

Water Resources Research

RESEARCH ARTICLE

10.1029/2022WR032344

Key Points:

- Both the onset of stem rehydration and transpiration in evergreen species overlap the spring snowmelt, while only rehydration for deciduous
- Trees used snowmelt water during stem rehydration and the onset of transpiration. Evergreen snowmelt water use was detected earlier
- Tree water transit time explained the time lag between the xylem water shift (at canopy-level) to snowmelt water signatures from soil water

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

M. F. Nehemy,
mnehem@trentu.ca

Citation:

Nehemy, M. F., Maillet, J., Perron, N., Pappas, C., Sonnentag, O., Baltzer, J. L., et al. (2022). Snowmelt water use at transpiration onset: Phenology, isotope tracing, and tree water transit time. *Water Resources Research*, 58, e2022WR032344. <https://doi.org/10.1029/2022WR032344>

Received 9 MAR 2022

Accepted 7 AUG 2022

Author Contributions:

Conceptualization: Magali F. Nehemy, Colin P. Laroque, Jeffrey J. McDonnell
Data curation: Magali F. Nehemy, Jason Maillet, Nia Perron
Formal analysis: Magali F. Nehemy
Funding acquisition: Oliver Sonnentag, Jennifer L. Baltzer, Colin P. Laroque, Jeffrey J. McDonnell
Investigation: Magali F. Nehemy, Jason Maillet, Nia Perron, Christoforos Pappas, Colin P. Laroque, Jeffrey J. McDonnell
Methodology: Magali F. Nehemy, Jason Maillet, Nia Perron, Christoforos Pappas, Colin P. Laroque, Jeffrey J. McDonnell
Project Administration: Magali F. Nehemy, Colin P. Laroque, Jeffrey J. McDonnell

Snowmelt Water Use at Transpiration Onset: Phenology, Isotope Tracing, and Tree Water Transit Time

Magali F. Nehemy^{1,2,3} , Jason Maillet^{2,4}, Nia Perron⁵ , Christoforos Pappas^{5,6,7,8} , Oliver Sonnentag⁵, Jennifer L. Baltzer⁹ , Colin P. Laroque² , and Jeffrey J. McDonnell^{1,10} 

¹School of Environment and Sustainability, Global Institute for Water Security, University of Saskatchewan, Peterborough, SK, Canada, ²Department of Soil Science, Mistik Askiwin Dendrochronology Laboratory (MAD Lab), University of Saskatchewan, Peterborough, SK, Canada, ³Trent School of the Environment, Trent University, Peterborough, SK, Canada, ⁴Department of Geography, The University of Winnipeg, Winnipeg, MB, Canada, ⁵Département De Géographie, Université de Montréal, Montréal, QC, Canada, ⁶Centre d'étude de la forêt, Université du Québec à Montréal, Montréal, QC, Canada, ⁷Département Science et Technologie, Université TÉLUQ, Montréal, QC, Canada, ⁸Department of Civil Engineering, University of Patras, Rio Patras, Greece, ⁹Department of Biology, Wilfrid Laurier University, Waterloo, ON, Canada, ¹⁰School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, UK

Abstract Studies of tree water source partitioning have primarily focused on the growing season. However, little is yet known about the source of transpiration before, during, and after snowmelt when trees rehydrate and recommence transpiration in the spring. This study investigates tree water use during spring snowmelt following tree's winter stem shrinkage. We document the source of transpiration of three boreal forest tree species—*Pinus banksiana*, *Picea mariana*, and *Larix laricina*—by combining observations of weekly isotopic signatures ($\delta^{18}\text{O}$ and $\delta^2\text{H}$) of xylem, soil water, rainfall and snowmelt with measurements of soil moisture dynamics, snow depth and high-resolution temporal measurements of stem radius changes and sap flow. Our data shows that the onset of stem rehydration and transpiration overlaps with snowmelt for evergreens. During rehydration and transpiration onset, xylem water at the canopy reflected a constant pre-melt isotopic signature likely showing late fall conditions. As snowmelt infiltrates the soil and recharges the soil matrix, soil water shows a rapid isotopic shift to depleted-snowmelt water values. While there was an overlap between snowmelt and transpiration timing, xylem and soil water isotopic values did not overlap during transpiration onset. Our data showed 1–2-week delay in the shift in xylem water from pre-melt to clear snowmelt-depleted water signatures in evergreen species. This delay appears to be controlled by tree water transit time that was in the order of 9–18 days. Our study shows that snowmelt is a key source for stem rehydration and transpiration in the boreal forest during spring onset.

Plain Language Summary Are trees thirsty for snowmelt when they wake up in the spring? Most studies have investigated the source of transpiration in the summer. Here we investigate the water source for transpiration prior, during and after snowmelt in the boreal forest. Our data shows that when the snow melts and recharges soil water storage, trees also refill internal water stores and rehydrate. Evergreen species start to transpire during snowmelt. While there is a clear overlap between snowmelt and when trees begin to transpire, the tracer data does not show the same. The tracer signature in the canopy did not reflect the snowmelt soil-water signature until one or 2 weeks after the onset of transpiration. Our transpiration age estimates suggest that this mismatch in tracer signature between trees and soil results from the time it takes for water to travel inside the trees, from roots to canopy. We conclude that trees use snowmelt water to rehydrate and start transpiring in the spring. Our findings shed light on ecohydrological investigations and highlight the importance of snowmelt water input to boreal forest spring onset and carbon uptake.

1. Introduction

Tree water uptake for transpiration is the largest terrestrial water flux (Schlesinger & Jasechko, 2014; Wei et al., 2017) and is increasing as the world warms (Pascolini-Campbell et al., 2021). Thus, investigating and identifying the water sources for tree transpiration and how those sources vary in time and space is fundamental to our understanding on the impacts of vegetation on the hydrological cycle. Whilst many studies in the past decade have revealed important insights into tree water use within the growing season (e.g., Brooks et al., 2010; Carrière et al., 2020; Geris et al., 2015; Hahm et al., 2020; Hervé-Fernández et al., 2016), we still know very little

Supervision: Oliver Sonnentag, Jennifer L. Baltzer, Colin P. Laroque, Jeffrey J. McDonnell

Visualization: Magali F. Nehemy

Writing – original draft: Magali F. Nehemy

Writing – review & editing: Magali F. Nehemy, Jason Maillet, Nia Perron, Christoforos Pappas, Oliver Sonnentag, Jennifer L. Baltzer, Colin P. Laroque, Jeffrey J. McDonnell

about patterns of tree water use in ecosystems that experience winter dormancy (Snelgrove et al., 2020; Tetzlaff et al., 2021). Furthermore, identifying what water sources are used during post-winter rehydration and during the onset of growing season transpiration is crucial for understanding the connectivity between sources of transpiration, streamflow and groundwater recharge. Beyond hydrology, forest productivity in northern latitudes is largely explained by spring onset conditions (Pulliainen et al., 2017; Richardson et al., 2013; Rossi et al., 2011). Thus, identifying tree water availability and uptake during spring onset is key to establishing links between water sources and photosynthetic carbon uptake in cold regions. This knowledge is especially important under climate change where the onset of spring snowmelt is trending earlier in many regions (Chen et al., 2015), with reduced snow water stores (Lawrence & Slater, 2010), shortened winters and longer growing seasons (Barichivich et al., 2013; Linderholm, 2006).

One promising tool for quantifying tree water sources are stable isotopes of oxygen and hydrogen (^{18}O and ^2H , respectively) as tracers. In the past decade, these naturally-occurring tracers have revealed that transpiration seems to be supplied by resident soil water pools tightly bound to the soil matrix and seasonally lagged from precipitation inputs (Brooks et al., 2010). Many studies have shown that water that sustains transpiration throughout the growing season appears to be recharged during the previous wet season (Allen et al., 2019; Brinkmann et al., 2018; Xu et al., 2019). Tree water source investigations have also shown that the xylem water isotopic composition tends to be more similar to soil matrix water (i.e., less mobile), and distinct from the more mobile soil water that travel via preferential flow paths and feeds the streams (Brooks et al., 2010; Evaristo et al., 2015; Goldsmith et al., 2012; Knighton et al., 2019). This apparent lack of hydrologic connectivity between sources of transpiration and streams—ecohydrological separation (Brooks et al., 2010) — means that transpiration may be supplied by water that is stored in small pores within the soil matrix that are *disconnected*, or temporally *disconnected* (Hervé-Fernández et al., 2016; Zhao et al., 2018), from recent precipitation inputs that bypass the soil matrix and recharge groundwater and later becomes streamflow. The mechanisms behind observed ecohydrological separation are still debated (Barbeta et al., 2019; Chen et al., 2020; Sprenger & Allen, 2020) and new research is advancing model-based understanding (Finkenbiner et al., 2021). Clearly, identifying tree water sources is key to understanding the coupling of precipitation inputs and transpiration (Miguez-Macho & Fan, 2021), and how transpiration affects streamflow processes and depletes subsurface water storage (McDonnell et al., 2018).

Subsurface water storages are mainly recharged during spring snowmelt in northern latitudes (Harpold et al., 2015; Jasechko et al., 2014). Trees, too, seem to rehydrate and recharge internal water storages (i.e., inner bark and sapwood) in the spring following snowmelt, storing large volumes of water (Young-Robertson et al., 2016). Studies in northern forests have also shown that the onset of transpiration can occur when snow still covers the ground (Chan & Bowling, 2017; Turcotte et al., 2009) and that freezing soil temperatures reduce, but not eliminate, transpiration and photosynthetic activity (Bergh & Linder, 1999; Sevanto et al., 2006). The question thus becomes: Do trees wake up thirsty and use this season's snowmelt water, or do they rely on pre-melt soil water and groundwater for their rehydration and early onset of transpiration? How can we better understand tree water use for ecosystems coming out of winter dormancy?

Understanding the timing of stem rehydration and the onset of transpiration is critical because of its role in determining ecosystem carbon and water fluxes (Richardson et al., 2013). While both deciduous and evergreen species experience the same environmental conditions in a plot or foreststand, these functional groups show distinct timing in their transpiration phenological phases (Pierrat et al., 2021). Deciduous species drop their leaves in the fall, consequently, the production of leaves is required before transpiration can resume in the following season. In contrast, evergreen taxa retain their needles but undergo biochemical changes to downregulate transpiration and photosynthetic activity (Adams III et al., 2002; Oh et al., 2013; Oquist & Huner, 2003). These seasonal life history differences have the potential to alter the timing of transpiration initiation in the spring. As such, information about dynamic spring onset by the different taxa or functional groups is important. Canopy “greenness” indices, such as the green chromatic coordinate (G_{cc}), measured using phenocams have been successfully applied to identify the timing of phenological transition phases of leaf-level physiological changes associated with photosynthetic capacity (Richardson, 2019; Seyednasrollah et al., 2021). Stem radius change monitored with high-resolution dendrometers can provide information on the timing of specific phenological transition phases from dormant (i.e., freeze-thaw stem cycles) to actively transpiring trees (i.e., transpiration driven stem cycles), thus indicating periods of stem rehydration and onset of transpiration (Pierrat et al., 2021; Sevanto et al., 2006; Turcotte et al., 2009; Zweifel & Hasler, 2001). Thus, combining phenological measurements along with stable

isotope tracing is key to understanding mechanisms that drive tree water use in ecosystems that experience winter dormancy.

Here we use a cold region environment to test the ecohydrological separation hypothesis during spring onset. We question how connected is transpiration onset to incoming mobile snowmelt relative to pre-melt matrix water? We combine measurements of the phenological transition from winter dormancy to the onset of transpiration using tree hydraulic measurements and canopy greenness index with isotope tracing during the largest hydrological event of the year in northern ecosystems—snowmelt—to understand the connectivity between source water of transpiration and streams. We sample tree water and available source waters (i.e., soil, precipitation, snowmelt) for isotopic analysis ($\delta^{18}\text{O}$ and $\delta^2\text{H}$) on a weekly basis before, during and after snowmelt in two boreal forest stands in central Saskatchewan, Canada. We couple isotopic sampling with tree hydraulics monitoring using sap flow sensors, high-frequency circumference dendrometers and G_{cc} to monitor the phenological transition from winter dormancy to the onset of transpiration at both sites. We then use our combined approaches to address the specific questions: (a) When do evergreen and deciduous conifers initiate water uptake in relation to snowmelt? (b) What is the source of transpiration during spring onset for both evergreen and deciduous trees and how does it evolve in the first weeks? (c) Do we observe an ecohydrological separation between trees and streams during the snowmelt-transpiration period?

2. Material and Methods

2.1. Site Description

We conducted our study in two sites that are part of the long-term Boreal Ecosystem Research and Monitoring Sites (BERMS) located in the Boreal Plains ecozone in Saskatchewan, Canada (Figure S1 in Supporting Information S1). The sites are the Old Jack Pine (OJP; 53.92°N, 104.69°W, elevation 579.3 m) and the Old Black Spruce (OBS; 53.98°N, 105.12°W, elevation 628 m). The canopy at OJP is dominated by jack pine (*Pinus banksiana*) (Figure S2 in Supporting Information S1), while the canopy at OBS is composed mainly of black spruce (*Picea mariana*) with some sparse larch (*Larix laricina*) (Figure S3 in Supporting Information S1). The soils at OJP are classified as well- or rapidly-drained fine sandy soils with properties of the orthic eutric Brunisolic order (Barr et al., 2012; Kalyn & Van Rees, 2006). The water table depth is located between 5 and 8 m below the ground surface. The soils at OBS have properties of the gleyed eluviated eutric Brunisolic order, overlain by approximately 10–20 cm of peat. The soil at OBS are classified as imperfect to poor drainage sandy loam to loam till soils (Kalyn & Van Rees, 2006). The water table depth varies between 0 and 1 m throughout the year (Barr et al., 2012). The region's climate is classified as continental humid (Dfb; Köppen climate classification) with short warm summers and long, cold winters. The region's mean annual air temperature (1989–2010) is 1.4°C and the mean annual precipitation is 423 mm (Environment and Climate Change Canada meteorological station at Prince Albert; 53.22°N, 105.67°W; https://climate.weather.gc.ca/climate_normals/). Snowfall represents 30% of the total precipitation (Barr et al., 2012).

2.2. Meteorological and Hydrometric Recording at BERMS

Both BERMS sites log air temperature (HMP45C, Vaisala Inc., Oy, Finland) above the canopy level (OBS 25 m; OJP 29 m). Rain gauges are in small forest clearings and precipitation is recorded using an accumulating gauge (Geonor model T-200B all weather weighting precipitation gauge with an Alter shield, GEONOR, Inc., Augusta, NJ, USA). OJP and OBS monitor soil volumetric water content (VWC) with water content reflectometers (CS615, Campbell Scientific, Logan, UT, USA) at two locations per depth. Soil volumetric water content is recorded at 15, 30, 60, 90, 120, and 150 cm depths at OJP and 2, 7.5, 22, 45, and 60 cm depths at OBS. Soil temperature measurements were taken at 2, 5, 10, 20, 50, and 100 cm depths using Type-T (copper-constant) thermocouples at two locations per depth and averaged together. All environmental data is recorded at 30-min time resolution. We downloaded all data from the Wiski web server containing the BERMS database using the R package WISKIr (Shook, 2015).

Continuous snow depth is monitored at OJP and OBS using an ultrasonic snow depth gauge (UDG01, Campbell Scientific, Logan, UT, USA) situated within the forest canopy. Additionally, snow surveys are conducted at least once a month between October and April at both sites. At OJP, a networked digital camera (P1357, Axis Communications, Lund, Sweden) is mounted to the tower that allows for visual canopy and snow ground cover

monitoring through repeat photography. This study combined snow depth, photographic visual ground cover information, site visits, and surface soil temperature (i.e., the snowpack insulates the soil near the surface resulting in near-constant soil temperatures until snow melt, when surface soil temperature raise above zero and shows variability after melt (Zhang, 2005)) to determine the first snow free day.

