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Water sources for red maple trees in a northern hardwood forest under a changing climate

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Abstract

Climate models project increased growing season air temperatures and decreased depth and duration of winter snowpack for the north-eastern United States, leading to greater frequency of soil freeze/thaw cycles in winter over the next century. We utilized the Climate Change Across Seasons Experiment (CCASE) at Hubbard Brook Experimental Forest in New Hampshire to determine how projected changes in climate in this region affect the depth from which trees take up water, which to our knowledge has yet to be determined. We determined the stable isotopic composition of water in soils and branch xylem three times throughout the growing season to partition potential sources of water for red maple (*Acer rubrum*) trees. Using a Bayesian mixing model approach, we determined that all trees used similar water sources in the early (June) and mid (July) growing season. However, in the late growing season (August), trees exposed to ambient and warmer growing season soil temperatures took up more than 40% of their water from between 90- and 100-cm soil depth, likely due to greater water availability at this depth. In contrast, those trees exposed to soil freeze/thaw cycles in winter utilized water from all depths (0- 100 cm) evenly (8- 10%), possibly due to soil freezing causing compensatory root growth in the following growing season, compared with trees in the reference and warmed plots. These results demonstrate that the projected changes in climate for the north-eastern United States are likely to alter the depth from which trees access water, especially in the late growing season.

KEYWORDS

Acer rubrum, climate change, soil depth, stable isotopes, water uptake

1 INTRODUCTION

The north-eastern United States is projected to experience a rise in air temperatures throughout the growing season, a decrease in the winter snowpack, and an increased frequency of droughts over the next century (Hayhoe et al., 2007), which together will alter soil temperatures and water availability throughout the snow-free season (hence-forth 'growing season'). By the end of the next century, it is expected that mean annual air temperatures in the north-eastern United States will be 2.9- 5.3°C greater than the 1970- 1999 mean (Hayhoe et al., 2007). In winter, the snowpack is expected to shrink in depth and duration (Reinmann, Susser, Demaria, & Templer, 2019), causing increased frequency of soil freeze/thaw cycles in winter (Campbell et al., 2010) in this region. With projected changes in climate that will alter soil temperatures, it is important to understand how these changes in climate might affect water uptake by dominant trees. Trees in temperate forests such as those in the north-eastern United States have a large effect on water cycling patterns because

water uptake, the process resulting from transpiration, makes up the majority of evapotranspiration(Jasechko et al., 2013). Droughts that cause a reduction in water availability can impair the ability for trees to get sufficient water, possibly leading to desiccation for trees in temperate forests (Breda, Hue, Granier, & Dreyer, 2006; Granier et al., 2007).

Warmer soils in the growing season increase rates of water uptake by temperate trees in the north-eastern United States (Juice, Templer, Phillips, Ellison, & Pelini, 2016; Harrison et al., in press). However, soil freezing that is associated with a smaller snowpack in winter induces root damage (Comerford et al., 2013; Tierney et al., 2001) and decreases rates of water (Harrison et al., 2020; Robitaille, Boutin, & Lachance, 1995) and nutrient uptake capacity (Sanders-DeMott,Sorensen, Reinmann, & Templer, 2018) by roots. In order to examine the combined effects of climate change across seasons, we exposed temperate forest trees to soil warming (+5°C) in the growing season and increased frequency of soil freeze/thaw cycles in winter in forests at the Hubbard Brook Experimental Forest **(HBEF)** in New Hampshire to determine how changes in soil temperatures affect forest ecosystem processes such as water uptake (Templer et al., 2017). We previously found in the same soil temperature manipulation experiment we utilize here that redmaple trees had higher rates of water uptake in response to soil warming, and surprisingly, these elevated rates of water uptake were not affected by soil freeze/thaw cydes in the previous winter when also exposed to soil warming in the growing season (Harrison et al., in press). It is possible that because of the negative effects of soil freeze/thaw cycles on fine roots, uptake of water from various depths of the soil profile is also affected, which, combined with increased drought frequency, could have harmful effects on the water dynamics of northernhardwood forests.

It is possible that when combined with growing season warming, the lack of effect of soil freeze/thaw cycles in winter on water uptake by red maple trees in the growing season at Hubbard Brook, as indicated by Harrison et al. (in press) in this same study, is due to changes in depth from which these trees access water. Trees are known to have belowground rooting strategies that enable them to access water, where it is most available throughout the growing season. For example , past work in arid environments, where roots often grow throughout the soil surface to 2- to 3-m depth to enhance nutrient and water uptake (McCulley, Jobbagy, Pockman, &Jackson, 2004), shows that plants in these areas often switch their water source seasonally from shallow to deep soil water when water is more available at greater soil depths than in shallow soil depths (G6mez-Navarro , Pataki, Bowen, & Oerter, 2019; Liu et al., 2019; Schwinning, Davis, Richardson, & Ehleringer, 2002; Smith, Wellington, Nachlinger, & Fox, 1991). Trees in arid environments also change their water source to deeper soils as shallow water becomes less available in response to weather events, such as heat waves and droughts (Eggemeyer et al., 2009; Goebel & Lascano, 2019; Moore, Li, Kui , & West, 2016; Snyder & Williams, 2003; Williams & Ehleringer, 2000). With climate change, tree species that are able to switch between water sources may be at an advantage over those that are limited in their ability to access water from a variety of soil depths. However, the ability to switch between water sources is limited by the depth and distribution of functional roots (Ehleringer& Dawson,1992), and trees in northern hardwood forests, such as those at **HBEF,** have more than 90% of their fine root biomass in the top 10 cm of the soil profile (Yanai, Park, & Hamburg, 2006). The greater root biomass in shallow soils may constrain the ability for northern hardwood to switch to deeper soils when water is more available there, but to our knowledge, the depth from which northern hardwood trees take up water has not yet been determined. In addition, the known detrimental effects of soil freezing on root health (Comerford et al., 2013; Tierney et al., 2001) and nutrient uptake capacity (Campbell, Socci, & Templer, 2014; Sanders-DeMott et al., 2018) could also diminish the ability of these trees to change the depths from which they access water throughout the growingseason.

Natural abundance stable isotopic composition of water provides a powerful and minimally destructive way of determining the depth from which trees take up water. Given sufficient differences in the isotopic signatures of oxygen (O) and hydrogen (H) across various depths in soil, plant xylem water canbe analysed for its stable isotopic content of water, and the depths from which trees take up water can be determined. Evaporation, which causes fractionation of water isotopes at the soil surface, typically results in enrichment of heavy isotopes (both ^{18}O and ^{2}H) in the remaining water pools. Because of decreased rates of evaporation with increased soil depth, isotopic values of water typically decrease with soil depth (e.g., Barnes & Allison, 1983; Ehleringer & Dawson, 1992; Grossiord et al., 2017),allowing researchers to use the gradient in soil water isotopic composition to examine sources of water for plants. In addition, relatively low values of deuterium-excess (hereafter 'd-excess1 indicate a water source that has relatively high rates of evaporation, suggesting a relatively shallow depth from which roots take up water compared with higher values of d-excess that indicate a water source less affected by evaporation and a relatively deep source of water for plants (Flanagan, Orchard, Tremel, & Rood, 2019; Matheny et al., 2017; Simonin et al., 2014).

