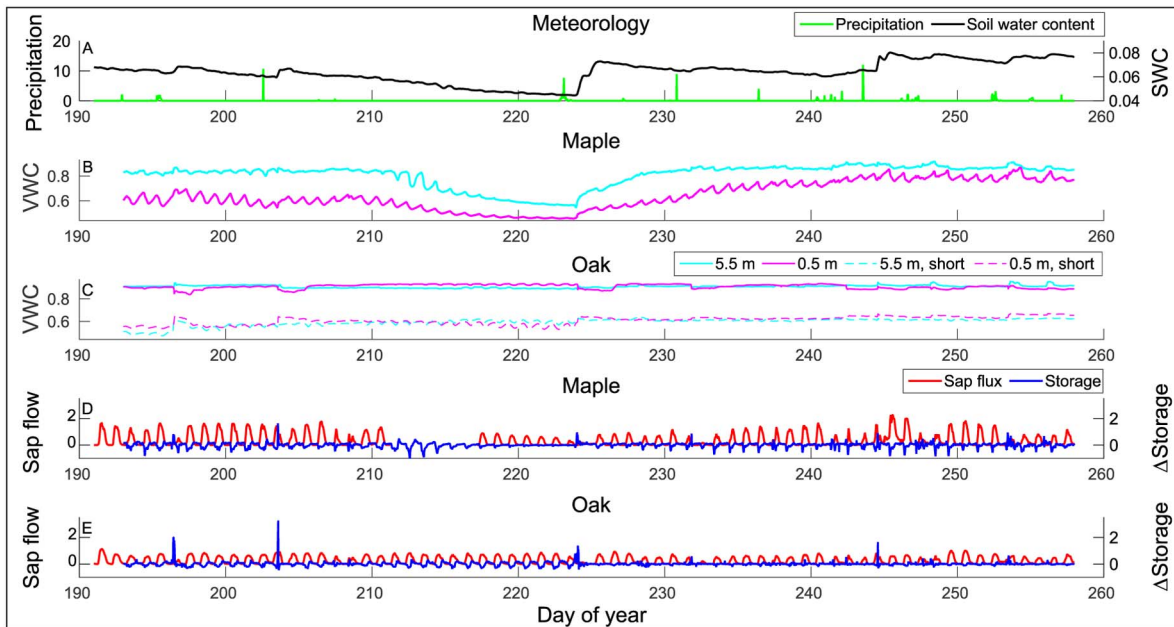

Fig. 2. Time series of precipitation (mm), soil water content (SWC; m^3/m^3) (A), volumetric wood water content (VWC; m^3/m^3) at the top and bottom locations in the maple (B) and oak (C), and sap flow (g/s) and ΔStorage (g/s) in the maple (D) and oak (E). Spikes in ΔStorage coincide with rapid increase in soil water content following precipitation events. Missing sap-flux data is indicative of temporary instrument failure.
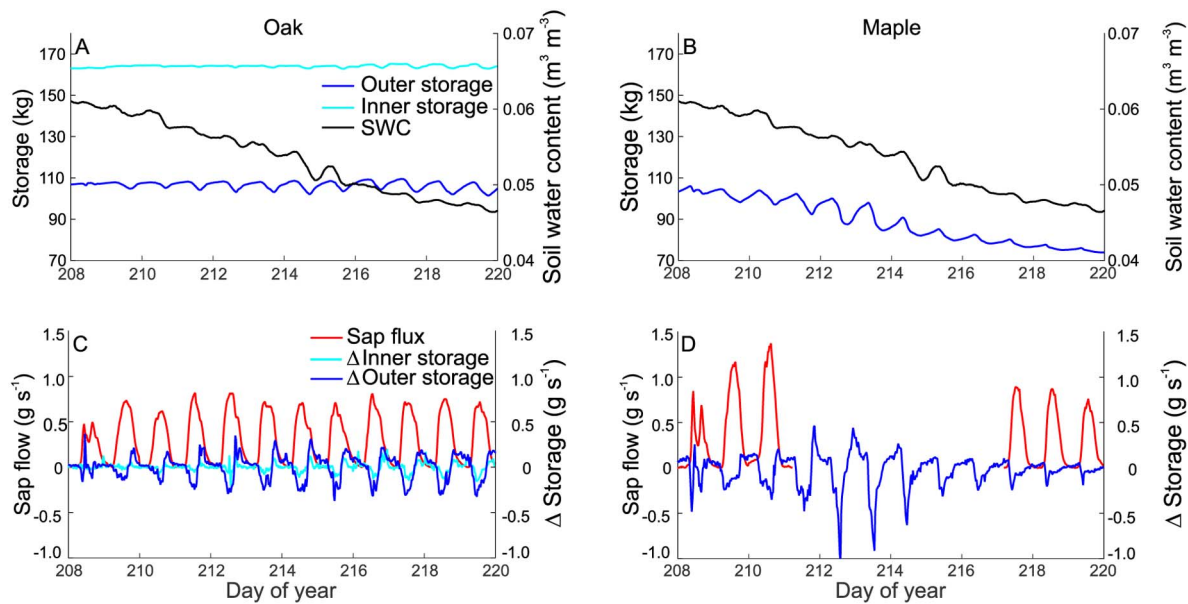
Fig. 3. During DOY 206–223, the site experienced extended soil drying. Storage and soil water content are presented for the oak (A) and the maple (B). Panels (C) and (D) show sap flow and ΔStorage for oak and maple, respectively, during the drying period. For the oak measurements "inner" refers to measurements made by sensors having full length probes, and "outer" refers to measurements made by sensors having cut probes.