2.3. Stable Isotope Dynamics

We sampled the isotopic values of water from xylem ($n = 280$), soil ($n = 556$), groundwater ($n = 20$) and the stream ($n = 60$) weekly between March and May 2018. We collected snowmelt water ($n = 2$; sub-samples = 6) in the last week of April. We collected precipitation from November of 2017 to October of 2018 at both sites ($n = 420$). We used three randomly located permanent plots (radius = 25 m) at OJP and OBS for sample collection. We used the plots to understand the spatial variability in soil and tree water isotopic composition within each sampling campaign. We randomly sampled trees within the same plot.

2.3.1. Stable Isotope Sampling: Xylem, Soil, Precipitation, Snowmelt, and Stream

We sampled xylem water by collecting suberized branches at canopy height (Figure S4 in Supporting Information S1) (approximate diameter of 2–4 cm). Each week we sampled 15 jack pine trees (five per plot), 15 black spruce trees (five per plot), and only one larch tree because of the low stem density. We immediately processed branches in the field. We did this by rapidly removing all bark from the branch, storing xylem samples in glass vials, and sealing the vial with parafilm. Next, we sampled bulk soil within the same plot (Figure S5 in Supporting Information S1). We paired xylem and soil samples by sampling all trees and the soil within the closest proximity possible. We sampled bulk soil by gently removing the lichen and moss from the soil surface and collecting samples using a soil auger. We sampled soil every 20 cm from 20 to 200 cm depths at OJP and at 10 cm intervals from 10 to 100 cm at OBS. This difference reflects each species' characteristic root depth distribution and water table depth at OBS. Black spruce and larch trees are described as shallow-rooted species (<60 cm) that invest in near-surface lateral roots (Liefers & Rothwell, 1987; Strong & Roi, 1983). Jack pine trees in eutric Brunisolic soils show <2 m depth root systems, most commonly not extending beyond depths of around 1.3 m (Strong & Roi, 1983). The Supporting Information S1 provides a more detailed description of xylem and soil sampling (Sections 2.1 and 2.2 in Supporting Information S1).

We collected total weekly snowfall using an open container (diameter = 25 cm) placed in the center of each sampling plot. We sampled snowfall on the morning of each weekly sampling campaign. Later in the spring, we switched to rainfall collectors. We installed rainfall collectors in an open clearing at approximately 1 m above the ground at each site. We also placed rainfall collectors inside each plot to collect throughfall. We sampled rainfall and throughfall weekly. Prior to the beginning of the 2017 snow season, we installed small snowmelt lysimeters at both sites inside one of the plots, underneath the canopy, following the method used by Coles and McDonnell (2018). After the last week of snowmelt in the spring, we retrieved the collected bulk snowmelt water. We also collected grab samples of stream water at locations on White Gull Creek draining the catchment area of both OJP and OBS.

All samples were transported to the Hillslope Hydrology Lab, University of Saskatchewan and stored in a fridge at approximately 4°C until water extractions and further isotopic measurements were completed. Because of the distance between site locations and the duration of each extensive field sampling, we were not able to sample both sites within the same day. However, we sampled both sites within a day of each other and on one occasion, within 3 days.

2.3.2. Isotope Analysis

Snowfall, rainfall, snowmelt and stream water samples were analyzed for isotope ratios using a liquid water off axis integrated-cavity output spectroscopy analyzer (IWA-45EP OA-ICOS; Los Gatos Research Inc., San Jose, CA, USA). Laboratory repeatability was 0.2 and 1.0 ‰ $\delta^{18}\text{O}$ and $\delta^2\text{H}$, respectively.

We extracted xylem and soil water using a cryogenic vacuum distillation method following Koeniger et al. (2011) (Figure S6 and Section S3 in Supporting Information S1). All water samples were filtered using a 45 μm nylon disk filter and stored in solid capped 2 ml glass vials until isotopic analysis. The extracted soil water was also analyzed using an IWA-45EP OA-ICOS. Xylem water isotope analyses were carried out at the National Hydrology Research Centre Stable Isotope Laboratory using an Isoprime isotope ratio mass spectrometer (IRMS)

(Elementar UK Ltd, Cheadle Hulme, UK). Hydrogen isotope values were measured by on-line reduction of the water sample to hydrogen by reaction with elemental chromium (Morrison et al., 2001). The oxygen isotopic values were determined using the CO₂-water equilibration method (Epstein & Mayeda, 1953). The IRMS laboratory precision was ± 0.12 ‰ and ± 0.81 ‰ $\delta^{18}\text{O}$ and $\delta^2\text{H}$, respectively.

2.4. Supporting Tree Water Source Investigation During Spring Onset: Tree Physiological and Phenological Monitoring

2.4.1. Sap Flow Measurements and Tree Water Transit Time

We installed Granier-type thermal dissipation sensors to measure sap flow density (Granier, 1987) of jack pine ($n = 30$), black spruce ($n = 24$) and larch ($n = 10$). We installed sensors at OBS and OJP in May 2016 and May 2018, respectively. The sensors were self-manufactured following Pappas et al. (2018) and previously described in detail elsewhere (Matheny et al., 2014). Briefly, each sensor comprised of two hollow needles of 20 mm in length, containing type T thermocouples. We installed sensors in the outermost 20 mm of sapwood of each tree on the north-facing aspect. The lower needle was installed 100 mm vertically below the upper heated needle. We recorded each monitored tree's height and diameter at breast height (DBH). A data logger (CR1000; Campbell Scientific, Logan, UT, USA) recorded sap flow data at 1-min resolution. We further measured the sapwood depth of trees of different diameters at both sites (see Section 3 in Supporting Information S1 for additional details). This measurement allowed us to identify individuals where the probe (=20 mm) is inserted in non-conducting wood, which can underestimate sap flux measurements if not corrected (Clearwater et al., 1999; Peters et al., 2018).

We processed sap flow data using the TREX R package (Tree sap flow Extractor; R Core Team, 2019) (Peters et al., 2021). Small data gaps due to power loss at the end of May at the OJP site remained unfilled. Following the processing workflow implemented in TREX, we converted the raw measurements to sap flux density ($\text{cm}^3 \text{cm}^{-2} \text{sapwood}^{-1} \text{h}^{-1}$) (Granier, 1987). Briefly, the sap flux density is calculated using the temperature difference between a heated and an unheated probe relative to the maximum temperature difference during zero flow conditions (ΔT_{max}). Because of the lack of species- and site-specific calibration, we used calibration coefficients from the literature as implemented in TREX, in combination with a best-fit assessment (Peters et al., 2021). We used the “genus” level calibration coefficients for black spruce and larch (“Picea” and “Larix,” respectively), and “wood” level calibration coefficients for jack pine (“Coniferous”) when calculating sap flux densities (using function: `tdm_cal.sfd`). Next, we converted sap flux density to sap velocity (m d^{-1}) and tree water travel time (d) (Meinzer et al., 2006). We calculated the latter by integrating sap flux density to daily values per individual tree and dividing the specific height (m; water travel distance) by the sap flux density, allowing us to compute the standard error per species. For sap velocity (m d^{-1}) and tree sap travel time (d) calculations we did not use trees that required large sapwood corrections (DBH <9 cm) to reduce uncertainties in these estimates. We also excluded trees that showed signs of wounding effect (e.g., Figure S7 in Supporting Information S1). We used the tree water transit time as an estimation of the time it takes for a water parcel to travel from the roots (entry point) to the canopy (exit point).

2.4.2. Stem Radius Measurements

We monitored changes in stem diameter using automatic circumference dendrometers (DC2 and DC3, Ecomatik, Dachau, Germany) in black spruce and larch ($n = 13$; each) and jack pine trees ($n = 18$) at breast height for 5 years (2016–2020). We used HOBO data loggers (HOBO UX120-006M; ONSET, Bourne, MA, USA) to record the data at 30-min resolution. Each data logger recorded data for up to four dendrometers from the same species. We converted dendrometer measurements to μm following the manufacturer's specification. We further processed the data to identify periods that indicated sensor malfunctioning due to battery failure and/or wildlife interference. We omitted short data periods that indicated malfunctioning or sensor failure with no attempt at gap filling.

We isolated tree hydraulic signals by using the empirical stem diurnal cycle approach of King et al. (2013). We used the stem diurnal cycle and hydraulic signal to determine the phenological timing of stem rehydration and the onset of transpiration in the spring described previously in Pierrat et al. (2021). Briefly, we identified stem rehydration by the continuous increase in stem radius after the detected end of freeze-thaw stem diurnal cycle (Améglio et al., 2001; Sevanto et al., 2006; Zweifel & Häsler, 2000). Stem rehydration is followed by the characteristic transpiration-induced stem diurnal cycle indicating the onset of transpiration in the spring. The transpiration induced-diurnal cycle reflects the balance between water loss from transpiration and water uptake

from soil (Kozłowski & Winget, 1964; Steppe et al., 2006). The transpiration induced-diurnal cycle shows a maximum amplitude in the morning and a minimum in the afternoon, opposite to the freeze-thaw cycle (Améglio et al., 2001; Servanto et al., 2006; Zweifel & Häsler, 2000).

Beyond our phenological assessment of transpiration using stem diurnal cycle information, we also report the sub-hourly stem radius in relation to its maximum radius recorded in the previous growing season (Zweifel et al., 2016). This assessment allows direct observations of stem rehydration and when trees completely refill tree water storage (Zweifel et al., 2016). We did this by subtracting the maximum stem radius recorded in the previous growing season (i.e., zero-growth line) from the 30-min measurement of each specific tree. The spring stem rehydration ceases when trees surpass the zero-growth line and recover tree water status (i.e., storages are fully hydrated). During the monitoring period, we observed synchronous and homogeneous variations in stem size between individuals of the same species. We thus report the species stem radius average per site and sub-hourly standard deviations.

2.4.3. Canopy Greenness Index Measurements

We used the G_{cc} to track the onset of canopy level photosynthetic activity and leaf out period in the spring. For evergreen species (i.e., black spruce), greenness raising (i.e., greening up) indicates changes in leaf pigmentation and photosynthetic capacity. For deciduous conifers the green-up is direct evidence of leaf emergence (Richardson, 2019). At OBS, a “phenocam” is mounted to a tower at canopy height level contributing to the PhenoCam Network. The phenocam takes time lapse images of the canopy at 30-min intervals (see <https://phenocam.sr.unh.edu/webcam/>; Richardson et al., 2018, 2019). The PhenoCam Network processes the images providing the G_{cc} data for both black spruce and larch. G_{cc} time series analysis offers the greenness rising transition dates based on predefined thresholds (10%, 25%, and 50%) of the seasonal G_{cc} amplitude per species (Richardson et al., 2018; Seyednasrollah et al., 2019).

2.5. Data Analysis and Visualization

To identify if the onset of rehydration and transpiration overlapped with snowmelt, we first carried out a phenological assessment of transpiration using the stem diurnal cycle approach. We did this by determining the timing of the rehydration phase by identifying the end of the freeze-thaw cycle and the continuous increase in stem radius in the spring (described in Section 2.4.2). Then, we determined the onset of transpiration by identifying when the transpiration-induced cycles started. We also used the greenness index to identify the leaf out period for the deciduous species to contrast with the phenological assessment from the stem cycle approach. Finally, we compared transpiration onset dates with snow depth timeseries to understand when trees start to transpire in relation to snowmelt.

We used the weekly isotope data to evaluate the temporal evolution of soil and xylem water. First, we evaluated assumptions of normality in xylem and soil isotope data using quantile-quantile plots, histograms, and the Shapiro–Wilk test. Because the data were not normally distributed, we used non-parametric Kruskal–Wallis (Kruskal & Wallis, 1952) and Dunn's multiple comparison tests (Dunn, 1964) to assess changes in soil and xylem water isotopic composition. We first assessed if the xylem and soil isotopic composition differed between the three sampling plots within each site (OJP and OBS). We did this to evaluate whether there was a significant difference in xylem water across the canopy of sampling trees between plots and in the soil in any given week. Then, we assessed the temporal trajectory of the xylem and soil water. We also used the non-parametric Kruskal–Wallis and Dunn's tests to detect significant changes in the isotopic composition of xylem and soil water across the multiple sampling weeks. We did this to understand how (i.e., more depleted or more enriched) and when we observed changes in the isotopic composition of xylem and soil in relation to snowmelt (i.e., prior, during or after snowmelt). We adjusted p -values according to Benjamini and Hochberg (1995) to control false discovery rates (Benjamini & Hochberg, 1995). The significance level for all statistical tests was set to the 95% confidence interval.

Finally, we used the identified onset of transpiration date to compare with changes in xylem isotopic composition per species. We contrast identified shifts in xylem isotopic composition with species-specific transit times obtained from sap flow measurements. We used dual-isotope inference to compare the isotopic composition between xylem, soil, precipitation, and snowmelt and identify tree water sources guided by phenological

observations of transpiration and physiological observations of tree water transit times. All data analyses and visualizations were done using R, version 3.5.1 (R Core Team, 2019).

3. Results

3.1. The Overlap of Stem Rehydration and Transpiration With Snowmelt

The onset of stem rehydration for the three species was observed during the snowmelt period (Figures 1 and 2). Stem rehydration initiated on April 18 for jack pine and black spruce, followed by the onset of transpiration for jack pine (Figure 1a; Figure S13 in Supporting Information S1) and black spruce on April 25 (Figure 2b; Figure S14 in Supporting Information S1). Stem rehydration is observed by the rapid increase in stem radius, prior to the onset of a transpiration-induced diurnal cycle, and after the end of the freeze-thaw cycle (Figures 1a and 2b). The onset of rehydration is also aligned with the start of canopy greenness rising, derived from the black spruce G_{CC} time series (Figure 2a). Transpiration onset for larch occurred on May 12, consistent with the needle-unfolding period observed with canopy greenness rising for this species (Figure 2a). On May 18, the larch canopy reached 50% amplitude of G_{CC} .

The primary snowmelt period occurred during the last 2 weeks of April at both sites (Figures 1c and 2c). The snow “end date” (i.e., no snow left on the ground) was observed on May 1 at OJP and May 5 at OBS. The end of the snowmelt melt period occurred after the onset of stem rehydration and transpiration.

Volumetric water content from shallow soil layers increased rapidly and synchronously with the decline in snow depth. We acknowledge that water content reflectometers are notoriously poor at recognizing ice in the soil profile. Nevertheless, measured soil volumetric water content behaved in an expected manner where water content started to increase on April 18 with the infiltration of melt water at both sites (Figures 1b and 2b). The average pre-melt soil water content at the shallow soil layer at OJP was $0.04 \text{ cm}^3 \text{ cm}^{-3}$. Soil volumetric water content after the melt onset reached field capacity ($0.13 \text{ cm}^3 \text{ cm}^{-3}$; Barr et al., 2012) on April 24 and maintained values above field capacity until April 26. On the first snow-free day (May 1), volumetric water content in the shallow layer was $0.11 \text{ cm}^3 \text{ cm}^{-3}$ and declined rapidly thereafter. At OBS, the volumetric water content was $0.16 \text{ cm}^3 \text{ cm}^{-3}$ prior to the snowmelt period for the shallow soil layer (below the peat surface) and peaked on April 26. Values reached $0.41 \text{ cm}^3 \text{ cm}^{-3}$ during melt and started to decline on May 7. A rainfall event later in May increased shallow soil water content in both sites (Figures 1b and 2c).