Some recent studies indicate there might be fractionation with water uptake, but the mechanisms are not fully understood (Vargas, Schaffer, Yuhong, & Sternberg, 2017; Barbeta et al., 2018), whereas other studies show that fractionation with water uptake does not ocrur (Dawson & Ehleringer, 1993; Zimmerman, Ehhalt, & Munnich, 1967). The natural abundance stable isotopic composition of water has been used extensively in the past for partitioning water sources, primarily in arid environments and across natural environmental gradients such as with proximity to surface water (Dawson & Ehleringer, 1991; Mensforth, Thorburn, Tyerman, & Walker, 1994; Wei, Fang Liu, Zhao, & Li, 2013; White, Cook, Lawrence, & Broecker , 1985). We are aware of one study in a semi-arid woodland that evaluated the sources of water for co-existing grasses and trees in response to experimentally induced increases in year-round soil temperature (Grossiord et al., 2018). In that study soil warming led grasses to take up more water from deeper soils and juniper trees to take up more water from shallow soil depths, whereas pilion pines did

notalter the depth from which they took up water, compared with under ambient soil temperature conditions. However, we are unaware of any studies that have utilized measurements of stable isotopic composition of plant and soil water to determine how experimental changes in soil temperatures impact the depth from which trees in a northern hardwood forest take up water.

Here, we describe the effects of experimental changes in soil temperatures throughout the year, with warmer soil temperatures in the growing season and increased frequency of soil freeze/thaw cycles in winter, on the depth from which red maple trees in a northern hardwood forest take up water. We determined the stable isotopic composition of water in soils and branch xylem three times throughout the 2018 growing season to partition potential sources of water for red maple *(Acer* rubrum) trees. We measured soil water availability across the growing season and used values of branch xylem and soil water in a Bayesian mixing model framework to determine the primary depth from which trees take up water throughout the growing season. The objective of our study was to understand how climate change across seasons affects the depth from which red maple trees take up water. We aimed to determine whether, despite similar rates of water uptake in plots that experienced warming or the combination of warming and freeze/thaw cycles (Harrison et al., in press), the negative effects of freeze/thaw cycles on root health (Sanders-DeMott et al., 2018) also affects the primary depth from which trees take up water. We expected that the depth from which red maple trees take up water depends on the distribution of fine root biomass, which is primarily located in the top 10 cm. Further, we expected red maples that experience soil freeze/thaw cycles in winter to switch their water source less frequently due to the documented root injury caused by soil freeze/thaw cycles.

2 METHODS

2.1 | Study site

Our research was conducted at the HBEF, in New Hampshire, USA (43°56'N, 71°45'W), a U.S. National Science Foundation Long-Term Ecological Research (LTER) site. Forests at HBEF are dominated by northern hardwoods, with coniferous species present on higher elevation and steeper slopes. Soils consist of base-poor spodosols, specifically Typic Haplorthods that developed in gladofluvial sand and gravel, and depth to bedrock is approximately 14 m deep (Winter et al., 2008). The climate is cool, humid, and continental with mean annual precipitation of 1,400 mm falling evenly throughout the year. Winter air temperatures average -4.7°C (Bailey, Hornbeck, Campbell, & Eagar, 2003; years 1969-2000), and soil frost is present approximately 2 out of every 3 years, with an average annual maximum depth of 6 cm (Campbell et al., 2010). The site for our experiment has been undisturbed since 1920, after 30-year logging of the conifer-hardwood forest (Bailey, Hornbeck, Campbell, & Eagar, 2003). Environmental data, including soil temperature and moisture, snow, and soil frost depth, and water potential were measured during the experimental period in 2018, and a description of our methods for these measurements is presented below.

2.2 | Climate Change Across Seasons Experiment

We established Climate Change Across Seasons Experiment (CCASE) in summer 2012 at HBEF [Templer et al., 2017) to examine the effects of the 5°C increase in temperature in the snow-free season (Hayhoe et al., 2007) and rise in soil freeze/thaw cycle frequency in winter (Campbell et al., 2010) projected in this region over the next century. The six plots (each 11 x 13.5 m^2) were purposefully located to have similar tree species composition and aboveground biomass. The six plots in our experiment are each centred on at least three mature red maple (A. *rubrum)* trees, a common canopy tree in northern hardwood forests of the north-eastern United States and the focus of this study. Red maples make up 63 ± 7% basal area, and litterfall mass of red maple trees was not significantly different across the six plots in 2012 (prior to the start of the experiment; t test, $p = 0.54$). The understorey is composed primarily of American beech *(Fagus grandifolia)* saplings.

Soil temperature and snow-manipulation treatments are ongoing and began in December 2013. There are two plots with soils warmed 5°C above ambient *('warmed)* between spring snowmelt (early April) and the first snowfall in November or December (hereafter referred to as the growing season), two plots with the same warming treatment combined with soil freeze/thaw cycles induced in winter *('warmed + FTC),* and two plots with ambient soil temperature ('reference'). The *wanned* and *warmed + FTC* plots together make up the four 'treatmen't plots and are equipped with heating cables that were buried by hand 10 cm deep using a flat shovel in 2012 in parallel lines spaced 20 cm apart. *Reference* plots were similarly cut to mimic cable installation disturbance, but no cable was installed.

In the *wanned+ FTC* treatment plots, the first snow of winter is gently packed down to maintain albedo and minimize disturbance to the forest floor with subsequent shovelling. We induced soil freezing by removing snow within 24-h of snowfall events in winter. Soil freezing is operationally defined as soil temperature less than -0.5°C. After soils are frozen for 72-h, the heating cables are turned on to warm soils to 1°c to induce a 72-h thaw. The entire process of frozen 72-h and a thawing for 72-h total constitutes one soil FTC. We achieved four FTCs in the winters of both 2013/2014 and 2014/2015, two in 2015/2016, and one in 2016/2017 and two in 2017/2018.

2.3 | Environmental variables

Soil temperature (Betatherm type 10K3A1; n = 6 at 10-cm depth for all plots) and volumetric soil moisture (m^3 H_2O m^{-3} soil volume; CS 616; n = 4 per plot integrated across 0- to 30-cm depth) were logged every 5 s, and half-hourly means were stored on a CR1000 multichannel data logger (Campbell Scientific, Utah, USA). Air temperature (n = 2 sensors total) and relative humidity (RH; n = 2 sensors total)

were measured in two locations (CS215; Campbell Scientific, Utah, USA).

