



Transpiration of Dominant Tree Species Varies in Response to Projected Changes in Climate: Implications for Composition and Water Balance of Temperate Forest Ecosystems

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ABSTRACT

The climate is changing in many temperate forests with winter snowpack shrinking and an increasing frequency of growing season air temperatures exceeding long-term means. We examined the effects of these changes on growing season rates of transpiration (sap flow) in two snow removal experiments in New Hampshire and Massachusetts, USA. Snow was removed during early winter, resulting in greater depth and duration of soil freezing compared to untreated plots. We exam-

ined the dominant tree species at each site, *Acer saccharum* at Hubbard Brook, NH and *Acer rubrum* and *Quercus rubra* at Harvard Forest, MA. Trees responded to a smaller snowpack, but with distinct species-specific responses consistent with ecological traits. Snow removal decreased rates of sap flow per kPa vapor pressure deficit (VPD) in sugar maples in the early growing season and red maples throughout the growing season. In contrast, sap flow rates per kPa VPD increased for red oak with snow removal. Downscaled climate projections from the Coupled Model Intercomparison Project indicate increases in heat stress days at both sites by the end of the century, leading to increased rates of whole-season transpiration across all three tree species, which will be offset in red maples and increased in red oaks with a smaller snowpack and increased frequency of heat stress days. Results of this study demonstrate that the combined effects of changes in climate during the growing season and winter will impact transpiration differently among

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tree species, with implications for forest water balance and tree species composition in the northeastern USA

Key words: maple trees; oak trees; rising temperature; sap flow; water; winter climate change.

HIGHLIGHTS

- Smaller snowpack increases transpiration in oaks, but decreases in maple trees
- Increased air temperatures increase rates of transpiration in oak and maple trees
- Variable response to climate change will affect forest composition and function

INTRODUCTION

Increased mean annual air temperatures across many mid- and high-latitude ecosystems have reduced winter snowpack depth and duration (Campbell and others 2010; Hamburg and others 2013) and increased the frequency of heat waves in the growing season (Hayhoe and others 2007). Over the next century in the northeastern USA, mean annual air temperatures are expected to rise up to 5.5°C higher than mean values for the years 1976–2005 (USGCRP 2017) and the amount of forest area experiencing an insulating snowpack is expected to shrink between 49 and 95% compared to 1951–2005 values (Hayhoe and others 2007; Brown and DeGaetano 2011; Reinmann and others 2019). The absence of insulating snow cover can lead to colder soil temperatures and a greater depth and duration of soil frost (Boutin and Robitaille 1995; Groffman and others 2001; Hardy and others 2001; Decker and others 2010). Currently, shallow (< 10 cm depth) soil frost occurs in some temperate forests (Bailey and others 2003), but may increase in frequency over the next century due to colder minimum annual soil temperatures (Brown and DeGaetano 2011) and increased frequency of soil freeze–thaw events (Campbell and others 2010). The rise in air temperatures is also expected to increase heat wave frequency during the growing season (Hayhoe and others 2007; IPCC 2014), which can reduce forest net primary productivity (Allen and others 2010; Tang and others 2010; Filewod and Thomas 2014; Allen Craig and others 2015; Martin-Benito and Pederson 2015; Reinmann and Hutrya 2017).

Reduced winter snowpack and increased depth and duration of soil frost can increase mortality and injury of fine roots (Tierney and others 2001; Cleavitt and others 2008; Repo and others 2008; Comerford and others 2013), which are essential for plant water and nutrient uptake (Eissenstat 1992; Coners and Leuschner 2002). Thus, impaired root function and/or mortality due to winter climate change could hinder plant processes such as water uptake, a crucial component of the soil–tree–atmosphere continuum that regulates transpiration (that is, sap flow) rates, plant and ecosystem productivity, and ecosystem latent heat flux during the growing season (see Bréda and others 2006). One study in Quebec, Canada, showed that severe soil freezing reduced transpiration rates during the following growing season (Horsley and others 1995), but the specific role of soil freezing was likely confounded with water limitation caused by complete removal of the winter snowpack. It therefore remains uncertain whether a decrease in snowfall and increase in soil frost impact water uptake and transpiration independently from water limitation.

Transpiration is driven by both tree physiology (for example, stomatal regulation) and environmental factors (for example, air and soil temperature, soil moisture, vapor pressure deficit (VPD); Day and others 1990; Bergh and Linder 1999; Fredeen and Sage 1999; Oren and others 1999; Sun and others 2000; Yin and others 2004; Bovard and others 2005; Daley and Phillips 2006; Chang and others 2014; Juice and others 2016). Contrasts in tree physiology among species may therefore modulate the response of trees to increased depth and duration of soil frost in winter and increased frequency of heat waves in the growing season, which may alter competition dynamics and induce shifts in tree species composition of temperate forest ecosystems.