3.2. Spring Water Isotope Dynamics

3.2.1. Precipitation and Snowmelt Water

The isotopic composition of precipitation for both OJP and OBS showed large variability when compared to streamflow and groundwater δ -values (Figure 3). Throughfall samples were not statistically distinct from precipitation collected at either site ($p > 0.05$, Kruskal Wallis test – KW). The integrated snowmelt water δ -values collected by the snow lysimeter were $-20.30 \text{ ‰} \pm 0.02$ (Mean $\pm$ SE) $\delta^{18}\text{O}$ and $-159.18 \text{ ‰} \pm 0.18$ $\delta^2\text{H}$ at OJP, and $-21.05 \text{ ‰} \pm 0.01$ in $\delta^{18}\text{O}$ and $-165.04 \text{ ‰} \pm 0.04$ in $\delta^2\text{H}$ at OBS by the end of the melt season.

3.2.2. Temporal Evolution of Soil Water

Soil water $\delta^{18}\text{O}$ and $\delta^2\text{H}$ did not differ significantly between the three sampling plots within each site, at OJP ($p > 0.05$, KW) and OBS ($p > 0.05$, KW). Weekly soil $\delta^{18}\text{O}$ and $\delta^2\text{H}$ data showed a small difference between the three sampling plots after snowmelt at OJP (Figure S11 in Supporting Information S1) and during the first week of snowmelt at OBS (Figure S12 in Supporting Information S1). The data suggested that soil water isotopic composition was somewhat similar across plots but presented some heterogeneity during and after the onset of snowmelt. Because of general similarities in soil $\delta^{18}\text{O}$ and $\delta^2\text{H}$ across plots (Figures S11 and S12 in Supporting Information S1), we grouped them per depth and similarity in isotopic composition for temporal assessment of soil water isotopic dynamics.

Soil water $\delta^{18}\text{O}$ and $\delta^2\text{H}$ at OBS and OJP showed a constant temporal isotopic composition in early spring (March 24–April 20; $p > 0.05$, KW), but a clear shift to more lighter-snowmelt water δ -values during the last week of snowmelt (Figure 4). When compared to weeks prior to melt, OJP soil water $\delta^{18}\text{O}$ and $\delta^2\text{H}$ became statistically more negative across the soil profile, from shallow (20–60 cm) to medium (80–140 cm) and deep

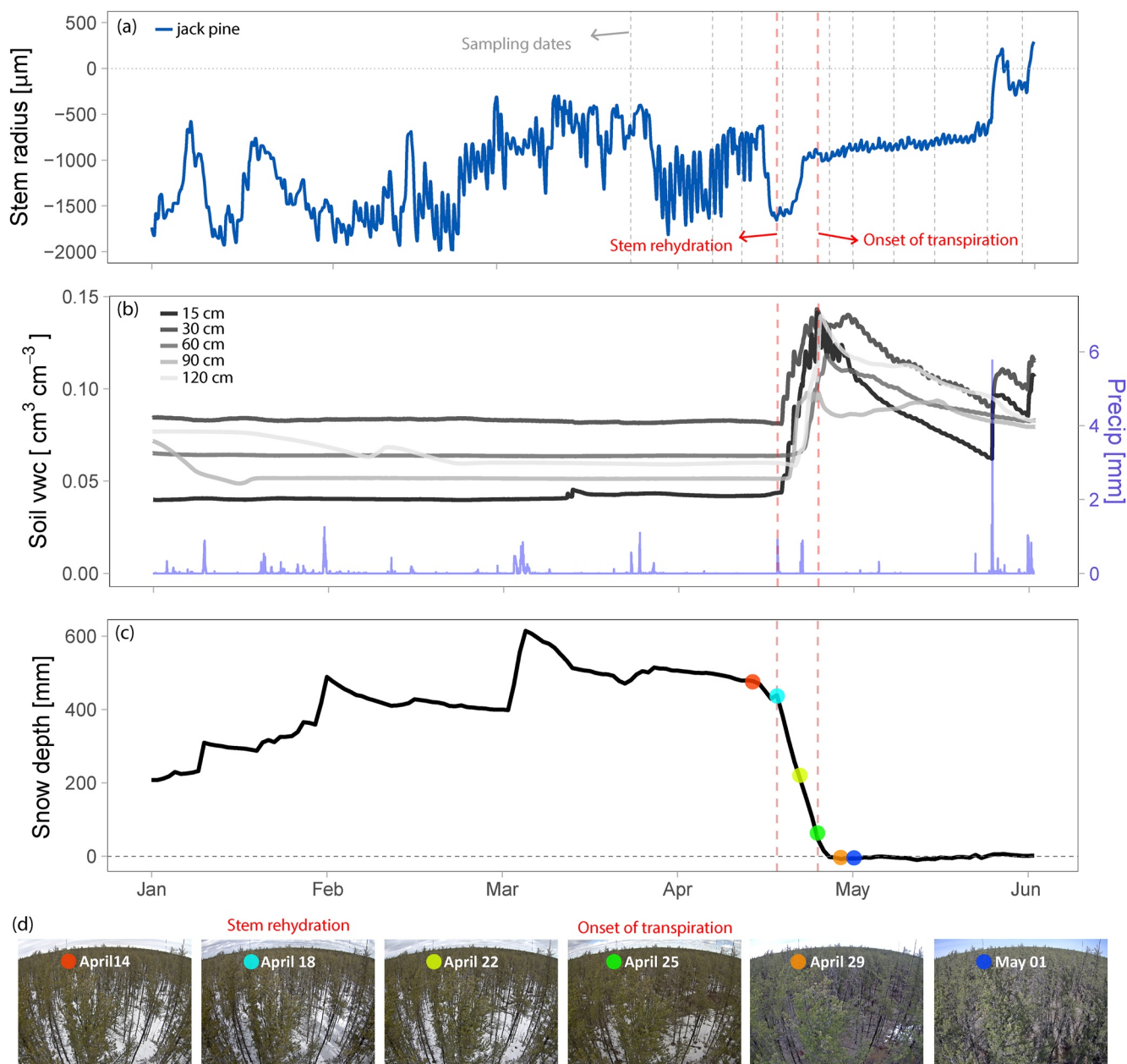


Figure 1. The phenological transition from winter to spring and onset of stem rehydration and transpiration at the Old Jack Pine site (OJP) in 2018. Panel (a) shows the mean stem radius variability of jack pine in relation to its maximum radius recorded in the previous growing season (2017) (zero-growth line; Zweifel et al., 2016). The stem radius shows negative values below the zero-growth line as a result of fall and winter stem dehydration. The onset of stem rehydration indicated by the first red dashed line shows a rapid increase in stem radius as a result of the refilling of internal water storage. The onset of transpiration indicated by the second red dashed line shows when trees started to transpire and present transpiration-induced stem diurnal cycles. Specific stem diel-cycle analysis of rehydration transpiration onset can be found Figure S13 in Supporting Information S1. Sampling dates (dashed gray line) indicate days when samples were collected for isotope analysis at the site. Panel (b) shows soil volumetric water content (VWC) across the different soil depths. Panel (c) shows snow depth. Panel (d) shows tower images from OJP indicating the transition periods. April 18 image shows conditions during stem rehydration with snow covering the ground and the beginning of the snowmelt period (blue dot; Panel d). April 25 image shows conditions during the onset of transpiration. May 1 image shows the first snow free day.

layers (160–200 cm) ($p < 0.05$, KW) (Figures 4b–4d, respectively). We observed the same shift in soil water $\delta^{18}\text{O}$ and $\delta^2\text{H}$ at OBS during the same week (Figure 4e). OBS soil water δ -values became statistically more negative on shallow (20–40 cm), medium (50–60 cm), and deep layers (70–100 cm) ($p < 0.05$, KW) (Figures 4g–4i, respectively). This change occurred 1 week earlier in the peat layer, the upper 10 cm, although not statistically significant (Figure 4f). Because the peat δ -values were consistently distinct from the sandy-loam layers below

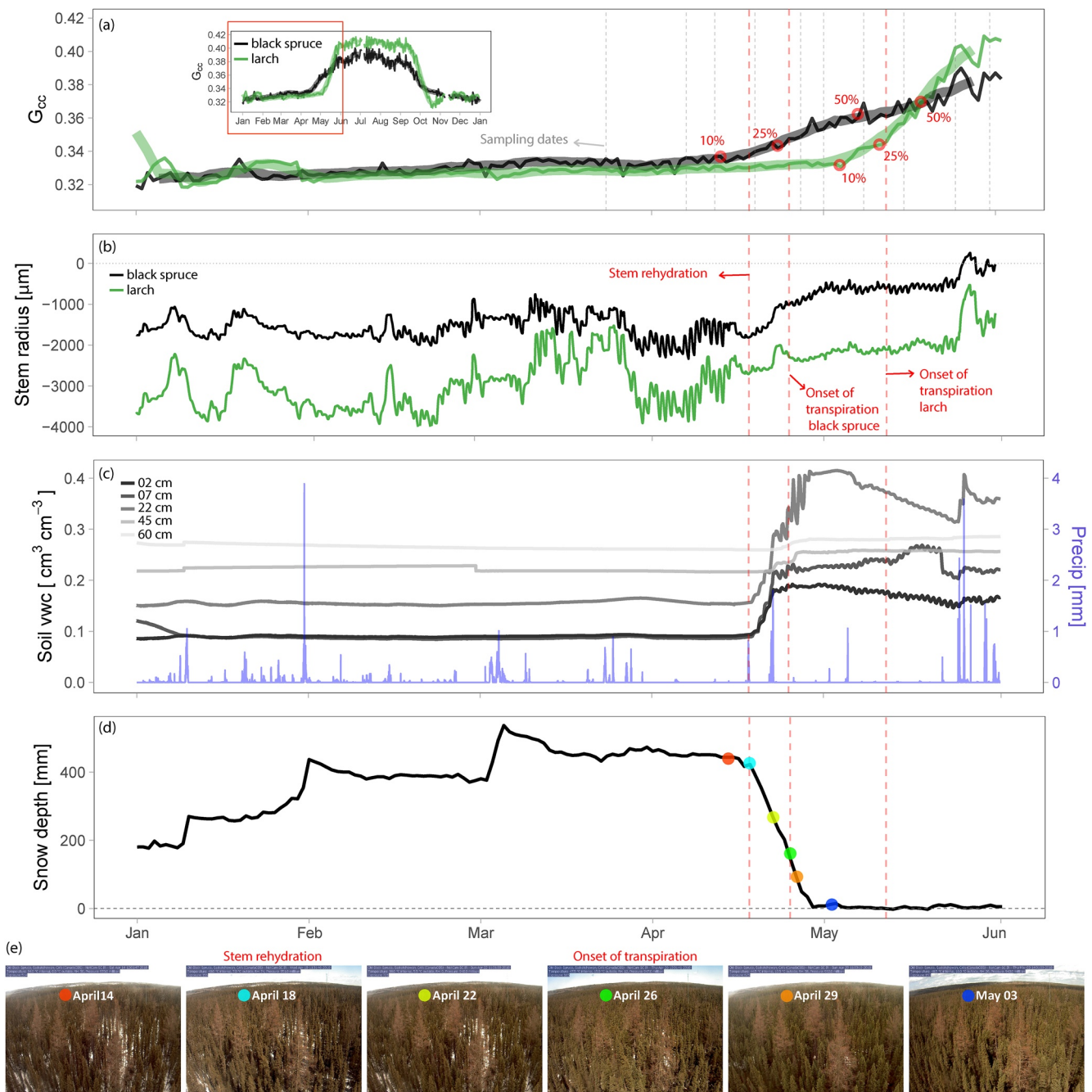


Figure 2. The phenological transition from winter to spring and onset of stem rehydration and transpiration at Old Black Spruce site (OBS) in 2018. Panel (a) shows G_{cc} (“greenness index”) for black spruce and larch along with “greenness raising” transition dates (10%, 25%, and 50%). Sampling dates (dashed gray lines) indicate days when samples were collected for isotope analysis at the site. Insert in Panel (a) shows the annual pattern in canopy G_{cc} , with the red box indicating the main plot period. Panel (b) shows the mean stem radius variability of black spruce and larch in relation to their maximum radius recorded in the previous growing season (2017) (zero-growth line; Zweifel et al., 2016). The stem radius shows negative values below the zero-growth as a result of fall and winter stem dehydration. Stem rehydration indicated by the first red dashed line shows both species’ onset of stem rehydration. The onset of transpiration indicated by the second red dashed line shows when black spruce started to transpire and showed a transpiration-induced stem diurnal cycle. Specific stem diel-cycle information of rehydration transpiration onset can be found in Supporting Information S1 (Figure S14 and S15, for black spruce and larch, respectively). Panel (c) shows soil volumetric water content (VWC) across the different soil depths and precipitation inputs. Panel (d) shows snow depth. Panel (e) shows tower images from OBS indicating the transition periods. April 18 image shows conditions during stem rehydration with snow covering the ground at the beginning of the snowmelt period (blue dot; Panel e). April 25 image shows conditions during the onset of transpiration of black spruce at the end of the snowmelt period. May 03 image shows just before the first snow-free day.

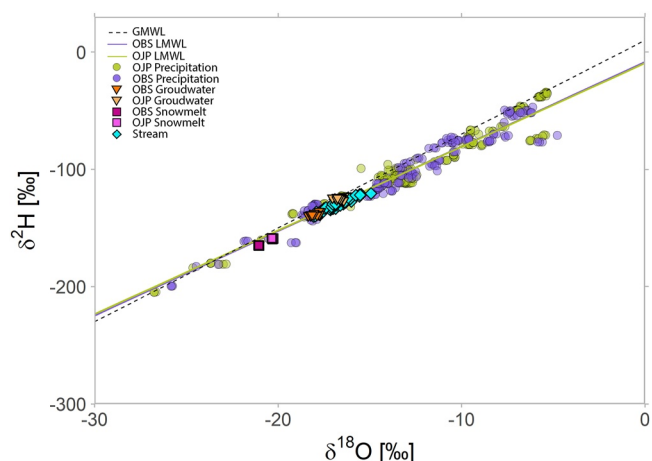


Figure 3. Local Meteoric Water Line (LMWL) from the Old Jack Pine site (OJP) and Old Black Spruce site (OBS) sites, along with individual samples of precipitation, groundwater and snowmelt from each site and nearby stream.

(20–40 cm), peat was not grouped with below layers during $\delta^{18}\text{O}$ and $\delta^2\text{H}$ temporal assessment.

3.2.3. Xylem Water Isotopic Values Prior, During and After Snowmelt

Weekly assessment of xylem water showed that black spruce and jack pine isotopic composition ($\delta^{18}\text{O}$ and $\delta^2\text{H}$) did not differ significantly between the sampling plots within each site ($p > 0.05$, KW). There was only one exception for jack pine during the last week of March that showed distinct $\delta^{18}\text{O}$ and $\delta^2\text{H}$ in one of the sampling plots compared to the other two plots ($p < 0.05$, KW). Because of overall similar xylem water isotopic signatures within species, we pooled species data to evaluate temporal isotopic dynamics.

Xylem water of jack pine, black spruce and larch at canopy level showed a continuous temporal isotopic composition without significant variability in early spring (Figure 5). However, after snowmelt and onset of transpiration, xylem data showed an asynchronous species temporal shift in $\delta^{18}\text{O}$ and $\delta^2\text{H}$ (Figure 5). This shift in $\delta^{18}\text{O}$ and $\delta^2\text{H}$ showed a change in xylem water to a more depleted isotopic composition in both ^{18}O and ^2H . We collected branches from the canopy in this study. Thus, when referring to xylem water hereafter, we refer to xylem water δ -values at the canopy level.

Jack pine xylem were consistent in both $\delta^{18}\text{O}$ and $\delta^2\text{H}$ across the initial six sampling weeks (March 24–May 2) ($p > 0.05$, KW; Mean $\pm$ SE: $-13.25 \text{‰} \delta^{18}\text{O} \pm 0.12$ and $-116.10 \text{‰} \delta^2\text{H} \pm 0.77$; $n = 89$) (Figure 5a). On May 9 jack pine xylem water δ -values became more negative ($-16.56 \text{‰} \delta^{18}\text{O} \pm 0.17$ and $-140.14 \text{‰} \delta^2\text{H} \pm 0.96$; $n = 15$) in comparison to previous weeks ($p < 0.001$, KW), and showed an overlap with soil water isotopic composition from the last week of snowmelt (Figure 6). Jack pine xylem water $\delta^{18}\text{O}$ and $\delta^2\text{H}$ values continued to become more negative in the following week and became more positive at the end of May (Figure 5a).