Soil frost and snow depth were measured weekly throughout winter using frost tubes (n = 4 per plot; Ricard, Toabiasson, & Greatorex, 1976) and a metre stick inserted into snowpack from November 30 to April 30 for all years. We report winter data only for the winter that preceded the growing season of 2018 (November 15, 2017 to April 4, 2018) as it is the focus of this study. Soil frost duration (i.e., number of days with frost) during winter was calculated as days when depth of soil frost was greater than O cm.

Soil water potential (kPa) was measured in 2018 at a nearby site at HBEF, approximately 1,500 m from the CCASE plots. Soil texture at both sites is similar, composed of loamy sand in the upper soil layers, eventually switching to gravelly sand at deeper layers (Scott Bailey, personal communication). Using four dielectric permittivity water potential sensors, one at 10-, 20-, 30-, and 50-cm soil depths (n = 4 sensors total), we processed data in 30-min intervals. We present soil water potential data for June, July, and August 2018, the months that overlap with our water isotope data.

2.4 | Root water uptake patterns

We quantified the depths from which red maple trees took up water throughout the 2018 growing season using branch xylem and soil samples collected on 3 days that represented the early (June 11), peak (July 9), and late (August 16) growing season. For the trees, branch xylem water from a 2- to 5-cm-long excised branch xylem sample from each of three mature red maple trees in each plot (n = 18 trees on each sampling day) was sampled between hours 07:00 and 12:00. Samples were taken by shooting down sunlit branches with a shotgun and taking subsamples with clippers. The samples were immediately placed in airtight scintillation vials and stored in a cooler to avoid evaporation. On the same day as branch xylem collection, we collected integrated, duplicated soil samples from the organic soil layer (Oe and Oa) and across every 10 cm down to 1 m in two soil pits but only analysed one sample for isotopic composition: one pit sampled adjacent (<5 m) to *reference* plots (n = 1 soil sample for each depth; n = 11 samples on each date; n = 33 samples total throughout the growing season) and one pit adjacent (<5 m) to treatment plots (*warmed* and *wanned*+ FTC; n = 1 soil sample for each depth; n = 11 samples on each date; n = 33 samples total throughout the growing season). Pits were 2 m wide and 1 m deep, and samples were collected from the edge of the pit facing the plots. We gently scraped away soil from the 2 cm of the soil pit exposed to air (area of soil facing the opening of the soil pit) prior to sample collection throughout the 0- to 1-m depth soil pit in case evaporation occurred from the side of the pit that was exposed to air. Soil samples were placed directly into scintillation vials and stored in a cooler with ice. Once in the laboratory, all samples were frozen until analysis. We could not collect soil samples from within the six experimental plots due to the large area of destruction required when digging soil pits and concern about damaging the buried heating cables.

Water from branch xylem and soil was extracted using a cryogenic vacuum distillation system at the Boston University Stable Isotope Lab (Boston, MA, USA). We first evacuated the extraction system, made of 0.5-in diameter glass tubing, to a baseline vacuum reading of 20 mTorr to test for leaks before the sample was extracted. A frozen sample was placed in a 1-inch diameter glass extraction system tube and further frozen with liquid nitrogen after which the system was evacuated once again. We then removed the sample from the liquid nitrogen and submerged it in boiling water, while the collection vessel (0.5-in diameter glass tubing) was submerged in liquid nitrogen. During distillation, vacuum reading went up to about 2,000 mTorr. The extraction time was approximately 60 min for both branch xylem and soil samples. We believe this extraction time is sufficient based on previous research that found that 60 min was a sufficient extraction time for all plant and soil materials (West, Patrickson, & Ehleringer, 2006). After extraction, water samples in the collection vessels were transferred to plastic cone cap scintillation vials and stored at 4°C until analysis.

All branch xylem and soil water samples were analysed for stable isotopic composition using a Liquid Isotope Water Analyser (LIWA) cavity ringdown spectrometer (Model DLT-100; Los Gatos Research, Mountain View, CA, USA) at Plymouth State University (Plymouth, NH, USA). For each date, the stable isotope ratios of hydrogen and oxygen in each water sample were determined and expressed in standard delta notation (6^2H and 6^{18}0 , respectively, %0). Deuterium-excess (=6^2H - 8 • 6^{18} 0 ; Dansgaard, 1964) was calculated for all branch xylem water samples. Precision of measurements for this analysis was ±1.0%0 for 6^2H and ±0.5%0 for 6^{18}0 , based on repeated analyses of lab standards.

We corrected for narrow and broadband spectral interference due to the presence of organic compounds using the LGR-SCI software (Version 1.0.0.69; Schultz, Griffis, Lee, & Baker, 2011). Of our 126 samples, 17 were flagged as potentially having organic compounds and corrected with the software. Past studies show that cavity ring-down spectrometers can report incorrect isotope values due to organic compounds causing spectral contamination (Leen, Berman, Liebson, & Gupta, 2012; Schultz, Griffis, Lee, & Baker, 2011). We confirmed that organic compounds in our water samples did not interfere with the UWA analysis by also running a variety of soil samples across eight depths and branch xylem samples across all three treatments on an isotope ratio mass spectrophotometer (IRMS; GV Instruments IsoPrime, Manchester) coupled with a Pyr-OH liquid auto-sampler (Eurovector, Milan) at the Boston University Stable Isotope Lab (Boston, MA, USA). We found a significant (p < .001) and strong (R^2 = 0.91) positive relationship when comparing the results on the LIWA and IRMS (Figure 51) and therefore have confidence in the data from the cavity ring-down spectrometer.

2.5 | Statistical analyses

We conducted a repeated measures analysis of variance (ANOVA) to examine differences in soil water potential for each depth, each

month separately. To examine potential differences in stable isotopic composition of water across the 11 depths in each soil profile, we conducted ANOVAs on each sampling date. We used linear mixed effects (LMEs) models to compare $\delta^{18}O$, $\delta^{2}H$, and d-excess for branch xylem water within a given time period (early, peak, or late growing season) across treatments. The package 'nlme' in R (Pinheiro, Bates, DebRoy, & Sarkar, 2012) was used for all LME models. For all LME models, tree nested within plot was designated as the random effect with the treatment as the fixed effect. All post hoc pairwise comparisons among treatments for ANOVAs and LMEs were conducted using Tukey's honestly significant difference (HSD) tests.