Sugar maple (*Acer saccharum*) trees dominate northern hardwood forest ecosystems of northeastern North America. Fine roots of this tree species, which actively transport water and nutrients, have been shown to be particularly susceptible to soil freezing-induced root mortality (Tierney and others 2001), injury (Cleavitt and others 2008; Comerford and others 2013), and reduced nutrient uptake (Campbell and others 2014). Rates of aboveground growth of sugar maple trees also decline in response to soil freezing (Reinmann and others 2019). In contrast, red maple (*Acer rubrum*) roots are less sensitive to soil freezing (Sanders-DeMott and others 2018) and this species is increasing in relative abundance across the region,

while red oak (*Quercus rubra*) abundance is declining (Fei and Steiner 2007). Red oaks tend to have deeper roots than maples, potentially suffering fewer adverse impacts of soil freezing on root vitality and transpiration (Lyford and Wilson 1964; Lyford 1980).

Maple and oaks also tend to differ in how their stomatal regulation responds to water stress. Maple trees tend to be isohydric (Roman and others 2015), closing their stomata to maintain leaf water potential, while anisohydric oaks tend to leave their stomata open (Roman and others 2015; Yi and others 2017) during drought conditions. These different responses to water stress could cause more reduced water uptake in maples compared to red oaks under extremely high temperatures. However, due to the strong correlation between air temperature and transpiration (Granier and others 1996; Bovard and others 2005), it is possible that transpiration could increase in both maples and oaks with increased air temperatures. Further, since soil freezing likely induces greater root injury in sugar maples than red maples and red oaks, it is possible that sugar maples experiencing greater depth and duration of soil freezing may have the largest reductions in rates of transpiration on high air temperature days in the following growing season. However, it is unknown how the combined effects of higher temperatures and root injury from soil freezing may affect transpiration by trees, especially in the early growing season when root damage effects are greatest (Tierney and others 2001; Cleavitt and others 2008; Campbell and others 2014).

Transpiration constitutes more than 80% of annual surface water flux across terrestrial ecosystems (Jasechko and others 2013), demonstrating how trees can influence soil moisture and hydrology in northern temperate forests (Campbell and others 2011). Thus, if differential effects of climate change on tree species induce shifts in forest composition or change transpiration rates, temperate forest biogeochemical cycling, soil moisture, and hydrology may be altered. To examine the impacts of a reduced snowpack and increased depth and duration of soil frost on transpiration by common tree species, we removed snow for the first 6 weeks of winter from two mixed temperate hardwood forests: Hubbard Brook Experimental Forest (hereafter “Hubbard Brook”) in New Hampshire, USA, and Harvard Forest in Massachusetts, USA, in 2010 and 2011, respectively.

During the growing season following snow removal, we used continuous measurements of xylem sap flow to quantify transpiration in the

dominant tree species at each site, including mature sugar maple trees at Hubbard Brook and red maple and red oak trees at Harvard Forest. We defined heat stress days as those with air temperatures above the long-term (years 2001 through 2017) average daily maximum for a given site. We used projected regional changes in air temperatures in conjunction with our in situ measurements of sap flow to estimate how transpiration might change in the future under increased air temperatures and reduced winter snowpack. We hypothesized that reduced snowpack and increased depth and duration of soil frost in winter reduce rates of sap flow and whole tree transpiration by trees due to root damage, particularly for sugar maples. Because of the relatively deeper rooting depth of red oak than maple trees (Lyford and Wilson 1964; Lyford 1980), we further hypothesized that soil freezing in winter would more negatively impact transpiration in sugar maple and red maple compared to red oak trees. Finally, we hypothesized that while rates of sap flow may increase with projected increases in air temperature in the growing season across all species, these increases may be offset by species-specific levels of root damage caused by a smaller snowpack and greater soil freezing in winter.

MATERIALS AND METHODS

Site Description

Hubbard Brook Experimental Forest is located in the White Mountain National Forest in New Hampshire (43° 56′ N, 71° 45′ W) and is a long-term ecological research (LTER) site. The climate is cool, humid, and continental. The mean annual precipitation is 1400 mm, evenly distributed throughout the year, with between one-quarter and one-third falling as snow (Bailey and others 2003; years 1969–2000). Soils typically consist of base-poor spodosols, mostly Haploreggids, that developed in glacial till, and the bedrock is generally shallow. Soil frost over the last 50 years has occurred approximately one out of every 3 years, but typically to a depth of less than 10 cm (Bailey and others 2003; Fuss and others 2016). Sugar maple, American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Brit.) dominate the canopy, with red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* Mill.) dominant at higher elevations. The site was a mixed conifer–hardwood forest logged in the 1890s to 1920 for sawtimber and fuelwood, which generated the current mixed hardwood forest. In 1938,

there was a hurricane, but besides that disturbance, the site has been relatively undisturbed since 1920.

Harvard Forest is located in central Massachusetts (42° 30' N, 72° 10' W) and is also a LTER site. The climate is cool, temperate, and humid. Mean annual precipitation is 1100 mm, distributed evenly throughout the year with a quarter falling as snow (years 2001–2017). Soils are of the Montauk series (coarse-loamy, mixed, mesic Oxyaquic Dystrudepts) and Whitman series (loamy, mixed, mesic, shallow Typic Humaquepts). Plots were located in the Prospect Hill Tract, an area that is dominated by red oak and red maple trees. The site was a pasture until the end of the nineteenth century and then regenerated naturally into forest. In 1938, there was a stand-replacing hurricane. The site is comprised of trees that survived and trees that have since regenerated.