Black spruce xylem water shifted to lighter δ -values following snowmelt 1 week earlier than jack pine (Figure 5b). Prior to the shift, the black spruce xylem water $\delta^{18}\text{O}$ and $\delta^2\text{H}$ were fairly stable across the previous weeks ($p > 0.05$, KW; $-13.84 \text{‰} \delta^{18}\text{O} \pm 0.13$ and $-120.79 \text{‰} \delta^2\text{H} \pm 0.31$; $n = 60$) and like jack pine xylem water δ -values became statistically more negative after snowmelt ($p < 0.001$, KW). The average black spruce water δ -values became more negative on May 1 ($-17.21 \text{‰} \delta^{18}\text{O} \pm 0.14$ and $-142.06 \text{‰} \delta^2\text{H} \pm 0.96$; $n = 15$) and overlapped with the previous week's soil water (April 27) during snowmelt (Figure 7). Black spruce xylem water δ -values became more negative in the two consecutive weeks (May 8 and 15), indicating a continued use of snowmelt water. Larch showed the most delayed change among all species in xylem water δ -values. The shift to lighter δ -values in both $\delta^{18}\text{O}$ and $\delta^2\text{H}$ occurred on May 15 (Figure 5c) and became more positive on May 23 along with black spruce (Figure 7).

3.3. Tree Apparent Velocity

We used the sap flow data to estimate when the snowmelt water left the tree transport system. During early spring, the transport velocity of water calculated using sap velocities and tree height in jack pine, black spruce, and larch was $0.27 \text{ m d}^{-1} \pm 0.03$ ($n = 23$), $0.57 \pm 0.09 \text{ m d}^{-1}$ ($n = 13$) and $0.50 \pm 0.10 \text{ m d}^{-1}$ ($n = 8$), respectively. Based on this information, the resultant tree water transit time was 18.7 ± 1.6 days for jack pine, 9.4 ± 1.4 days for black spruce, and 9.9 ± 1.4 days for larch during the sampling period.

3.4. Tree Water Status

As expected, trees were in water deficit in early spring (Figures 1a and 2b). During spring rehydration, the current stem radius measurement was below the previous maximum growing season's stem radius as a result of fall and winter dehydration (2017 – zero line in Figures 1a and 2b). The negative stem radius indicates that tree water status was below its maximum hydration and trees were still using water to refill internal water storage in early spring. Jack pine and black spruce refilled internal water storages and recovered previous maximum stem radius on May 25 (Figures 1a and 2b, respectively), after a rainfall event that also recharged soil water storages and increased volumetric water content (Figures 1b and 2c, respectively).

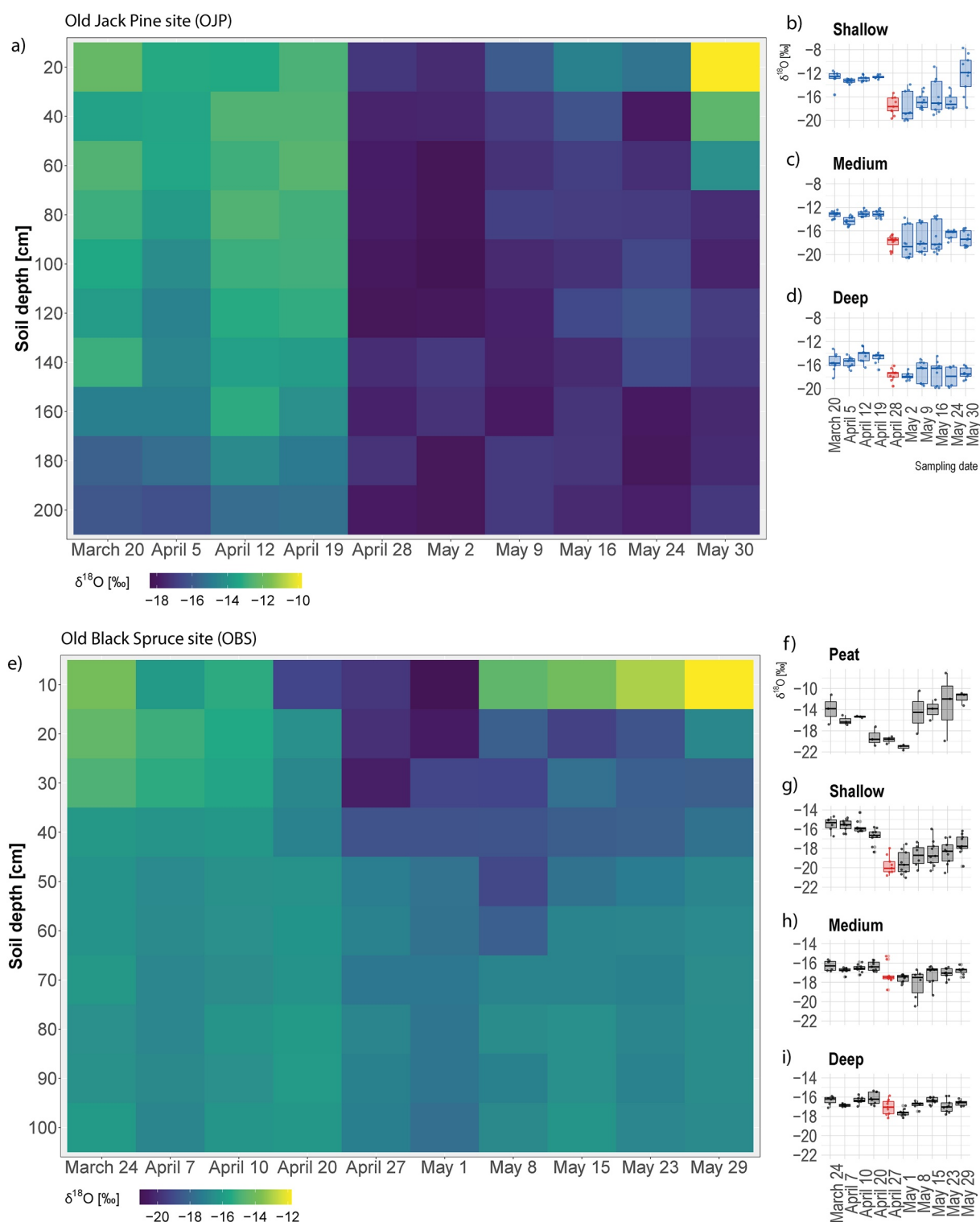


Figure 4. Temporal dynamics of soil water across different depths at the Old Jack Pine site (OJP) ($n = 290$) and Old Black Spruce site (OBS) ($n = 276$) in the spring of 2018. Panel (a) shows OJP mean $\delta^{18}\text{O}$ per depth across the 10-week spring transition period with a marked change in soil water δ -values on April 28. Panel (b–d) show transition in soil isotopic composition for shallow (20–60), medium (80–140) and deep (160–200) soil layers at the OJP site. Panel (e) shows OBS mean $\delta^{18}\text{O}$ value per depth across the 10-week spring transition period with marked change in soil water isotopic composition on April 27. Panel (f–i) show the transition in soil δ -value for peat (10 cm), shallow (20–40), medium (50–60) and deep (50–60) soil layer (70–100) at OBS. Red box plots indicate a statistically significant shift in soil water isotopic values ($p < 0.05$; KW).

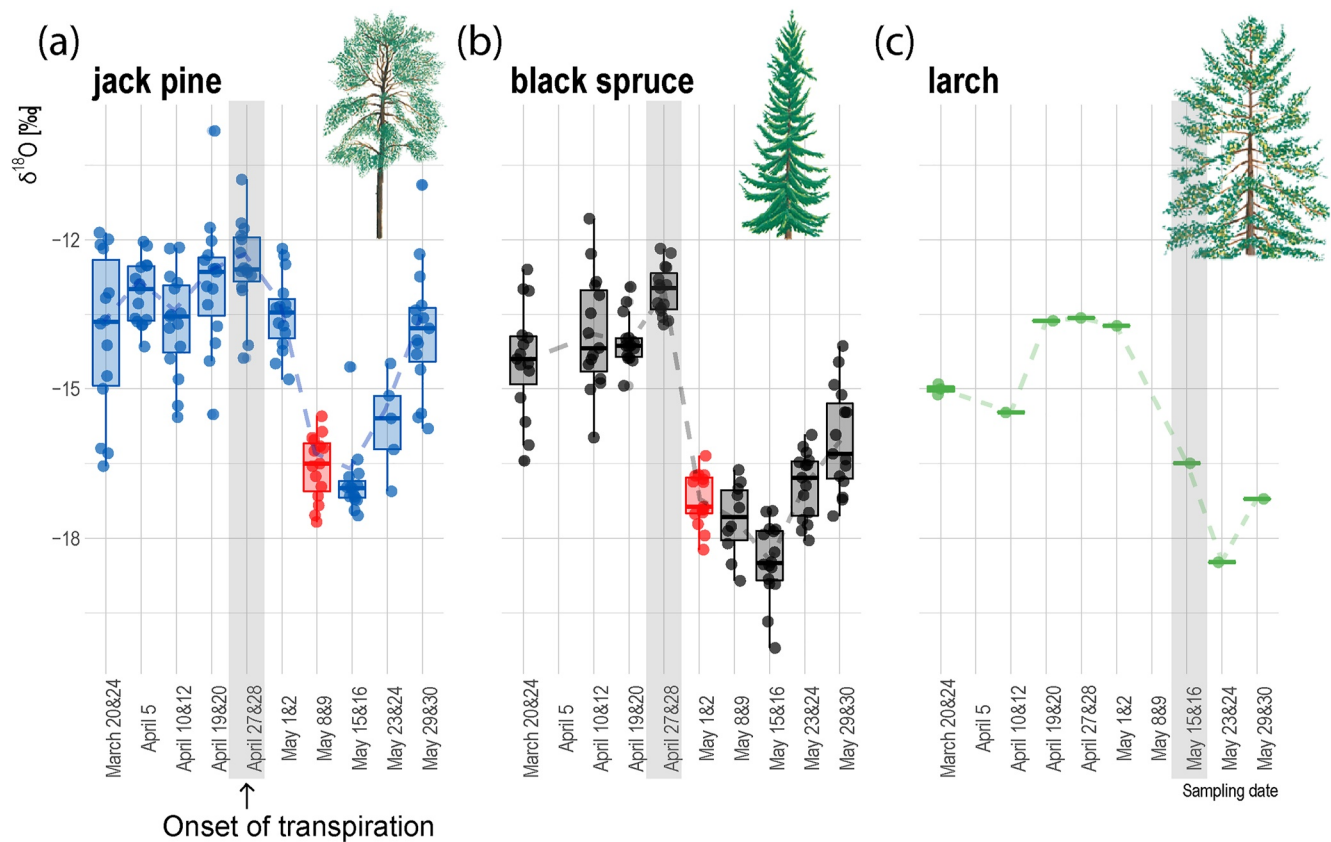


Figure 5. Temporal dynamics of $\delta^{18}\text{O}$ in xylem water from jack pine ($n = 139$) (a), black spruce ($n = 131$) (b) and larch ($n = 10$) (c) during spring onset. Gray bars indicate the week when the onset of transpiration occurred. The red box plot indicates a statistically significant shift in xylem water δ -values ($p < 0.05$) in relation to the previous weeks (March 20–May 2 for jack pine; March 24–April 27 for black spruce). Larch's shift to more depleted signatures occurred during and after the observed onset of transpiration. Tree sketches were obtained from: treesofmnapp.com. See Figure S8 in Supporting Information S1 for temporal dynamics of $\delta^2\text{H}$ in xylem water.

4. Discussion

4.1. Stem Rehydration and Onset of Transpiration Occurs During Snowmelt

We used stem radius phenological assessment of spring onset, snow depth measurements, soil moisture content and phenocams to understand the phenological overlap between tree transpiration and snowmelt. This hydrometric data showed that the onset of spring stem rehydration overlapped with the beginning of the main snowmelt period in both OJP and OBS (Figures 1 and 2). Stem rehydration coincided with the increase in soil moisture and the decline in snowpack depth. Our observations of spring rehydration were consistent with published records of stem radius data in cold regions. After long periods of stem desiccation and winter shrinkage trees show marked rehydration prior to resuming physiological functioning in spring (Deslauriers et al., 2003; Eitel et al., 2020; Tardif et al., 2001; Turcotte et al., 2009). Young-Robertson et al. (2016) had previously investigated this overlap between snowmelt and stem rehydration. They suggested that stem rehydration results in a large sink of snowmelt water in boreal trees across Alaska and the Yukon. They showed a rapid increase in tree volumetric water content at the end of the snowmelt period for both evergreen and deciduous species. The broadleaf deciduous taxa (*Betula neoalaskana* and *Populus tremuloides*; paper birch and trembling aspen, respectively) showed higher rehydration volumes in their study. Young-Robertson et al. (2016) estimated that about 25% of total snowmelt input was routed to deciduous rehydration; whereas small proportion of snowmelt available water (<1%) contributed to evergreen (*Picea mariana*; black spruce) rehydration. We also found relatively small stem rehydration volumes in our sites, which is mainly dominated by evergreens (data not shown).