We used a Bayesian mixing model to quantify the relative contribution of water from each soil sampling depth for trees on each sampling date with the package 'simmr' in R (Parnell, 2015). Bayesian mixing models use typical end member mixing equations (e.g., Dawson & Ehleringer, 1993) but implement Bayesian techniques that allow the probability of many sources to be estimated. Specifically, we used Markov chain Monte Carlo (MCMC) methods to determine proportions and probability distributions of potential water sources from 11 depths in the soil for plants to take up. We calculated the average isotopic value of both elements (hydrogen and oxygen) at all 11 soil depths across the two soil pits for a given sampling date, each representing a potential source of water. For all depths, the input into the Bayesian mixing model induded mean for stable isotopic composition of both elements. In addition, the model includes standard deviation for each input to account for uncertainty within a sample. The model uses MCMC sampling combined with Bayesian updating to update prior distributions and to create a posterior distribution of uncertainty surrounding estimates. We assumed no isotopic fractionation during water uptake (Dawson & Ehleringer, 1993; Zimmerman, Ehhalt, & Munnich, 1967).

The Bayesian mixing model was run with three chains and 100,000 iterations for each sampling date for each treatment. The first 50,000 iterations were discarded and considered the 'burn-in' period. We assumed water uptake from all potential sources was equally likely. The result of the Bayesian mixing model provides probability distributions and mean fractional contribution for each depth, accounting for uncertainty in these sources. Recent studies highlight the robustness of the Bayesian mixing model compared with other analytical techniques (two-end member, graphical inference, and multisource mixing models; Beyer, Hamutoko, Wanke, Gaj, & Koeniger, 2018; Evaristo, McDonnell, & Clemens, 2017; Rothfuss & Javaux, 2016).

Due to the cost and infrastructure required to implement the experimental treatments, it was not possible to have more than two *reference,* two *warmed,* and two *warmed* + FTC plots. Therefore, we used $\alpha = .10$ to evaluate significant treatment effects, unless otherwise noted. All statistical analyses were conducted with R statistical software (version 3.0.3; R Core Team, 2013). All error is reported as standard error (SE) of the mean.

3 RESULTS

3.1 | Growing season and winter environmental variables

Plots that were warmed throughout the growing season had higher soil temperatures relative to the reference plots by 5.1 ± 0.05°C and 5.0 ± 0.05°C, for *wanned* and *warmed* + *FTC,* respectively (April 4-November 15, 2018; Table 2 and Figure 1). This pattern is consistent with soil temperature increases reported for the years 2013-2017 in previous papers by our group (Harrison et al., in press; Sanders-DeMott, Sorensen, Reinmann, & Templer, et al., 2018; Sorensen et al., 2018; Templer et al., 2017). Also consistent with past years, soil warming did not affect soil moisture integrated from O to 30 cm throughout the growing season ($p = .73$) in 2018 or in the 2017/2018 winter prior to the growing season when we analysed

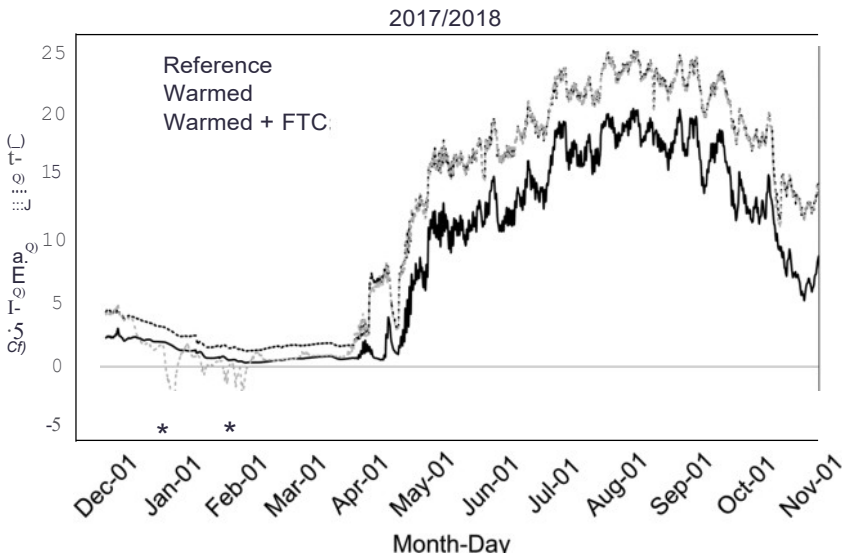


FIGURE 1 Soil temperatures at 10-cm depth for three treatments for December 1-November 30 for the 2017/2018 winter and growing season at Hubbard Brook. Asterisks indicate dates when experimentally induced soil freeze/thaw cycles in winter occurred (two in 2017/2018)

TABLE 1 Environmental variables by experimental treatment for the 2017-2018 winter (November15, 2017-April 4, 2018) and growing season in 2018 (April 4, 2O18-November 15, 2018)

	Reference	*Wanned*	*Warmed + FTC*
Minimum soil temperature (°C)°"	0.32• ± 0.044	1.23• ±0.052	- 3.64b± 0.061
Maximum snow depth (cm)°""	66.25• ± o.84	65.13· ± 1.33	23.38b ± 0.68
Maximum frost depth (cm)°"	9.44. ± 1.44	9_43• ±0.99	25.69b ± 1.30
Number of soil freeze/thaw cycles	0	0	2
Growing season soil temperature (° C)°"	12.62. ± 0.19	17.81b ±023	17.74b ± 0.062

Note: Soil temperatures are averaged at 1O-cm depth. Values are means with standard error across plots unless otherwise noted. Distinct letters within a row indicate statistically significant differences among treatments.
°$p < .05$.
..$p < .05$.
... $p < .0001$.

plant samples ($p = .34$). Snow removal in the *warmed* + FTC led to lower snow depths and minimum winter soil temperatures and greater soil frost depths and number of soil FTCs in 2017/2018 (Table 1).

Soil water potential significantly increased with greater soil depth (Figure 2; $p < .001$on all three sampling dates) and was consistently greater at 50-cm depth compared with 10-, 20-, and 30-an depths throughout the growing season (Figure 2; $p < .001$ on all dates). In addition, the range in water potential values throughout the growing season was smaller at SO-cm depth (-13.1 to - 12.6kPa) compared with shallower depths (-18.8 to - 17.4kPa, - 16.7 to -15.9 kPa, and - 14.2 to - 14.8 kPa, at 10-, 20-, and 30-cm depths, respectively; Figure 2).