have less fluctuation in ΔStorage when soil was wet compared to when soil was dry, whereas the maple tended to have higher daily variation in ΔStorage when comparing wet to dry periods.

Storage in the active xylem of the oak, as measured by the short probes, was lower and more responsive to depletion by sap flux than storage in the oak's entire xylem system as measured by the long probes (Fig. 3A). The longer probes in the oak consistently measured higher storage than the shorter probes, but were less responsive to depletion. Furthermore, the long probes' measurements do not display the typical spike in storage after precipitation events (data not shown).

Storage in the maple was strongly correlated with soil water potential during both wet and dry days (Fig. 4A). The maximal daily withdrawal by the maple was significantly correlated with soil water potential during dry days ($R^2 = 0.75$, $P = 0.003$), but not during wet days (Fig. 4B). Similarly, daily integrated sap flux from the maple was correlated with soil water potential only during dry days ($R^2 = 0.93$, $P = 0.0005$; Fig. 4C). For the oak tree, only mean daily storage within the outer xylem was correlated with soil

water potential during wet days, while storage in the entire xylem system, as measured by the long probe, did not show any significant relationships with soil moisture (Fig. 4D). Daily withdrawal from the oak was related to soil water potential only during dry days, and only from the entire xylem (Fig. 4E). It is interesting that this correlation is negative, indicating that this tree uses its internal storage most when soil water potential is highly negative. Sap flux in the oak was never significantly related to soil water potential (Fig. 4F).