Stem rehydration continued until late-May for jack pine and black spruce, when trees recovered stem water status and reached the previous year's maximum radius. But our stem radius data also showed a distinct transpiration-induced cycle starting about 1 week after the onset of rehydration on April 25 during the later stages

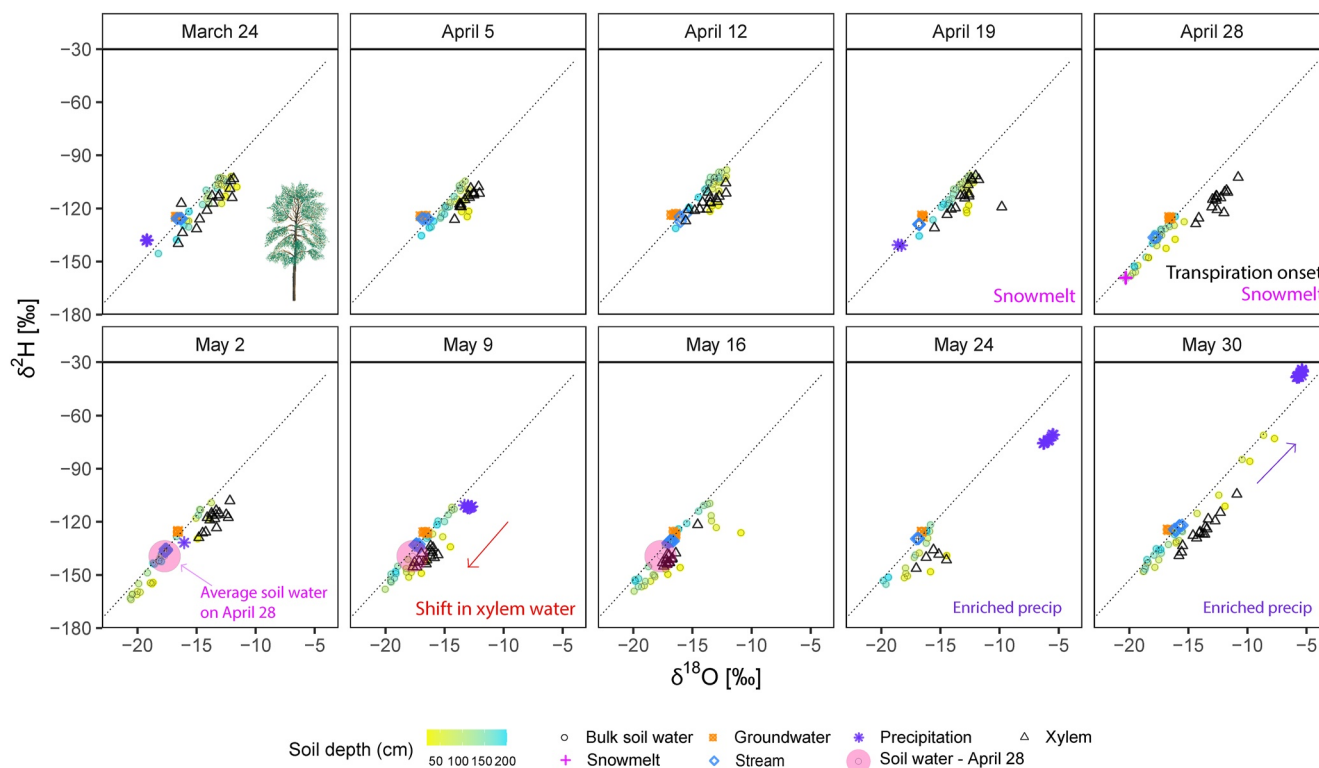


Figure 6. Weekly dual-isotope plots of xylem along with snowmelt and soil water dynamics during the phenological transition from winter dormancy to spring onset at the jack pine site in 2018. The dotted line shows the Local Meteoric Water Line (LMWL). The rapid decrease in snow depth (main melt period) was observed between the week of April 19 and the week of April 28 (no snow on ground on May 1). Jack pine onset of transpiration was observed on April 25 during the last days of snowmelt. Large circle (pink) represents the average soil water isotopic composition from April 28 (-139.42 ± 9.77 $\delta^{18}\text{O}$ and -17.70 ± 1.20 $\delta^2\text{H}$; Mean $\pm$ SD). The significant shift in xylem δ -values was observed on May 9 and showed a great overlap with soil water isotopic composition from April 28 (large pink circle). See Figure S9 in Supporting Information S1 for data displayed with reduced x and y axis range.

of the snowmelt period and along the observed peak in soil moisture at both sites (Figures 1 and 2). This lagged activation of the diurnal transpiration cycling is likely to occur only after trees reach minimum sapwood and inner bark water storage that can offset changes in xylem water potential driven by transpiration (Steppe et al., 2006; Zweifel et al., 2016). Our results support observations from other boreal sites where evergreen trees begin transpiration *before* the snowpack completely melts (Bowling et al., 2018; Chan & Bowling, 2017).

Larch, the deciduous species, showed onset of transpiration in mid-May, approximately 3 weeks after the onset of transpiration for co-occurring black spruce. This period overlapped with the increase in the larch greenness index, indicating leaf unfolding. In 2019 and 2020, larch onset of transpiration also occurred approximately three weeks after the onset of black spruce at OBS (on May 22 and May 18, respectively) (Pierrat et al., 2021). Young-Robertson et al. (2016) also reported the onset of deciduous transpiration in May in Alaska and the Yukon.

4.2. Snowmelt Water Use and Observed Lags Due To Tree Transit Time

Knowing that the onset of rehydration and transpiration overlaps with snowmelt, the next question is: Are trees actually using snowmelt water to rehydrate and start transpiring? Young-Robertson et al. (2016) have speculated that snowmelt water stored in the stem during rehydration can contribute to transpiration after leaf-out of deciduous trees and through the early growing season. However, their work did not use any tracer data. Without that line of evidence, it is difficult to know whether trees use infiltrated snowmelt water and if snowmelt water stored in stems sustains transpiration during the following weeks and summer. In an earlier investigation of tree water use after snowmelt, Bowling et al. (2017) using stable isotopes ($\delta^{18}\text{O}$ and $\delta^2\text{H}$) revisited the stream side trees from Dawson and Ehleringer (1991). They showed that xylem from *Acer negundo* and *A. gradidentatum* (box elder and bigtooth maple, respectively) did not overlap in dual-isotope space with snowmelt signatures or even any

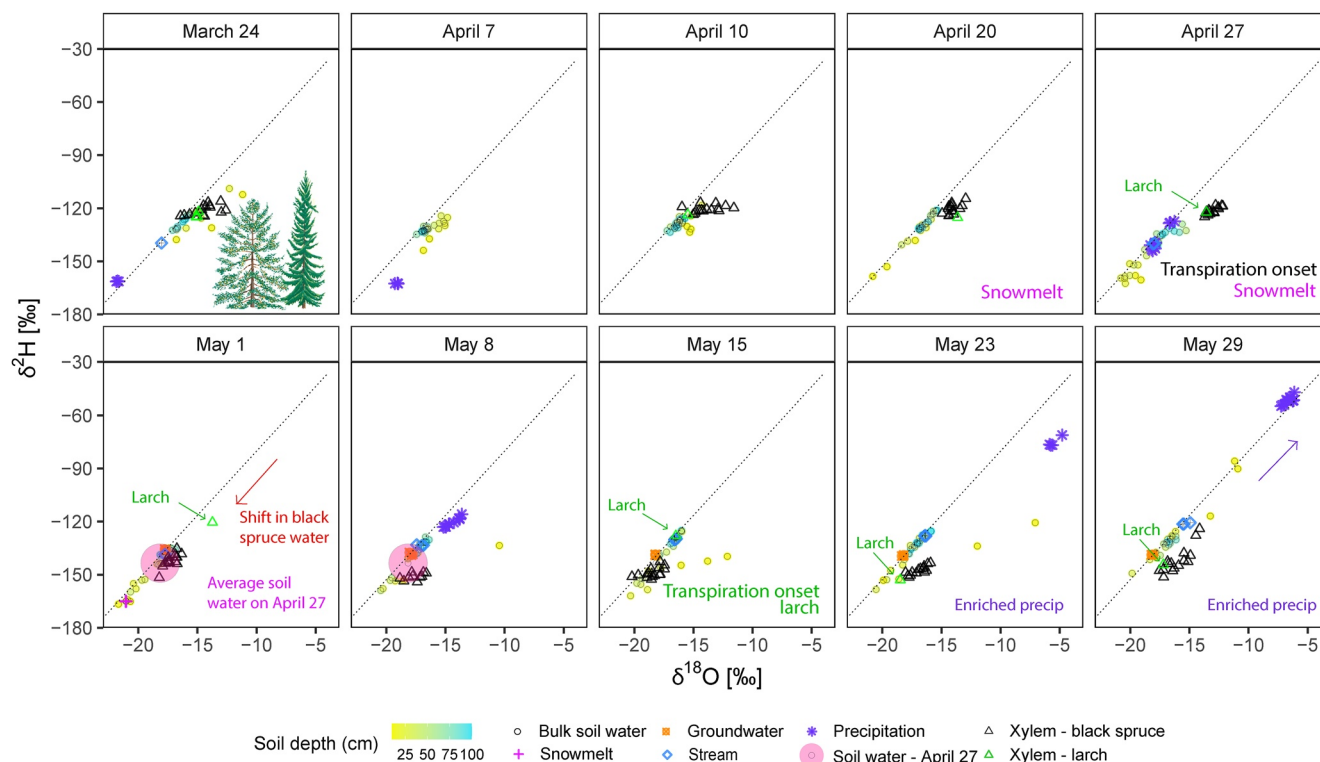


Figure 7. Weekly dual-isotope plots of xylem along with snowmelt and soil water dynamics during the phenological transition from winter dormancy to spring onset at the black spruce site (OBS). The dotted line shows the Local Meteoric Water Line (LMWL). The decrease in snow depth (main melt period) was observed between the week of April 20 and the week of April 27. The black spruce onset of transpiration was observed on April 25 during the last days of snowmelt. The significant shift in xylem δ -values for black spruce was observed on May 1. Large circle (pink) represents the average soil water isotopic composition from April 28 ($\delta^{18}\text{O} -143.47 \pm 10.88$ and $\delta^2\text{H} -18.16 \pm 1.56$ Mean $\pm$ SD). Larch showed onset of transpiration on May 15 and returned to the LMWL during the same week of transpiration onset for larch (May 12). Larch xylem water is represented by a few to one individual tree and is indicated by a green arrow. Xylem water is not available from April 7. See Figure S10 in Supporting Information S1 for data displayed with reduced x and y axis range.

other available sources during early spring (May and later in June). Their data refuted the hypothesis that trees would use snowmelt water that had infiltrated the soil during the melt season and supported the ecohydrological separation hypothesis of Brooks et al. (2010).

In contrast to Bowling et al. (2017), our hydrometric observations support the notion that trees use snowmelt water during the snowmelt season (Figures 1 and 2). Melt infiltration increased soil water availability providing a water source for stem rehydration and transpiration in these otherwise dry soils (i.e., following fall and early winter conditions), with low soil water content (Figures 1b and 2c). Our tracer data shows evidence of snowmelt water use. However, the detection of snowmelt isotopic signature at canopy level was lagged in relation to hydrometric observations of transpiration onset and likely relative to root water uptake (Figure 8). High-frequency sampling of xylem water was able to characterize this lag. We observed a clear shift in black spruce xylem water to more negative $\delta^{18}\text{O}$ and $\delta^2\text{H}$ values 1 week after the onset of transpiration and the change in soil δ -values following snowmelt (Figure 5). This same shift occurred 2 weeks later for jack pine (Figure 5). Prior to the shift in xylem water to more depleted-snowmelt water values, the constant xylem water in early spring in both species likely reflected a mixture of pre-winter soil water sources and/or evaporative enrichment of resident water in the stem. Trees in northern sites show patterns of stem dehydration (i.e., shrinkage) later in the fall in preparation for winter hardening (Chang et al., 2021; Winget & Kozlowski, 1964). A late fall isotopic investigation at the same sites showed an enrichment in xylem isotope values in comparison to summer water after stem shrinkage (data not shown). For larch, the deciduous species, the shift to more depleted-snowmelt δ -values happened after leaf unfolding (Figure 8). At this time larch xylem water moved onto the Local Meteoric Water Line (LMWL) in the dual-isotope plot (Figure 7). Our observations support an earlier investigation by Phillips and Ehleringer (1995) that showed that the xylem of winter-deciduous species deviated from the LMWL before leaf flush and returned near LMWL after complete leaf flushing.

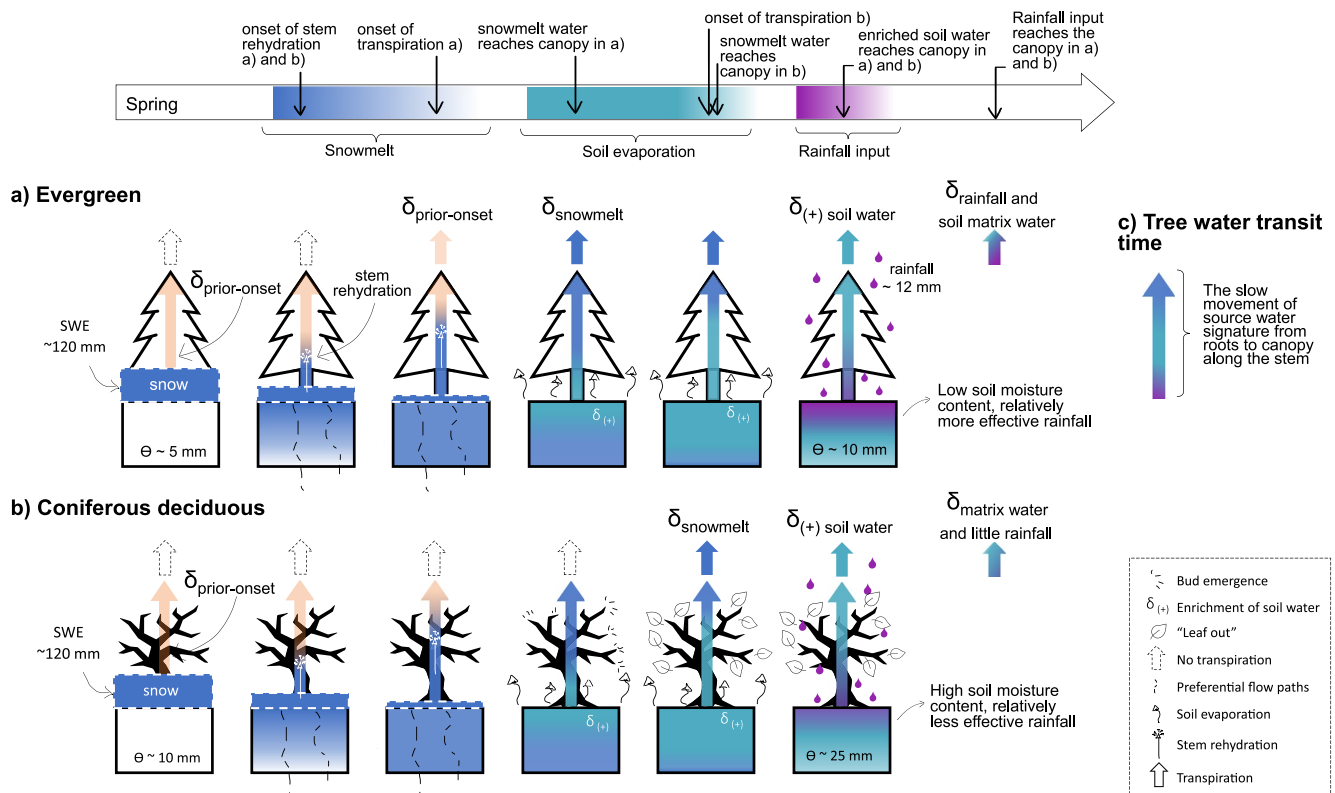


Figure 8. Perceptual model for tree water use in the boreal forest during spring onset. Panel (a) Evergreen onset of stem rehydration overlaps with the onset of snowmelt while snowmelt water infiltrates the soil. The onset of transpiration overlaps with the end of snowmelt period. Xylem water δ -values shows a pre-melt isotopic signature during onset of transpiration. The shift in xylem water δ -values to snowmelt isotopic signatures at canopy level occurs weeks later because of slow tree water transit times (c). Shallow soil water shows evaporative enrichment (indicated by δ "positive sign") weeks after snowmelt, and only soil matrix water is available for transpiration. Later, rainfall inputs recharge shallow soil volumetric water content. Rainfall inputs mixes with shallow soil water and contributes to xylem water. Like snowmelt, but in small proportions, this uptake results in an expansion of stem radius and recharge of internal tree water storage. The shift in xylem δ -values at the canopy is delayed again because of tree water transit times. Panel (b) Coniferous deciduous (larch) onset of stem rehydration overlaps with evergreens and snowmelt, but the onset of transpiration occurs weeks later, only after leaf out. During the onset of transpiration, xylem water δ -values at canopy shift to snowmelt water isotopic signature. Later rainfall inputs also contribute to transpiration, but its isotopic contribution is more negligible than the other site (a). The larger antecedent wetness conditions and relatively smaller rainfall fraction to total water stored in the soil available for uptake might explain isotopic observations. Note: coniferous deciduous have needles, and the broadleaf representation is for illustration purposes only.

It is possible that because of the "snapshot" sampling approach, Bowling et al. (2017) might have missed the possibility of observing the potential overlap between trees and soil by sampling a bit too early in May when leaves were only beginning to emerge. A lower sampling frequency might have resulted in sampling before the shift in xylem water resulting in a mismatch between trees and soils isotopic composition. Similar to our observations in dual-isotope space at the end of April during the end of snowmelt (Figures 6 and 7). Bowling et al. (2017) described that in May xylem water was highly evaporatively enriched and that while in June they observed xylem water closer to LMWL, xylem water did not overlap with soil water or any other available water pools. Their monthly sampling frequency may have reduced their ability to detect tree water sources, where trees might have been lagging in relation to soil water δ -values. We would have faced similar challenges had we not sampled weekly in combination with continuous phenological monitoring with stem radius change and phenocams.