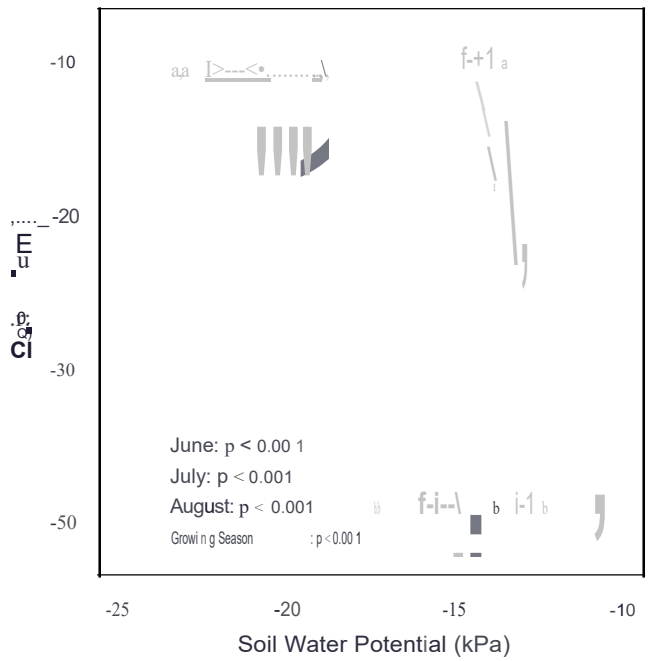


FIGURE 2 Soil potential measured at five depths at a nearby flux tower with similar soil texture composition to our site, with means± SE values for June, July, and August of 2019, the year with the finest resolution in data available. Mean± SE values for the entire growing season also provided. Pvalues indicate significance for potential differences in water potential across depths. Different letters represent statistically significant differences across the depths

3.2 | Stable isotopic composition of water in branch xylem and soil

Throughout the 2018 growing season, soil water $\delta^{18}O$ values ranged from - 3.3‰ to - 13.3‰ and $\delta^{2}H$ ranged from - 34.4‰ to - 1O1.I o/oo $\delta^{18}O$ and $\delta^{2}H$ values were generally more enriched at the soil surface compared with more depleted deeper soil layers (Figure 3). We also observed significant variation in isotopic values across the growing season with August (late growing season) values (-4.9 ± O.3o/oo for $\delta^{18}O$ and -42.9 ± 2.0o/oo for $\delta^{2}H$) relatively enriched than June or July (-10.5 ± O.So/oo for $\delta^{18}O$ and - 82 .2 ± 3.4o/oo for $\delta^{2}H$ in June and - 10.1 ± 0.3o/oo for $\delta^{18}O$ and -76.1 ± 3.2o/oo for $\delta^{2}H$ in July; $p < .001$ for $\delta^{18}O$ and $\delta^{2}H$, respectively). There was a positive and significant relationship between $\delta^{18}O$ and $\delta^{2}H$ across all depths of soil (Figure 52; $p < .001$), with slight $\delta^{18}O$ enrichment compared with the global meteoric water line (GMWL) and the local meteoric water line (LMWL; Green, Laursen, Campbell, Mcguire, & Kelsey, 2015).

Throughout the growing season, $\delta^{18}O$ values in branch xylem ranged from -5.lo/oo to - 9.5oo/o, and $\delta^{2}H$ ranged from -43.3o/oo to - 7O.?o/oo (Figure 4). There were significant differences in the mean isotopic values of branch xylem across the growing season ($p < .001$ for both $\delta^{18}O$ and $\delta^{2}H$), with August having greater values than June and July. June branch xylem $\delta^{18}O$ values were -7.4 ± O.2oo/o, and $\delta^{2}H$ were -65.5 ± 1.Oo/oo; July branch xylem $\delta^{18}O$ values were -8.00 ± O.2oo/o, and $\delta^{2}H$ were - 60.8 ± O.9o/oo; August branch xylem $\delta^{18}O$ values were - 6.1 ± O.2o/oo, and $\delta^{2}H$ were - 48.3 ± O.6o/oo. Branch xylem had similar isotopic values across the treatments in July, but trees in the *warmed + FTC* plots were significantly more enriched in both ^{18}O and ^{2}H compared with the *reference* and *warmed* plots in June and August (Figure 4; $p < .05$ across plots for both $\delta^{18}O$ and $\delta^{2}H$). Similarly, *d-excess* in xylem branch water was not statistically different across treatments in July, but values were significantly lower in *warmed + FTC* compared with *reference* and *warmed* plots in June and August (Figure 4; $p < .05$).

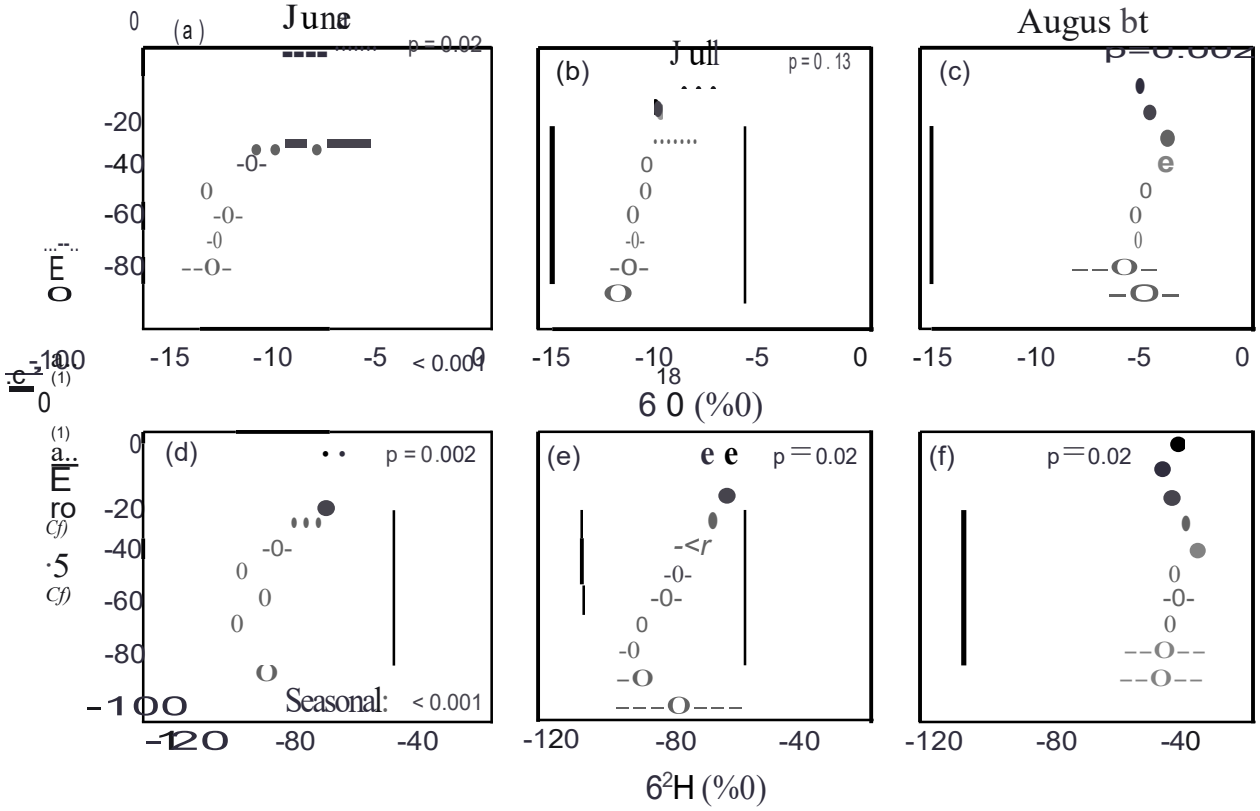


FIGURE 3 Differences in soil water isotopic values ($\delta^{18}O$ and $\delta^{2}H$) with means and standard error for two soil pits during each sampling time across the growing season. The shaded region represents the range of values in June for comparison across the growing season. Different letters represent statistically significant differences across the season