Further analysis revealed that the maple's daily withdrawal was tightly correlated with mean daily storage levels only during dry days (Fig. 5A). On both wet and dry days, integrated sap flux from the maple was significantly correlated to daily withdrawal from storage ($R^2 = 0.89$ and $P = 0.0159$, $R^2 = 0.46$ and $P < 0.001$, respectively; Fig. 5B). Contrary to the behaviors observed in the maple tree, withdrawal from the oak's storage was significantly, negatively correlated to mean daily storage in the outer xylem on both wet and dry days, and in the interior on dry days (Fig. 5C). These negative relationships may indicate that in times of high storage, recharge flow is
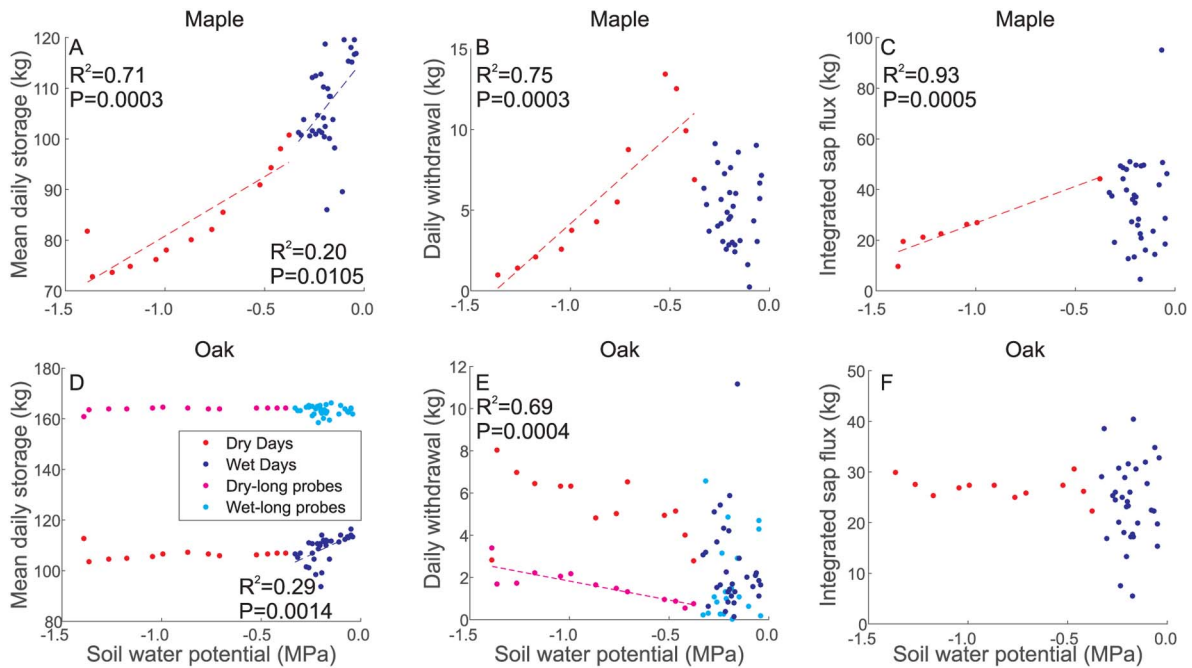
Fig. 4. Relationships between mean daily storage, daily withdrawal, and integrated daily sap flux, and soil water potential for dry days (red) and wet days (blue). Readings for oak long sensors are shown for wet days (cyan) and dry (magenta).
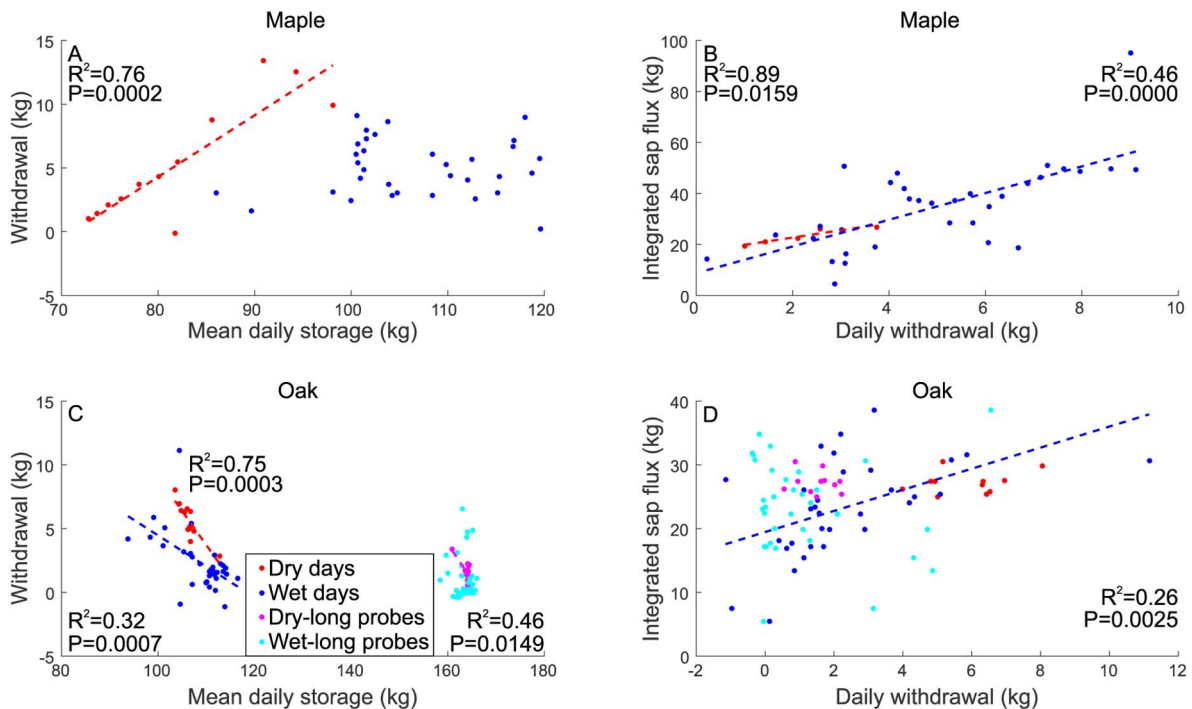