The observed delay in the shift of xylem water signatures to snowmelt water use in evergreen species is likely related to the slow tree water transport velocity and associated tree water transit time (Gaines et al., 2016; Mennekes et al., 2021). Our estimated boreal species tree water transit times were between approximately 9–18 days during early spring. Tree water transit time estimates are close to our observed time lag for snowmelt water to be detected in the xylem at canopy level. This lag is also relative to the observed onset of transpiration and shift in soil water δ -values. Previous comparisons between apparent velocity estimates from sap flow density and tracer velocity measurements under field conditions have shown that sap flow velocities tend to

underestimate “real” tracer velocities (Gaines et al., 2016; Meinzer et al., 2006). However, these comparisons have used more invasive tracer measurements by drilling into the stem of trees and artificially injecting the tracer in the stem (above the ground). Additionally, radial and circumferential movement of water influenced by wood anatomy can result in heterogeneous tracer concentration within the tree (Treydte et al., 2021). A recent field in situ isotope measurements on *Fagus sylvatica* (European beech) xylem water using vapour probes across different tree heights also showed a delay in tracer signature (Seeger & Weiler, 2021). Like our snowmelt water observations, Seeger and Weiler (2021) showed a rapid change in the soil water isotopic signature after tracer irrigation, but tracer values only peaked 14 days after irrigation at 8 m tree height monitoring probe. Magh et al. (2020) investigated tree water use strategies using artificial tracer irrigation to *F. sylvatica* and *Abies alba* (silver fir) and observed changes in xylem δ -values 12 days after tracer irrigation, while change in soil δ -values occurred within the first 2 days. Our results also corroborate with a recent tree water use investigation in a Mediterranean climate (island of Corsica; France) that showed varying time lags between new rainfall inputs and canopy-level xylem water δ -values shifts (Juhlke et al., 2021).

Hamilton (2019) performed a labelled ^2H -enriched tracer irrigation experiment at a site nearby the OJP (Narrow Hills Provincial Park; approximately 15 km from OJP). Their ^2H -enriched irrigation experiment was conducted on the same soil type and tree species, and xylem δ -values showed an 11 day-lag for irrigation to be detected at the canopy level of jack pine. This experiment, however, was conducted in August (2016), a much warmer month. Considering the sap flow velocities from our jack pine site for the same period of the year (August), our tree water transit time estimate reduces to 12.5 days ± 1.1 . If we refine this estimate by removing rain days in August, our sap flow estimates achieve the same tracer transit time as Hamilton (2019): In our case, 11.6 days ± 1.1 . This corroborates the tree water transit times estimated from sap flow velocity. Our tree water transit time observations and lag also corroborate with model simulations that indicate a more “piston-flow” like water movement of tracer within the trees, rather than a complete mixing of root water uptake with internal sapwood water stores (Knighton et al., 2020).

Unlike jack pine and black spruce, larch showed continuous stem rehydration following snowmelt. Larch rehydration time was long before the onset of transpiration when compared to only 1 week for jack pine and black spruce (from April 18 to 25). The long rehydration may explain the rapid shift in xylem water δ -values towards more depleted-snowmelt δ -values during the onset of transpiration in larch. This rapid shift without the delays seen in jack pine and spruce suggests that larch may rely on snowmelt water stored in the stem from the rehydration process during the onset of transpiration and leaf-out, since this species rehydrate for longer periods before starting to transpire. This would support the Young-Robertson et al. (2016) hydrometric observation that deciduous species use some stored water during leaf out given their relatively larger water storages (compared to evergreen species).

4.3. How Do the Findings From This Study Relate to Other Forest Environments and Ecohydrological Separation Observations?

Tree water transit times have also been used to investigate ecohydrological separation. Evaristo et al. (2019) in a large controlled experiment at the Biosphere 2-Tropical Rainforest mesocosm using a labeled rainfall, found transpiration transit times within our observed range or even longer (17–62 days). They also showed a variation in tree water transit times among different canopy species after a long-term drought (~60 days) followed by a rewetting event. This is somewhat analogous to our system where trees were in water deficit following winter stem shrinkage and started to recover their water storage during snowmelt. Evaristo et al. (2019) observed that tree water transit times were between 2 and 7 times slower than the movement of more mobile water into the soil profile. Our observations also support this by showing a much faster shift in soil water δ -values at different depths during snowmelt than at canopy level. Like our system, their longer delay in transit times can be attributed to a water deficit. Under deficit conditions, trees tend to show decreased sap flow velocities because tissue refilling needs are being met (He et al., 2020; Stohr & Losch, 2004), which increases travel time. Knighton et al. (2019) investigated tree water use from two temperate forest species (*F. grandifolia* and *Tsuga canadensis*, American beech and eastern hemlock, respectively). They suggested that transpiration was ecohydrologically separated from water moving in preferential flow paths (i.e., “percolate”) during fall rewetting events because xylem and percolate showed distinct age selection and lack of overlap in dual isotope-space. Our data, however, does not support the ecohydrological separation interpretation during rewetting (Evaristo et al., 2019; Knighton

et al., 2019). In contrast, our results indicate that, during the snowmelt rewetting period, trees may have been connected to the more mobile water (i.e., snowmelt) at the time of root water uptake, but that the snowmelt water signal is delayed at canopy level because of slow tree water transit times (Figure 8). Similarly, Hervé-Fernández et al. (2016) and Zhao et al. (2018) did not observe ecohydrological separation during wet conditions like our snowmelt period, which might have reflected soil water connectivity between transpiration sources and preferential flow paths. Higher-temporal resolution measurements of bulk soil water paired with suction cup sampling of mobile water would be helpful in understanding the exchange between the two flow domains. We argue that different ages between fast-flow soil domains and xylem water are natural and expected because of the distinct velocities and flow path lengths (i.e., tree height and depth of soil sampling). Thus, the mismatch between xylem water and preferential flow paths may not always indicate an ecohydrological separation per se because large trees may still be transpiring previous weeks' or months' root water uptake and rainfall inputs at the canopy level (Figure 8). It appears from our data that the separation in time (e.g., Evaristo et al., 2019; Knighton et al., 2019) between source water that feeds xylem and more mobile water in soils (i.e., percolate, snowmelt) can be an artifact of the time lag between percolation/rewetting rates, root water uptake and canopy transpiration, and not an ecohydrological separation between source of transpiration and water that feeds groundwater and streamflow (Brooks et al., 2010). Our hydrometric and tracer data indicate that the water that supplies transpiration and water that recharges groundwater is likely hydrologically connected during spring onset. Our data also showed that trees relied on snowmelt water during the first weeks after snowmelt. Figure 8 shows our perceptual understanding of tree water use during spring onset in the boreal forest.

In the weeks following snowmelt, the volumetric water content of soil showed a continuous decline (Figures 1c and 2d). Xylem water δ -values became heavier 4 weeks after snowmelt (May 23 and 24) (Figures 5a and 5b) and plotted further away from the LMWL in dual-isotope space (Figures 6 and 7). The xylem water likely reflected more soil bounded water as the soil dried and there is a lack of available mobile water (Figure 8). In response to enriched rainfall events (May 23–24; Figures 6 and 7), the soil showed an increase in volumetric water content in the shallow layers at OJP and OBS. On May 24 OBS and OJP received 12 mm of rainfall that continued on the next day. Besides recharging soil water stores, this rainfall led to the recovery of tree water status of jack pine and black spruce by showing the expansion in stem radius, surpassing the previous year's maximum and reaching a complete stem hydration at night (Figures 2a and 3b, respectively). The internal water storage recharge observed by the stem radius expansion after rainfall events have been observed previously (Güney et al., 2020; King et al., 2013; Maillet et al., 2022; Pierrat et al., 2021).

The rainfall on May 24 and other smaller events that occurred during the following week (Figures 1b and 2c) had enriched isotopic signatures (Figures 6 and 7) and resulted in a slight enrichment of soil water at surface layers at OJP (first 60 cm; Figure S11 in Supporting Information S1) and OBS (top 20 cm; Figure S12 in Supporting Information S1). When rainfall inputs enter the topsoil, rainfall water might mix with the existing soil matrix if the rainfall is not of high intensity (Germer & Braun, 2015; Radolinski et al., 2020). Following the observed rainfall events, jack pine xylem water δ -values became heavier (Figure 5a; May 30), and δ -values began to “move” in dual-isotope space toward precipitation δ -values (Figure 6). This observed change in xylem water δ -values after the rainfall shows similar trends to the first week after snowmelt (May 2), when jack pine xylem water δ -values became lighter and “moved” toward snowmelt water in dual-isotope space. The change in black spruce xylem water toward more positive δ -values following the rainfall event was observed but not as evident as the change in jack pine xylem water δ -values. We assume that the enrichment is more evident for jack pine because soil water conditions at OJP are much drier (Figure 8a) due to the well-drained nature of the sandy soil compared to OBS. OBS soil still showed relatively higher soil volumetric water content and more water available to trees (Figure 8b). Thus, the small change of black spruce and larch xylem δ -values in response to precipitation inputs might be due to antecedent soil wetness conditions. This understanding is supported by stem radius investigations at OBS and OJP that showed that jack pine has a stronger relationship to rainfall inputs than black spruce, likely because of drier soil conditions and well-drained sandy soil (Maillet et al., 2022). Thus, besides being influenced by the time lag relative to tree water transit time, the observation of ecohydrological separation might also reflect the antecedent soil moisture conditions, which also depends on soil texture (Sprenger et al., 2018). Before snow melt, little water was available as soil volumetric water content was low, and the snowmelt recharged the soil water matrix and activated preferential flow paths (Figure 8).

In May, the later rainfall event was likely more effective at recharging the OJP soil matrix because it had lower soil volumetric water content. In comparison, the OBS soil matrix stored larger volumes of water (Figure 8). Therefore, the xylem water of trees at OBS did not clearly show rainfall inputs and instead a more blended mixture of pre and post precipitation δ -values because of the higher antecedent wetness conditions in the soil (Figure 8b). The rainfall events differed from early snowmelt water input, where both sites' soils were much drier, and snowmelt volumes were larger than rainfall. Further research is needed to understand the relationship between tree water use, rainfall inputs across different sites, and soil textures during the growing season.

4.4. Measurement Uncertainty: Transpiration Age and Source

Whether bulk xylem measurements (i.e., cryogenic extracted water) represent source water uptake remains a pertinent question for the research community. One may alternatively sample the vessel water directly using, for example, the Scholander pressure chamber (Scholander et al., 1965) (e.g., Geißler et al., 2019; Zuecco et al., 2020), centrifugation (e.g., cavitron) (Barbeta et al., 2022), in situ vapor measurements (e.g., Kühnhammer et al., 2022), or direct vapor method in the lab (e.g., Millar et al., 2018; Nehemy et al., 2019), instead of obtaining the bulk xylem water via cryogenic extraction. We acknowledge the uncertainty with the cryogenic extraction method, given recent debates that show its limitations (Barbeta et al., 2022; Chen et al., 2020), but also others that challenge these views (Chen et al., 2020; Evaristo et al., 2021; Newberry et al., 2017). Additionally, recent studies showed that xylem water obtained from directly sampling vessel water using methods described above is not always distinct from cryogenic extracted water (Geißler et al., 2019; Kühnhammer et al., 2022; Zuecco et al., 2020), and the direct vapor method in woody species result in spectral contamination (Nehemy et al., 2019). Cryogenic extraction was likely not an issue within our observed species and observed period because our stable isotope results are supported by hydrometric observations. Our xylem water isotopic composition plotted within soil water distributions and was not more depleted in heavy isotopes than observed soil water sources.

We are aware that there are several sources of uncertainty in the estimation of sap flow (Flo et al., 2019; Peters et al., 2018; Steppe et al., 2010). Measurement redundancy showed good agreement between transpiration age estimates from tracer and sap flow velocities. Our age estimates corroborate with a labeling injection results from a site near the OJP with the same species (Hamilton, 2019). The close transit time estimates from sap flow and observed tracers may be because our sap flow sensors in monitored trees showed sapwood depth equal to or smaller than the probe length (20 mm) at OJP. We also avoided using trees that needed significant corrections (Clearwater et al., 1999; Peters et al., 2021) at OBS (e.g., smaller trees with DBH <9 cm, with sap wood depth smaller than 1/3 of probe length). However, sapwood depth estimates based on allometric equations also represent a potential source of error when corrections are necessary. We also allowed night-time sap flow activity by avoiding the use of predawn $\Delta T_{\max}$ (maximum temperature difference between the heated and a reference unheated probe) and further compared three other processing methods for determining the best $\Delta T_{\max}$ approach to our data (Peters et al., 2021). The species were coniferous which have also shown no effect of wood density on sap flow density estimates (Peters et al., 2018). Our main source of uncertainty is the lack of species-specific calibration. We compared different parameters from other species from the *Pinacea* family with similar water transport systems available in the literature (Flo et al., 2019; Peters et al., 2021) and applied the best fit to our data. All these combined factors described may have reduced uncertainties and resulted in a good agreement between tracers and sap flow velocities estimates. However, we acknowledge that our estimates contain uncertainties and more detailed sap flow monitoring (i.e., along with tree height and radially) and specific-species sap flow calibration would be helpful to improve this assessment.

5. Conclusions

We have presented a tree water use assessment during the onset of rehydration and transpiration in a southern boreal forest in Central Canada. Our analysis of when trees start to rehydrate and transpire in relation to snowmelt showed that stem rehydration and the onset of transpiration overlapped with the snowmelt period. Our stable isotope investigation showed that soil water shifted to lighter δ -values during the last week of snowmelt and this isotopic shift overlapped with the onset of jack pine and black spruce transpiration. However, crown-level xylem water did not show an immediate shift to lighter-snowmelt δ -values during the onset of transpiration. The shift in xylem water δ -values occurred approximately 1 week after the onset of transpiration in black spruce trees and approximately 2 weeks later in jack pine. Our hydrometric observations indicate that this delay was linked

to observed tree water transit times. Snowmelt water, therefore, is an important source of transpiration for trees in the spring. These findings highlight the importance of spring snowmelt onset time in relation to transpiration onset timing. As both the timing of snowmelt and vegetation phenology are likely to continue to change and snowpack is likely to continue to decline, understanding patterns in tree water sources during the spring onset is important to identify the impact of climate change on the evolution of forest composition and groundwater recharge.

Data Availability Statement

Stable isotope, tree hydraulic measurements and hydrometric data are available at Nehemy et al. (2022) <https://doi.org/10.20383/102.0554>. Phenocam data is available at <https://phenocam.sr.unh.edu/webcam/sites/canadaOBS/>.

Acknowledgments

The authors are grateful for the field assistance of Richard Belchamber, Megan Horachek, Bruce Johnson, Taylor Kosokowsky, Rafaella Mayrinck, Cody Millar, Dyan Pratt, and Beckett Stark (alphabetically). The authors thank Megan Horachek for her assistance in generating the map for this study. The authors are especially thankful to Taylor Kosokowsky and Beckett Stark for continued field assistance and Taylor for assistance with cryogenic extractions. The authors thank Kim Janzen for all the assistance with laser and mass spec analyses and edits. We thank many BERMS researchers and technicians that have maintained the sites. We are especially grateful to Alan Barr for providing the snow depth data. The authors thank Hillslope Hydrology Lab members for feedback on the perceptual model. The authors thank Pertti Ala-aho and two anonymous reviewers for constructive feedback. This study was supported by the American Geophysical – Horton Research Grant 2019 awarded to Nehemy, an NSERC CREATE in Water Security, and an NSERC Discovery Grant to Laroque and McDonnell. The BERMS sites (OJP and OBS) are located on Treaty 6 territory, which is the traditional territory of the Cree, Saulteaux, Stoney, Nakota, Dakota, and homeland of the Metis.