Our Bayesian mixing model revealed that in June, trees in the *reference*, *warmed*, and *warmed + FTC* plots used shallow water (0-10 cm) as their primary water source (Figure 5d; Table 2; 56.0 ± 9%, 49.8 ± 11.5%, and 65.5 ± 15% for reference, *warmed*, and *warmed + FTC* trees, respectively). In July, 14.9-20.3% of water in all trees came from 0- to 30-cm depth, with no apparent differences in water uptake depth by treatment (Figure 5e; Table 2). In August, trees in the *reference* and *warmed* plots took up more of their water from 90- to 100-cm depths than from shallower depths (Figure 5f; Table 2; 44.9 ± 10% and 40.2 ± 12.5% in reference and *warmed* plots, respectively). This pattern is in contrast to *warmed + FTC* plots, where trees utilized water from all depths evenly (8.1- 9.5% from each depth across the 1-m depth soil profile).

4 | DISCUSSION

Our isotope values throughout the soil profile show significant variation, allowing us to use natural abundance stable isotope values to calculate the proportion of water that trees take up from various soil depths (Figure 5a-c). In June and July, trees in all treatments took up the majority of their water from shallow depths (0- 30 cm). In August, trees in the *reference* and *warmed* plots took advantage of greater water availability at deeper soil depths, whereas the trees in the *warmed + FTC* plots did not. These results suggest that with warmer temperatures alone, we will not see significant shifts in the soil depths where trees get their water, but those trees that experience FTCs in winter may not be as responsive to changes in soil water availability in the future.

4.1 | Soil water potential

Values of water potential were similar to reported values for HBEF (Federer, 1979). In addition, the less variable water potential values we observed at greater depths are consistent with past studies (Eggemeyer et al., 2009; Eller, Burgess, & Oliveira, 2015). Throughout the growing season, water potential was significantly higher at 50 cm compared with shallower soil depths. The less variable and higher water potential at greater depths suggests that this depth experiences less removal (i.e., root uptake and evaporation) and/or more persistent inputs from redistribution of water from shallower soil layers (Gardner, Hillel, & Benyamini, 1970) or capillary rise of water from deeper soil layers (e.g., Brolsma & Bierkens, 2007).

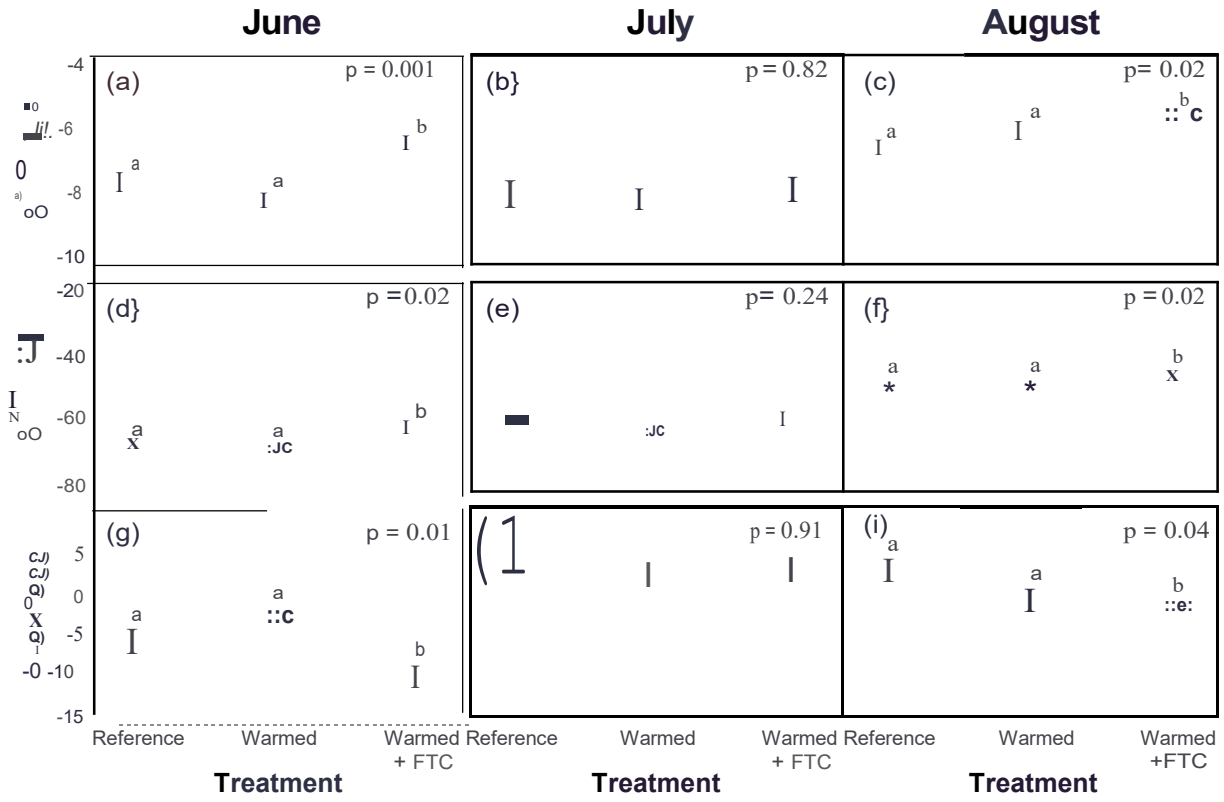


FIGURE 4 Stableisotopic values for branch xylem water ($\delta^{18}O$, $\delta^{2}H$, and d-excess) for red maple trees for each treatment for each sampling date in 2018. Values are means± SE. Different letters represent statistically significant differences between treatments on a samplingdate

4.2 | Stable isotopic composition of water in branch xylem andsoil

The relative enrichment of isotopic values of water at the soil surface compared with deeper soil layers is consistent with past studies in temperate environments (Brinkmann, Eugster, Buchmann, & Kahmen, 2018; Grossiord et al., 2014). Soils are generally more enriched in heavier isotopes at the surface due to fractionation during evaporation that causes enrichment of the residual water pools (Dansgaard, 1964). The increased enrichment of the heavy isotopes of oxygen and hydrogen from the early to late growing season we observed is likely also reflective of changes in the isotopic values of precipitation inputs for these forests (Green, Laursen, Campbell, Mcguire, & Kelsey, 2015). For example, in June and July, the mean isotopic values throughout the soil profile (- 10.3 and - 87.2 for $\delta^{18}O$ and $\delta^{2}H$, respectively) closely resembled values for snow in this region (-12.4 and- 86.3 for $\delta^{18}O$ and $\delta^{2}H$, respectively; averaged from 2006 to 2010), indicating that in June and July, most of the soil water was likely from winter snowmelt, especially at depth. In contrast, later in the growing season, mean isotopic values in the soil profile (-4.5 and - 42.0 for $\delta^{18}O$ and $\delta^{2}H$, respectively) began to reflect rain (-7.6 and - 54.8 for $\delta^{18}O$ and $\delta^{2}H$, respectively; Green, Laursen, Campbell, Mcguire, & Kelsey, 2015), indicating a seasonal shift from residual snowmelt to rainwater as the primary source of soil water in these forests in August.