Fig. 5. Regression analyses of daily storage withdrawal with respect to mean daily storage (left), and integrated sap flux with respect to daily storage withdrawal (right). Data are categorized by soil water potential into wet (blue) and dry (red) conditions. Long sensors in oak are shown for dry (magenta) and wet (cyan) conditions.

large enough that ongoing transpiration does not deplete the storage reservoir. Total daily sap flux from the oak was correlated with daily withdrawal on wet days and only in the outer xylem layer (Fig. 5D).

Discussion

On the basis of how well the dynamics of storage, withdrawal, and ΔStorage corresponded with dynamics observed in soil water potential and sap flow, we found use of the GS-3 sensors to be a reliable, effective means for the measurement of wood water content and water use dynamics in trees. The diurnal cycles of sap flow and storage withdrawal reported here match well with one another, as well as with the diurnal storage dynamics reported by Kumagai et al. (2009). The only other study to use FDR probes for the measurement of wood water content, of which the present authors are aware, was a study of xylem embolism in three adult *Betula papyrifera* conducted by Hao et al. (2013) who also found the GS-3 probes to provide reasonable measurements of volumetric water content that followed trends in rainfall and summer heat. We did not attempt to perform a mass balance using storage and sap flux due to our lack of knowledge of water storage in the whole tree. It is well known that storage in roots, branches, and leaves contributes significantly to the volume of water available for transpiration (Scholz et al. 2011). Future research regarding the scaling of storage in the bottom portion of the trunk to the whole tree would permit this type of analysis.

Our results from the long and short probes used to measure VWC in the oak indicate that water storage within the outermost layer of heartwood may play a role in water use dynamics, particularly when soil moisture conditions are limiting (Figs. 4E and 5C). For example, it is known that the outer parenchyma of woody savanna species is hydraulically connected to xylem and contributes significantly to storage and transpiration (Scholz et al. 2008). Similarly, outer heartwood, of which vessels may only be partially filled, could resupply depleted xylem water in times of water scarcity. In future studies, the use of multiple probe lengths may be most useful to fully capture storage at all radial depths. The use of multiple probe lengths is common in sap flux studies to capture differing flow velocities with depth (e.g., Phillips et al. 1996, Schäfer et al. 2000, Renninger et al. 2013, Shinohara et al. 2013).

Our analyses of maple and oak stem water storage reveal water use consistent with their wood densities and respective isohydric and anisohydric hydraulic strategies. Red maple, a diffuse porous and relatively isohydric species, showed strong positive relationships between storage and soil water potential demonstrating the governance of soil conditions on the ability to replenish stored water. This result is corroborated by the findings of Thomsen et al. (2013) who conducted a study of leaf water potentials in oak and maple trees in our study site. Predawn leaf water potentials for red maples were shown to be strongly correlated with soil water potential, whereas predawn leaf water potentials in oak were not significantly related to soil water potential within the top 3m of the soil column. This is further upheld by the significant relationships between withdrawal and soil water potential and sap flux and soil water potential, as well as between withdrawal and storage during periods of limiting soil water potential. A strong reliance of maple's transpiration on water withdrawn from trunk storage is revealed by the relationships between sap flux and storage withdrawal. This relationship was stronger during periods when soil water potential is limiting than in periods when it was not, indicating that storage withdrawal is particularly critical to maple's transpiration during times of water limitations. In a recent study of storage dynamics in temperate broad leaf species, Kocher et al. (2013) similarly found that diffuse porous species, including sycamore maple (*A. pseudoplatanus* L.), tended to be more storage reliant than ring porous species. The generally flat relationship between withdrawal and mean daily storage for the maple when soil water potential was not limiting is characteristic of an isohydric species; even in cases when stored water is available, withdrawal appears to be moderated. A strong reliance on stored water in two additional isohydric species (Japanese cedar (*Cryptomeria japonica*) and Japanese cypress (*Chamaecyparis obtusa*)) was also shown by Kumagai et al. (2009).