References

- Adams, W. W., III, Demmig-Adams, B., Rosenstiel, T. N., Brightwell, A. K., & Ebbert, V. (2002). Photosynthesis and photoprotection in overwintering plants. *Plant Biology*, 4(5), 545–557. <https://doi.org/10.1055/s-2002-35434>
- Allen, S. T., Kirchner, J. W., Braun, S., Siegwolf, R. T. W., & Goldsmith, G. R. (2019). Seasonal origins of soil water used by trees. *Hydrology and Earth System Sciences*, 23(2), 1199–1210. <https://doi.org/10.5194/hess-23-1199-2019>
- Améglio, T., Cochard, H., & Ewers, F. W. (2001). Stem diameter variations and cold hardiness in walnut trees. *Journal of Experimental Botany*, 52(364), 2135–2142. <https://doi.org/10.1093/jexbot/52.364.2135>
- Barbeta, A., Burlett, R., Martín-Gómez, P., Fréjaville, B., Devert, N., Wingate, L., et al. (2022). Evidence for distinct isotopic compositions of sap and tissue water in tree stems: Consequences for plant water source identification. *New Phytologist*, 233(3), 1121–1132. <https://doi.org/10.1111/nph.17857>
- Barbeta, A., Jones, S. P., Clavé, L., Wingate, L., Gimeno, T. E., Fréjaville, B., et al. (2019). Unexplained hydrogen isotope offsets complicate the identification and quantification of tree water sources in a riparian forest. *Hydrology and Earth System Sciences*, 23(4), 2129–2146. <https://doi.org/10.5194/hess-23-2129-2019>
- Barichivich, J., Briffa, K. R., Myneni, R. B., Osborn, T. J., Melvin, T. M., Ciais, P., et al. (2013). Large-scale variations in the vegetation growing season and annual cycle of atmospheric CO₂ at high northern latitudes from 1950 to 2011. *Global Change Biology*, 19(10), 3167–3183. <https://doi.org/10.1111/gcb.12283>
- Barr, A. G., van der Kamp, G., Black, T. A., McCaughey, J. H., & Nesic, Z. (2012). Energy balance closure at the BERMS flux towers in relation to the water balance of the White Gull Creek watershed 1999–2009. *Agricultural and Forest Meteorology*, 153, 3–13. <https://doi.org/10.1016/j.agrformet.2011.05.017>
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B*, 57(1), 289–300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>
- Bergh, J., & Linder, S. E. (1999). Effects of soil warming during spring on photosynthetic recovery in boreal Norway spruce stands. *Global Change Biology*, 5(3), 245–253. <https://doi.org/10.1046/j.1365-2486.1999.00205.x>
- Bowling, D. R., Logan, B. A., Hufkens, K., Aubrecht, D. M., Richardson, A. D., Burns, S. P., et al. (2018). Limitations to winter and spring photosynthesis of a Rocky Mountain subalpine forest. *Agricultural and Forest Meteorology*, 252, 241–255. <https://doi.org/10.1016/j.agrformet.2018.01.025>
- Bowling, D. R., Schulze, E. S., & Hall, S. J. (2017). Revisiting streamside trees that do not use stream water: Can the two water worlds hypothesis and snowpack isotopic effects explain a missing water source? *Ecohydrology*, 10(1), e1771. <https://doi.org/10.1002/eco.1771>
- Brinkmann, N., Seeger, S., Weiler, M., Buchmann, N., Eugster, W., & Kahmen, A. (2018). Employing stable isotopes to determine the residence times of soil water and the temporal origin of water taken up by *Fagus sylvatica* and *Picea abies* in a temperate forest. *New Phytologist*, 219(4), 1300–1313. <https://doi.org/10.1111/nph.15255>
- Brooks, R., Barnard, H. R., Coulombe, R., & McDonnell, J. J. (2010). Ecohydrologic separation of water between trees and streams in a Mediterranean climate. *Nature Geoscience*, 3(2), 100–104. <https://doi.org/10.1038/ngeo722>
- Carrière, S. D., Martin-StPaul, N. K., Cakpo, C. B., Patris, N., Gillon, M., Chalikhakis, K., et al. (2020). The role of deep vadose zone water in tree transpiration during drought periods in karst settings – Insights from isotopic tracing and leaf water potential. *Science of the Total Environment*, 699, 134332. <https://doi.org/10.1016/j.scitotenv.2019.134332>
- Chan, A. M., & Bowling, D. R. (2017). Assessing the thermal dissipation sap flux density method for monitoring cold season water transport in seasonally snow-covered forests. *Tree Physiology*, 37(7), 984–995. <https://doi.org/10.1093/treephys/tpx049>
- Chang, C. Y.-Y., Bräutigam, K., Hüner, N. P. A., & Ensminger, I. (2021). Champions of winter survival: Cold acclimation and molecular regulation of cold hardiness in evergreen conifers. *New Phytologist*, 229(2), 675–691. <https://doi.org/10.1111/nph.16904>
- Chen, X., Liang, S., Cao, Y., He, T., & Wang, D. (2015). Observed contrast changes in snow cover phenology in northern middle and high latitudes from 2001–2014. *Scientific Reports*, 5(1), 16820. <https://doi.org/10.1038/srep16820>
- Chen, Y., Helliker, B. R., Tang, X., Li, F., Zhou, Y., & Song, X. (2020). Stem water cryogenic extraction biases estimation in deuterium isotope composition of plant source water. *Proceedings of the National Academy of Sciences*, 117(52), 33345–33350. <https://doi.org/10.1073/pnas.2014422117>
- Clearwater, M. J., Meinzer, F. C., Andrade, J. L., Goldstein, G., & Holbrook, N. M. (1999). Potential errors in measurement of nonuniform sap flow using heat dissipation probes. *Tree Physiology*, 19(10), 681–687. <https://doi.org/10.1093/treephys/19.10.681>
- Coles, A. E., & McDonnell, J. J. (2018). Fill and spill drives runoff connectivity over frozen ground. *Journal of Hydrology*, 558, 115–128. <https://doi.org/10.1016/j.jhydrol.2018.01.016>
- Dawson, T. E., & Ehleringer, J. R. (1991). Streamside trees that do not use stream water. *Nature*, 350(6316), 335–337. <https://doi.org/10.1038/350335a0>
- Deslauriers, A., Morin, H., Urbinati, C., & Carrer, M. (2003). Daily weather response of balsam fir (*Abies balsamea* (L.) Mill.) stem radius increment from dendrometer analysis in the boreal forests of Québec (Canada). *Trees*, 17(6), 477–484. <https://doi.org/10.1007/s00468-003-0260-4>
- Dunn, O. J. (1964). Multiple comparisons using rank sums. *Technometrics*, 6(3), 241–252. <https://doi.org/10.1080/00401706.1964.10490181>

- Eitel, J. U. H., Griffin, K. L., Boelman, N. T., Maguire, A. J., Meddens, A. J. H., Jensen, J., et al. (2020). Remote sensing tracks daily radial wood growth of evergreen needleleaf trees. *Global Change Biology*, 26(7), 4068–4078. <https://doi.org/10.1111/gcb.15112>
- Epstein, S., & Mayeda, T. (1953). Variation of O18 content of waters from natural sources. *Geochimica et Cosmochimica Acta*, 4(5), 213–224. [https://doi.org/10.1016/0016-7037\(53\)90051-9](https://doi.org/10.1016/0016-7037(53)90051-9)
- Evaristo, J., Jameel, Y., & Chun, K. P. (2021). Implication of stem water cryogenic extraction experiment for an earlier study is not supported with robust context-specific statistical assessment. *Proceedings of the National Academy of Sciences*, 118(17). <https://doi.org/10.1073/pnas.2100365118>
- Evaristo, J., Jasechko, S., & McDonnell, J. J. (2015). Global separation of plant transpiration from groundwater and streamflow. *Nature*, 525(7567), 91–94. <https://doi.org/10.1038/nature14983>
- Evaristo, J., Kim, M., van Haren, J., Pangle, L. A., Harman, C. J., Troch, P. A., & McDonnell, J. J. (2019). Characterizing the fluxes and age distribution of soil water, plant water, and deep percolation in a model tropical ecosystem. *Water Resources Research*, 55(4), 3307–3327. <https://doi.org/10.1029/2018WR023265>
- Finkenbinder, C., Good, S., Brooks, J., Allen, S., & Sasidharan, S. (2021). *The physical basis for ecohydrologic separation: The roles of soil hydraulics and climate*. Research Square. preprint. In Review. <https://doi.org/10.21203/rs.3.rs-1024190/v1>
- Flo, V., Martínez-Vilalta, J., Steppe, K., Schuldt, B., & Poyatos, R. (2019). A synthesis of bias and uncertainty in sap flow methods. *Agricultural and Forest Meteorology*, 271, 362–374. <https://doi.org/10.1016/j.agrformet.2019.03.012>
- Gaines, K. P., Meinzer, F. C., Duffy, C. J., Thomas, E. M., & Eissenstat, D. M. (2016). Rapid tree water transport and residence times in a Pennsylvania catchment. *Ecohydrology*, 9(8), 1554–1565. <https://doi.org/10.1002/eco.1747>
- Geißler, K., Heblack, J., Uugulu, S., Wanke, H., & Blaum, N. (2019). Partitioning of water between differently sized shrubs and potential groundwater recharge in a Semiarid Savanna in Namibia. *Frontiers of Plant Science*, 10. <https://doi.org/10.3389/fpls.2019.01411>
- Geris, J., Tetzlaff, D., McDonnell, J., Anderson, J., Paton, G., & Soulsby, C. (2015). Ecohydrological separation in wet, low energy northern environments? A preliminary assessment using different soil water extraction techniques. *Hydrological Processes*, 29(25), 5139–5152. <https://doi.org/10.1002/hyp.10603>
- Germer, K., & Braun, J. (2015). Macropore-matrix water flow interaction around a vertical macropore embedded in fine sand-laboratory investigations. *Vadose Zone Journal*, 14(7), vzj2014.03.0030. <https://doi.org/10.2136/vzj2014.03.0030>
- Goldsmith, G. R., Muñoz-Villiers, L. E., Holwerda, F., McDonnell, J. J., Asbjornsen, H., & Dawson, T. E. (2012). Stable isotopes reveal linkages among ecohydrological processes in a seasonally dry tropical montane cloud forest. *Ecohydrology*, 5(6), 779–790. <https://doi.org/10.1002/eco.268>
- Granier, A. (1987). Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiol.* 3(4), 309–320. <https://doi.org/10.1093/treephys/3.4.309>
- Güney, A., Gülsoy, S., Şentürk, Ö., Niessner, A., & Küppers, M. (2020). Environmental control of daily stem radius increment in the montane conifer *Cedrus libani*. *Journal of Forestry Research*, 31(4), 1159–1171. <https://doi.org/10.1007/s11676-019-00983-0>
- Hahn, W. J., Rempe, D. M., Dralle, D. N., Dawson, T. E., & Dietrich, W. E. (2020). Oak transpiration drawn from the weathered bedrock vadose zone in the summer dry season. *Water Resources Research*, 56(11), e2020WR027419. <https://doi.org/10.1029/2020WR027419>
- Hamilton, I. L. (2019). *The interactions of jack pine trees (Pinus banksiana) and water* (Doctoral dissertation). University of Saskatchewan. Retrieved from <https://harvest.usask.ca/handle/10388/12336>
- Harpold, A. A., Molotch, N. P., Musselman, K. N., Bales, R. C., Kirchner, P. B., Litvak, M., & Brooks, P. D. (2015). Soil moisture response to snowmelt timing in mixed-conifer subalpine forests. *Hydrological Processes*, 29(12), 2782–2798. <https://doi.org/10.1002/hyp.10400>
- He, Q.-Y., Yan, M.-J., Miyazawa, Y., Chen, Q.-W., Cheng, R.-R., Otsuki, K., et al. (2020). Sap flow changes and climatic responses over multiple-year treatment of rainfall exclusion in a sub-humid black locust plantation. *Forest Ecology and Management*, 457, 117730. <https://doi.org/10.1016/j.foreco.2019.117730>
- Hervé-Fernández, P., Oyarzún, C., Brumbt, C., Huygens, D., Bodé, S., Verhoest, N. E. C., & Boeckx, P. (2016). Assessing the ‘two water worlds’ hypothesis and water sources for native and exotic evergreen species in south-central Chile. *Hydrological Processes*, 30(23), 4227–4241. <https://doi.org/10.1002/hyp.10984>
- Jasechko, S., Birks, S. J., Gleeson, T., Wada, Y., Fawcett, P. J., Sharp, Z. D., et al. (2014). The pronounced seasonality of global groundwater recharge. *Water Resources Research*, 50(11), 8845–8867. <https://doi.org/10.1002/2014WR015809>
- Juhlke, T. R., Van Geldern, R., Barth, J. A. C., Bendix, J., Bräuning, A., Garel, E., et al. (2021). Temporal offset between precipitation and water uptake of Mediterranean pine trees varies with elevation and season. *Science of the Total Environment*, 755, 142539. <https://doi.org/10.1016/j.scitotenv.2020.142539>
- Kalyn, A. L., & Van Rees, K. C. J. (2006). Contribution of fine roots to ecosystem biomass and net primary production in black spruce, aspen, and jack pine forests in Saskatchewan. *Agricultural and Forest Meteorology*, 140(1), 236–243. <https://doi.org/10.1016/j.agrformet.2005.08.019>
- King, G., Fonti, P., Nievergelt, D., Büntgen, U., & Frank, D. (2013). Climatic drivers of hourly to yearly tree radius variations along a 6°C natural warming gradient. *Agricultural and Forest Meteorology*, 168, 36–46. <https://doi.org/10.1016/j.agrformet.2012.08.002>
- Knighton, J., Kuppel, S., Smith, A., Soulsby, C., Sprenger, M., & Tetzlaff, D. (2020). Using isotopes to incorporate tree water storage and mixing dynamics into a distributed ecohydrologic modelling framework. *Ecohydrology*, 13(3), e2201. <https://doi.org/10.1002/eco.2201>
- Knighton, J., Souter-Kline, V., Volkmann, T., Troch, P. A., Kim, M., Harman, C. J., et al. (2019). Seasonal and topographic variations in ecohydrological separation within a small, temperate, snow-influenced catchment. *Water Resources Research*, 55(8), 6417–6435. <https://doi.org/10.1029/2019WR025174>
- Koeniger, P., Marshall, J. D., Link, T., & Mulch, A. (2011). An inexpensive, fast, and reliable method for vacuum extraction of soil and plant water for stable isotope analyses by mass spectrometry. *Rapid Communications in Mass Spectrometry*, 25(20), 3041–3048. <https://doi.org/10.1002/rcm.5198>
- Kozłowski, T. T., & Winget, C. H. (1964). Diurnal and seasonal variation in radii of tree stems. *Ecology*, 45(1), 149–155. <https://doi.org/10.2307/1937115>
- Kruskal, W. H., & Wallis, W. A. (1952). Use of ranks in one-criterion variance analysis. *Journal of the American Statistical Association*, 47(260), 583–621. <https://doi.org/10.1080/01621459.1952.10483441>
- Kühnhammer, K., Dahlmann, A., Iraheta, A., Gerchow, M., Birkel, C., Marshall, J. D., & Beyer, M. (2022). Continuous in situ measurements of water stable isotopes in soils, tree trunk and root xylem: Field approval. *Rapid Communications in Mass Spectrometry*, 36(5), e9232. <https://doi.org/10.1002/rcm.9232>
- Lawrence, D. M., & Slater, A. G. (2010). The contribution of snow condition trends to future ground climate. *Climate Dynamics*, 34(7), 969–981. <https://doi.org/10.1007/s00382-009-0537-4>
- Lieffers, V. J., & Rothwell, R. L. (1987). Rooting of peatland black spruce and tamarack in relation to depth of water table. *Canadian Journal of Botany*, 65(5), 817–821. <https://doi.org/10.1139/b87-111>