It is likely that changes in water availability combined with differences in root biomass throughout the soil profile affected seasonal water use by these trees. For example, throughout the entire growing season, water potential was significantly greater at SO cm compared with 10-, 20-, and 30-cm depths ($p < .001$; Figure 2). However, the difference in water potential across the different depths was less than 5 kPa in June, and the primary source of water (>49.8%) for trees in all plots was shallow water (<10 cm depth), suggesting that in the absence of a large variation in water potential, such as in the early growing season, trees access water from the depth that has the greatest root biomass, in other words, the shallowest soil layers (<10 cm depth; Yanai, Park, & Hamburg, 2006). In contrast, trees experiencing ambient or warmer growing season soil temperatures switched their primary water source from shallow (10- to 30-cm depth) in June and July to deep water (>90-cm depth) in August, which may have been a result of decreased (i.e., more negative) water potential in the shallow soil layers compared with less variable and higher (i.e., less negative and doser to zero) water potential in the deeper soil layers in August. In other words, in the late growing season, trees switched their primary water source to deeper water as it became more available and less variable than shallower water, despite the fact that most fine root biomass in this forest is in the top 10 cm of soil (Yanai, Park, & Hamburg, 2006). In August, water potential values at SO cm were greater and less variable (-13.4 ± 0.5 kPa) than at shallower (10-30 cm) depths (- 17.8 ± 1.1 kPa). Together, these

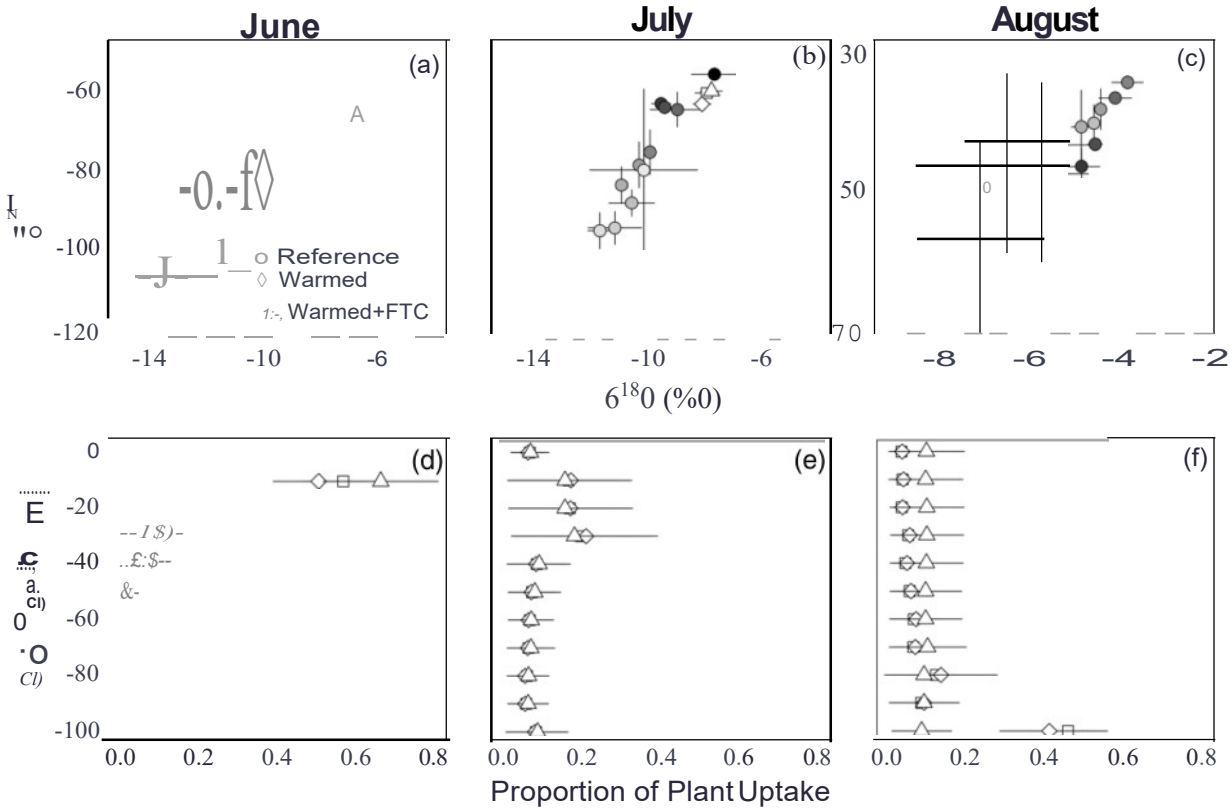
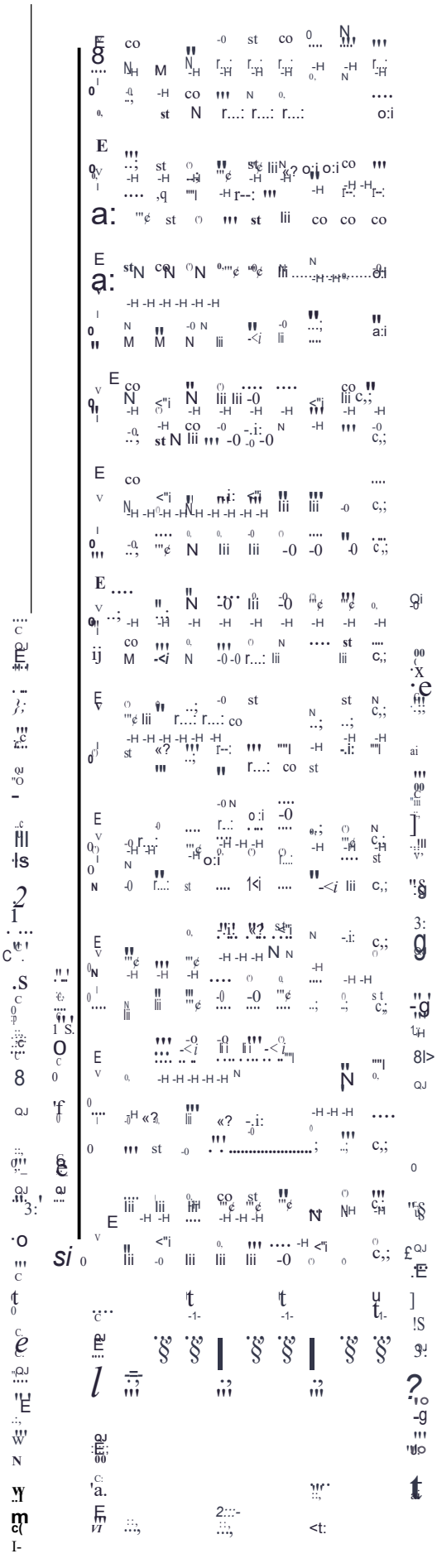