Red oak, a ring porous and relatively aniso-hydric species, presented an opposing hydraulic strategy. Red oaks maintained negative relationships between withdraw and soil water potential as well as between withdrawal and storage. We interpreted these negative relationships to suggest that withdrawal in oaks was more relevant in times of water scarcity, when soil water potential and storage were low. When storage was high, flows through the large xylem vessels characteristic of ring porous xylem may have been sufficient such that withdrawal could have been minimized by rapid refilling. The high withdrawal during periods of low storage and highly negative soil water potential coincides with behaviors typical of anisohydric species, which continue to transpire in spite of low leaf water potential. Withdrawal and sap flux for the oak were related in the outermost layer of xylem. Although storage in the outermost xylem was positively related to soil water potential during wet periods, during dry periods and as measured by the full length probes over the entire study period, mean daily storage levels tended to be constant. Similarly, sap flux from the oak was never correlated with soil water potential. Thomsen et al. (2013) also found that predawn leaf water potential in red oak was independent of soil water potential in our site. We hypothesize that the lack of relationship between soil moisture and sap flux and stem water storage may be due to a deep rooting strategy employed by red oaks at our site. Furthermore, in Wullschleger's (1996) study of storage in ring and diffuse porous species, the authors found the ring porous species, white oak (*Q. abla* L.) and chestnut oak (*Q. prinus* L.), to be less sensitive to low soil moisture from May through August during a particularly dry year compared to the diffuse porous species studied, red maple (*A. rubrum* L.) and black gum (*Nyssa sylvatica* Marsh.). The findings of Kocher et al. (2013) regarding the storage dynamics of the ring porous, anisohydric species European ash (*Fraxinus excelsior* L.) also agree with our results. In their study, European ash did not demonstrate a time lag between sap flux in root and branches, indicating a low relevance for storage during drying periods for this species.

Conclusion

Our results confirm the functionality of GS-3 probes for the measurement of wood water content and determination of trunk water storage. Measurements of wood water content and stem storage in the oak and maple were consistent with the expected behaviors for each species' hydraulic strategy and functional type as reported in the literature. For both anisohydric and isohydric species, trunk storage appeared to provide a buffer to water demands during transpiration. In red maple, storage and withdraw provided a reservoir that buffered the diurnal water requirements of transpiration on both wet and dry days. In contrast, the red oak used stored water primarily during times when moisture was limiting, and exhibited a strategy indicating the use of stored water to supplement the transpiration stream in order to reduce xylem tension during periods that would otherwise leave it vulnerable to cavitation. Although our study was limited to two trees of two hardwood species and designed principally as a test case of this new measurement methodology, these differences in storage reliance and water use dynamics are consistent with the observed behaviors of these species in this forest (Thomsen et al. 2013, Matheny et al. 2014*b*) and with the behaviors characteristic of their hydraulic strategy and wood density (Wullschleger et al. 1996, Pratt et al. 2007, Kumagai et al. 2009, Scholz et al. 2011, Kocher et al. 2013).

Internal water storage plays a key role in maintaining tree hydraulic functionality throughout the course of a day, and during periods of declining soil water. Improving technology to measure tree water storage levels complements improved modeling approaches that can resolve tree water storage and incorporate its role in the modulation of stomatal conductance (Bohrer et al. 2005, Bittner et al. 2012*a*, Bittner et al. 2012*b*). When combined, direct measurements and modeling improve our ability to accurately predict transpiration and photosynthesis in forest environments. The relationships between these components of the soil-plant-atmosphere continuum and how they vary between species, particularly those frequently grouped together into the same plant functional type, are increasingly important to recognize and quantify as we progress toward

more detailed and accurate simulation of plant hydrodynamics across large spatiotemporal scales.

Acknowledgments

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Supplemental Material

Data Accessibility

All eddy covariance and meteorological data used for this paper are publicly available through the Ameriflux website (Ameriflux.ornl.gov) under site ID US-UMB. The sap flux and storage data used for this paper are available by contacting the corresponding author.