- Linderholm, H. W. (2006). Growing season changes in the last century. *Agricultural and Forest Meteorology*, 137(1), 1–14. <https://doi.org/10.1016/j.agrformet.2006.03.006>
- Magh, R.-K., Eiferle, C., Burzlaff, T., Dannenmann, M., Rennenberg, H., & Dubbert, M. (2020). Competition for water rather than facilitation in mixed beech-fir forests after drying-wetting cycle. *Journal of Hydrology*, 587, 124944. <https://doi.org/10.1016/j.jhydrol.2020.124944>
- Maillet, J., Nehemy, M. F., Mood, B., Pappas, C., Bonsal, B., & Laroque, C. (2022). A multi-scale dendroclimatological analysis of four common species in the southern Canadian boreal forest. *Dendrochronologia*, 72, 125936. <https://doi.org/10.1016/j.dendro.2022.125936>
- Matheny, A. M., Bohrer, G., Vogel, C. S., Morin, T. H., He, L., de Frasson, R. P. M., et al. (2014). Species-specific transpiration responses to intermediate disturbance in a northern hardwood forest. *Journal of Geophysical Research: Biogeosciences*, 119, 2292–2311. <https://doi.org/10.1002/2014JG002804>
- McDonnell, J. J., Evaristo, J., Bladon, K. D., Buttle, J., Creed, I. F., Dymond, S. F., et al. (2018). Water sustainability and watershed storage. *Nature Sustainability*, 1(8), 378–379. <https://doi.org/10.1038/s41893-018-0099-8>
- Meinzer, F. C., Brooks, J. R., Domec, J.-C., Gartner, B. L., Warren, J. M., Woodruff, D. R., et al. (2006). Dynamics of water transport and storage in conifers studied with deuterium and heat tracing techniques. *Plant, Cell and Environment*, 29(1), 105–114. <https://doi.org/10.1111/j.1365-3040.2005.01404.x>
- Menekes, D., Rinderer, M., Seeger, S., & Orlowski, N. (2021). Ecohydrological travel times derived from in situ stable water isotope measurements in trees during a semi-controlled pot experiment. *Hydrology and Earth System Sciences Discussions*, 25(8), 1–34. <https://doi.org/10.5194/hess-2020-674>
- Miguez-Macho, G., & Fan, Y. (2021). Spatiotemporal origin of soil water taken up by vegetation. *Nature*, 598(7882), 624–628. <https://doi.org/10.1038/s41586-021-03958-6>
- Millar, C., Pratt, D., Schneider, D. J., & McDonnell, J. J. (2018). A comparison of extraction systems for plant water stable isotope analysis. *Rapid Communications in Mass Spectrometry*, 32(13), 1031–1044. <https://doi.org/10.1002/rcm.8136>
- Morrison, J., Brockwell, T., Merren, T., Fourel, F., & Phillips, A. M. (2001). On-line high-precision stable hydrogen isotopic analyses on nanoliter water samples. *Analytical Chemistry*, 73(15), 3570–3575. <https://doi.org/10.1021/ac001447t>
- Nehemy, M., Maillet, J., Perron, N., Pappas, C., Sonnentag, O., Baltzer, J., et al. (2022). Snowmelt water use at transpiration onset: Dataset. [Dataset]. Federated Research Data Repository. <https://doi.org/10.20383/102.0554>
- Nehemy, M. F., Millar, C., Janzen, K., Gaj, M., Pratt, D. L., Laroque, C. P., & McDonnell, J. J. (2019). 17O-excess as a detector for co-extracted organics in vapor analyses of plant isotope signatures. *Rapid Communications in Mass Spectrometry*, 33(16), 1301–1310. <https://doi.org/10.1002/rcm.8470>
- Newberry, S. L., Nelson, D. B., & Kahmen, A. (2017). Cryogenic vacuum artifacts do not affect plant water-uptake studies using stable isotope analysis. *Ecohydrology*, 10(8), e1892. <https://doi.org/10.1002/eco.1892>
- Oh, S., Adams, W. W., Demmig-Adams, B., & Koh, S. C. (2013). Seasonal photoprotective responses in needles of Korean fir (*Abies koreana*) over an altitudinal gradient on Mount Halla, Jeju Island, Korea. *Arctic Antarctic and Alpine Research*, 45(2), 238–248. <https://doi.org/10.1657/1938-4246-45.2.238>
- Oquist, G., & Huner, N. P. A. (2003). Photosynthesis of overwintering evergreen plants. *Annual Review of Plant Biology*, 54(1), 329–355. <https://doi.org/10.1146/annurev.arplant.54.072402.115741>
- Pappas, C., Matheny, A. M., Baltzer, J. L., Barr, A. G., Black, T. A., Bohrer, G., et al. (2018). Boreal tree hydrodynamics: Asynchronous, diverging, yet complementary. *Tree Physiology*, 38(7), 953–964. <https://doi.org/10.1093/treephys/tpy043>
- Pascolini-Campbell, M., Reager, J. T., Chandanpurkar, H. A., & Rodell, M. (2021). A 10 per cent increase in global land evapotranspiration from 2003 to 2019. *Nature*, 593(7860), 543–547. <https://doi.org/10.1038/s41586-021-03503-5>
- Peters, R. L., Fonti, P., Frank, D. C., Poyatos, R., Pappas, C., Kahmen, A., et al. (2018). Quantification of uncertainties in conifer sap flow measured with the thermal dissipation method. *New Phytologist*, 219(4), 1283–1299. <https://doi.org/10.1111/nph.15241>
- Peters, R. L., Pappas, C., Hurley, A. G., Poyatos, R., Flo, V., Zweifel, R., et al. (2021). Assimilate, process and analyse thermal dissipation sap flow data using the TREX R package. *Methods in Ecology and Evolution*, 12(2), 342–350. <https://doi.org/10.1111/2041-210X.13524>
- Phillips, S. L., & Ehleringer, J. R. (1995). Limited uptake of summer precipitation by bigtooth maple (*Acer grandidentatum* Nutt) and Gambel's Oak (*Quercus gambelii* Nutt). *Trees*, 9(4), 214–219. <https://doi.org/10.1007/BF00195275>
- Pierrat, Z., Nehemy, M. F., Roy, A., Magney, T., Parazoo, N. C., Laroque, C., et al. (2021). Tower-based remote sensing reveals mechanisms behind a two-phased spring transition in a mixed-species boreal forest. *Journal of Geophysical Research: Biogeosciences*, 126, e2020JG006191. <https://doi.org/10.1029/2020JG006191>
- Pulliainen, J., Aurela, M., Laurila, T., Aalto, T., Takala, M., Salminen, M., et al. (2017). Early snowmelt significantly enhances boreal springtime carbon uptake. *Proceedings of the National Academy of Sciences*, 114(42), 11081–11086. <https://doi.org/10.1073/pnas.1707889114>
- Radolinski, J., Pangle, L., Klaus, J., & Stewart, R. (2020). Testing the ‘Two Water Worlds’ hypothesis under variable preferential flow conditions. <https://doi.org/10.13140/RG.2.2.26773.35049>
- R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Richardson, A. D. (2019). Tracking seasonal rhythms of plants in diverse ecosystems with digital camera imagery. *New Phytologist*, 222(4), 1742–1750. <https://doi.org/10.1111/nph.15591>
- Richardson, A. D., Hufkens, K., Milliman, T., Aubrecht, D. M., Chen, M., Gray, J. M., et al. (2018). Tracking vegetation phenology across diverse North American biomes using PhenoCam imagery. *Scientific Data*, 5(1), 180028. <https://doi.org/10.1038/sdata.2018.28>
- Richardson, A. D., Keenan, T. F., Migliavacca, M., Ryu, Y., Sonnentag, O., & Toomey, M. (2013). Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology*, 169, 156–173. <https://doi.org/10.1016/j.agrformet.2012.09.012>
- Rossi, S., Morin, H., & Deslauriers, A. (2011). Multi-scale influence of snowmelt on xylogenesis of black spruce. *Arctic Antarctic and Alpine Research*, 43(3), 457–464. <https://doi.org/10.1657/1938-4246-43.3.457>
- Schlesinger, W. H., & Jasechko, S. (2014). Transpiration in the global water cycle. *Agricultural and Forest Meteorology*, 189(190), 115–117. <https://doi.org/10.1016/j.agrformet.2014.01.011>
- Scholander, P. F., Bradstreet, E. D., Hemmingsen, E. A., & Hammel, H. T. (1965). Sap pressure in vascular plants: Negative hydrostatic pressure can be measured in plants. *Science*, 148(3668), 339–346. <https://doi.org/10.1126/science.148.3668.339>
- Seeger, S., & Weiler, M. (2021). Temporal dynamics of tree xylem water isotopes: In-situ monitoring and modelling. *Biogeosciences Discussions*, 1–41. <https://doi.org/10.5194/bg-2021-35>
- Sevanto, S., Suni, T., Pumpanen, J., Grönholm, T., Kolari, P., Nikinmaa, E., et al. (2006). Wintertime photosynthesis and water uptake in a boreal forest. *Tree Physiology*, 26(6), 749–757. <https://doi.org/10.1093/treephys/26.6.749>

- Seyednasrollah, B., Bowling, D. R., Cheng, R., Logan, B. A., Magney, T. S., Frankenberg, C., et al. (2021). Seasonal variation in the canopy color of temperate evergreen conifer forests. *New Phytologist*, 229(5), 2586–2600. <https://doi.org/10.1111/nph.17046>
- Seyednasrollah, B., Young, A. M., Hufkens, K., Milliman, T., Friedl, M. A., Frolking, S., & Richardson, A. D. (2019). Tracking vegetation phenology across diverse biomes using Version 2.0 of the PhenoCam Dataset. *Scientific Data*, 6(1), 222. <https://doi.org/10.1038/s41597-019-0229-9>
- Shook, K. (2015). WISKI: Acquires data from a WISKI web server. Retrieved from www.usask.ca/hydrology/RPkgs.php/
- Snelgrove, J. R., Buttle, J. M., Kohn, M. J., & Tetzlaff, D. (2020). Assessing ecohydrological separation in a northern mixed forest biome using stable isotopes. *Hydrology and Earth System Sciences Discussions*, 1–30. <https://doi.org/10.5194/hess-2020-592>
- Sprenger, M., & Allen, S. T. (2020). What ecohydrologic separation is and where we can go with it. *Water Resources Research*, 56(7), e2020WR027238. <https://doi.org/10.1029/2020WR027238>
- Sprenger, M., Tetzlaff, D., Buttle, J., Laudon, H., Leistert, H., Mitchell, C. P. J., et al. (2018). Measuring and modeling stable isotopes of mobile and bulk soil water. *Vadose Zone Journal*, 17(1), 170149. <https://doi.org/10.2136/vzj2017.08.0149>
- Steppe, K., De Pauw, D. J. W., Doody, T. M., & Teskey, R. O. (2010). A comparison of sap flux density using thermal dissipation, heat pulse velocity and heat field deformation methods. *Agricultural and Forest Meteorology*, 150(7), 1046–1056. <https://doi.org/10.1016/j.agrformet.2010.04.004>
- Steppe, K., De Pauw, D. J. W., Lemeur, R., & Vanrolleghem, P. A. (2006). A mathematical model linking tree sap flow dynamics to daily stem diameter fluctuations and radial stem growth. *Tree Physiology*, 26(3), 257–273. <https://doi.org/10.1093/treephys/26.3.257>
- Stohr, A., & Losch, R. (2004). Xylem sap flow and drought stress of *Fraxinus excelsior* saplings. *Tree Physiology*, 24(2), 169–180. <https://doi.org/10.1093/treephys/24.2.169>
- Strong, W. L., & Roi, G. L. (1983). Root-system morphology of common boreal forest trees in Alberta, Canada. *Canadian Journal of Forest Research*, 13(6), 1164–1173. <https://doi.org/10.1139/x83-155>
- Tardif, J., Flannigan, M., & Bergeron, Y. (2001). An analysis of the daily radial activity of 7 boreal tree species, Northwestern Quebec. *Environmental Monitoring and Assessment*, 67(1), 141–160. <https://doi.org/10.1023/A:1006430422061>
- Tetzlaff, D., Buttle, J., Carey, S. K., Kohn, M. J., Laudon, H., McNamara, J. P., et al. (2021). Stable isotopes of water reveal differences in plant – Soil water relationships across northern environments. *Hydrological Processes*, 35(1), e14023. <https://doi.org/10.1002/hyp.14023>
- Treydte, K., Lehmann, M. M., Wyszczynski, T., & Pfautsch, S. (2021). Radial and axial water movement in adult trees recorded by stable isotope tracing. *Tree Physiology*, 41(12), 2248–2261. <https://doi.org/10.1093/treephys/tpab080>
- Turcotte, A., Morin, H., Krause, C., Deslauriers, A., & Thibeault-Martel, M. (2009). The timing of spring rehydration and its relation with the onset of wood formation in black spruce. *Agricultural and Forest Meteorology*, 149(9), 1403–1409. <https://doi.org/10.1016/j.agrformet.2009.03.010>
- Wei, Z., Yoshimura, K., Wang, L., Miralles, D. G., Jasechko, S., & Lee, X. (2017). Revisiting the contribution of transpiration to global terrestrial evapotranspiration. *Geophysical Research Letters*, 44(6), 2792–2801. <https://doi.org/10.1002/2016GL072235>
- Winget, C. H., & Kozlowski, T. T. (1964). Winter shrinkage in stems of forest trees. *Journal of Forestry*, 62(5), 335–337. <https://doi.org/10.1093/jof/62.5.335>
- Xu, X., Guan, H., Skrzypek, G., & Simmons, C. T. (2019). Root-zone moisture replenishment in a native vegetated catchment under Mediterranean climate. *Hydrological Processes*, 33(18), 2394–2407. <https://doi.org/10.1002/hyp.13475>
- Young-Robertson, J. M., Bolton, W. R., Bhatt, U. S., Cristóbal, J., & Thoman, R. (2016). Deciduous trees are a large and overlooked sink for snowmelt water in the boreal forest. *Scientific Reports*, 6(1), 29504. <https://doi.org/10.1038/srep29504>
- Zhang, T. (2005). Influence of the seasonal snow cover on the ground thermal regime: An overview. *Reviews of Geophysics*, 43(4). <https://doi.org/10.1029/2004rg000157>
- Zhao, P., Tang, X., Zhao, P., & Tang, J. (2018). Temporal partitioning of water between plants and hillslope flow in a subtropical climate. *Catena*, 165, 133–144. <https://doi.org/10.1016/j.catena.2018.01.031>
- Zuocco, G., Amin, A., Frenress, J., Engel, M., Marchina, C., Anfodillo, T., et al. (2020). A comparative study of plant water extraction methods for isotopic analyses: Scholander-type pressure chamber vs. cryogenic vacuum distillation. *Hydrology and Earth System Sciences Discussions*, 1–23. <https://doi.org/10.5194/hess-2020-446>
- Zweifel, H. M., Buchmann, N., & Eugster, W. (2016). Are trees able to grow in periods of stem shrinkage? *New Phytologist*, 211(3), 839–849. <https://doi.org/10.1111/nph.13995>
- Zweifel, R., & Häslér, R. (2000). Frost-induced reversible shrinkage of bark of mature subalpine conifers. *Agricultural and Forest Meteorology*, 102(4), 213–222. [https://doi.org/10.1016/S0168-1923\(00\)00135-0](https://doi.org/10.1016/S0168-1923(00)00135-0)
- Zweifel, R., & Häslér, R. (2001). Dynamics of water storage in mature subalpine *Picea abies*: Temporal and spatial patterns of change in stem radius. *Tree Physiology*, 21(9), 561–569. <https://doi.org/10.1093/treephys/21.9.561>