FIGURE 5 Panels (a)-(c): soil and branch xylem water ($\delta^{18}O$ and $\delta^{2}H$) that was used in the Bayesian Mixing Model. Note: axes in Panel c are different than other panels; values are mean ± SE. Panels (d)-(f): proportion of plant water uptake from each soil sampling depth on each sampling date in 2018. Values are means ± SE determined by a Bayesian Mixing Model

results suggest that trees take up water from depths that have both greater water potential and less variability. The trend of trees switching their water source to deeper water in the late growing season when water availability and water potential are greatest has been demonstrated in other temperate tree species (Brinkmann, Eugster, Buchmann, & Kahmen, 2018; Cramer, Thorburn, & Fraser, 1999; Meizner, Kohler, Schwendenmann, & Holscher, 2012; Sun, Meng, Zhang, & Wan, 2011) and in many other plant species (Bargues Tobella et al., 2017; Bleby, Aucote, Kennett-Smith, Walker, & Schachtman, 1997; Dardanelli, Bachmeier, Sereno, & Gil, 1997; Ewe, Sternberg, Childers, & Ewe, 2018; Goebel, Lascano, Paxton, & Mahan, 2015; G6mez-Navarro, Pataki, Bowen, & Oerter, 2019; Li et al., 2019; Liu et al., 2019; Wu et al., 2018).

Several studies have shown that d-excess values are a suitable proxy for understanding depths from whichplants take up water, with lower values implying a shallower water source (Flanagan, Orchard, Tremel, & Rood, 2019; Matheny et al., 2017; Simonin et al., 2014; West, Goldsmith, Matimati, & Dawson, 2011). Deuterium-excess values for red maple trees exposed to soil freeze/thaw cycles were generally lower compared with trees experiencing ambient or warmer growing season temperatures. Values of d-excess confirmed the results that we found with the Bayesian mixing model and further demonstrate that trees exposed to greater frequency of soil freeze/thaw cycles in winter t endedto use shallower water, especially in the late growing season, whereas those with ambient or warmer growing season temperatures switched their water source to deeper soils where water was more available (as indicated by water potential values).

In this study, we found that whereas trees in the *reference* and *warmed* plots took up water from the depths that had the greatest water potential (i.e. availability), the trees that experienced soil freeze/thaw cycles in winter did not respond to increases in soil water availability in the deepest soil layers and instead took up water equally across all depths in the late growing season, despite water potential being greater at deeper soil depths. In the same soil temperature manipulation experiment reported here, we found that growing season soil warming increased rates of water uptake in red maple trees, with these higher rates maintained despite trees experiencing soil freeze/thaw cycles in winter (Harrison et al., in press) and damage to roots in those plots (Sanders-OeMott et al., 2018). As such, we do not think that changes in water sources are due to changes in overall rates of water uptake and instead speculate that trees took up water equally across the depths after experiencing fr eeze/ thaw cycles due to compensatory root growthin shallow soils that ledto greater water uptake from shallower soil depths than expected. Members of our group demonstrated across a climate gradient at HBEF that soil freezing in winter causes compensatory root growth by 40% in the top 15 cm of soil in the following growing season (Sorensen et al., 2016),



meaning that the root biomass at the soil surface for trees experiencing soil freeze thaw cycles in winter may have been greater than in our plots with ambient or warmer soil temperatures. In contrast, soil warming has been shown to decrease fine root biomass due to greater rates of nitrogen cycling and availability (Melillo et al., 2011). Therefore, it is possible that trees with ambient or warmer soil temperatures responded to changes in soil water potential by switching their water source to the depth with the highest water potential in the late growing season. In contrast, those trees experiencing soil freeze/thaw cycles relied on soil depths where they may have had the majority of their root biomass due to compensatory root growth caused by soil freeze/thaw cycles. We did not measure root biomass in our soils and therefore cannot conclude definitively the connection between soil temperatures, root biomass, and depths from which trees take up water.

While water did not appear to be limiting to trees at HBEF in the summer of 2018 based on the water potential values, our results have implications for how this forest might respond to water stress, with the frequency of drought projected to increase in the future (Hayhoe et al., 2007). Past studies suggest that freeze/thaw cycles in winter may damage roots (Sanders-DeMott et al., 2018), lead to larger root density at the soil surface in the following growing season (Sorensen et al., 2016), and minimize the tendency for red maple trees to switch to deeper water sources. These findings combined with our results suggest that winter climate change may cause red maple trees at HBEF to become more vulnerable to drought.

5 CONCLUSIONS

Over the next century, air temperatures will continue to rise (Hayhoe et al., 2007), and the frequency of winter soil freeze/thaw events in winter is likely to increase (Campbell et al., 2010), which together are likely to impact the flexibility trees have to switch water sources in response to changing water availability in northern hardwood forests. Our methods represent a novel approach to studying water uptake dynamics in a northern hardwood forest, by utilizing natural abundance stable isotopic composition of water in response to experimental changes in soil temperatures in a northern hardwood forest. Our results suggest that warmer soils in the growing season are unlikely to affect the ability of trees to switch to more available water sources in the late growing season when water potential at shallow depth d ecreases. However, increased frequency of soil freeze/thaw cycles in winter will likely negatively impact the ability for trees to access deeper sources of water, which may hold greater water availability. Our findings demonstrate that trees experiencing soil freeze/thaw cycles respond differently to changes in soil water availability than those with ambient or warmer soil temperatures in the growing season, which could possibly be the result of compensatory root growth in the growing season following soil freezing. As the frequency of drought rises (Hayhoe et al., 2007), it will be increasingly important to understand the ability for trees to access different water sources under a changing climate.

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DATA AVAILABILITY STATEMENT

Our data are publidy available through the Hubbard Brook Experimental Forest data archives (Templer, Harrison, Blagden, Green, & Salvucci, 2020a,b).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of thisarticle.

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