Snow Removal

This study builds on research reported from snow removal experiments at Hubbard Brook (Templer and others 2012; Comerford and others 2013; Campbell and others 2014; Sorensen and others 2016; Maguire and others 2017; Reinmann and others 2019) and Harvard Forest (Reinmann and Templer 2016; Sorensen and others 2016). In October 2007, we established four paired reference and snow removal plots ($n = 8$ plots total, each plot 13×13 m) at Hubbard Brook. Each plot contained a minimum of three mature sugar maple trees in the overstory, with the exception of two reference plots that contained one red maple and two sugar maple trees, and thus, only two sugar maple trees from that plot were included in the analysis. We clipped understory vegetation, primarily hobblebush (*Viburnum lantanoides*), in both the reference and snow removal plots to facilitate snow removal. To reduce winter snowpack and induce soil frost, we shoveled snow from the snow removal plots within 48 h of snowfall for the first 6 weeks of snowfall in 2008/2009 (December 17, 2008, through January 19, 2009) and 2009/2010 (December 17, 2009, through January 16, 2010). In summer 2010, we established three paired reference and snow removal plots ($n = 6$ plots total, each plot 13×13 m) at Harvard Forest. Plots were each centered on two mature overstory red oak and two mature red maple trees, and understory vegetation was clipped. We removed snow from the snow removal plots via shoveling within 24 h following each snowfall for the first 5 weeks of snowfall in the 2010/2011 winter (December 29,

2010, through February 4, 2011) to reduce snowpack and induce soil frost.

At both sites, the first snow of winter was packed down gently on all plots to create a 3 cm deep buffer of snow that remained on the snow removal plots to prevent disturbance to the soil surface during shoveling and maintain albedo consistent with a snowpack on the forest floor throughout winter. We also wore snowshoes to minimize disturbance of the snowpack. A natural snowpack accumulated on reference plots throughout the winter and on the snow removal plots following the end of the treatment.

Snow, Soil, and Air Monitoring

At Hubbard Brook, snow depth and soil frost were measured every 7 to 10 days from late October to early May during pre-treatment (2007/2008) and treatment (2008/2009, 2009/2010) years. Snow depth was measured using a stainless-steel snow sampling tube (Model 3600 Federal, $n = 4$ per plot per date). Soil frost tubes (Ricard and others 1976) were installed in October 2007 ($n = 4$ per plot) using flexible PVC tubing (1.3 cm diameter) filled with a methylene blue dye in a rigid PVC pipe allowing us to measure depth of soil frost from the surface of the soil to 0.5 m depth. During measurement, tubes were removed from the PVC pipe, and the depth of the soil frost was identified by the contents' transparency, since freezing excludes methylene blue dye from solution. Soil temperature was measured within each plot with copper-constantan thermocouples inserted at three depths (1, 3, and 7 cm; Templer and others 2012). In 2009, we used hourly air temperature and relative humidity data from a nearby Soil Climate Analysis Network (SCAN) site, a project of the US Department of Agriculture Natural Resources Conservation Service, at Hubbard Brook. In 2010, we measured air temperature and relative humidity at 10 s intervals at each pair of plots using a RHA1 probe (Delta-T Devices, Ltd., Cambridge, UK). Gaps in 2009/2010 air temperature and relative humidity due to equipment malfunction were substituted with the Hubbard Brook SCAN site data. Hourly averages of soil and air temperature and relative humidity were logged on multichannel dataloggers (Campbell Scientific CR1000 with AM16/32 multiplexers). Vapor pressure deficit (VPD) was calculated from air temperature and relative humidity using relationships determined by Goff (1946).

At Harvard Forest, we measured snow and soil frost depth weekly in four locations within each plot to characterize snowpack and soil frost depth

conditions during the winter of 2010/2011. Snow depth was measured using meter sticks that were permanently affixed to stakes. Soil frost depth was measured using the same procedure described above at Hubbard Brook. One Campbell Scientific HMP45C-L was used to measure air temperature and relative humidity at 2 m height in one location central to all plots. All sensors were connected to CR1000 dataloggers (Campbell Scientific), and the average of measurements scanned at 30 s intervals was recorded every 30 min. For both sites, snow cover duration was defined as the number of days with measurable snow on the ground.

Sap Flow

To measure sap flow during the 2010 growing season at Hubbard Brook and 2011 growing season at Harvard Forest, we used a constant heat-flow method (Granier 1987; Lu and others 2004) consisting of three thermal dissipation probes per tree installed at about 1.4 m height in the bole of each tree. Sap flow sensors were installed at Hubbard Brook in May 2010 (before leaf-out; $n = 3$ sensors per tree, evenly distributed around the bole of the tree; $n = 10$ trees in reference plots; and $n = 12$ trees in snow removal plots) and left in place until late September in 2010. Sap flow sensors at Harvard Forest were installed in April 2011 (before leaf-out) and left in place until November 2011. They were installed at about 1.4 m height in the bole of two red maple and two red oak trees in each plot (two sap flow sensors per tree; one north-facing and one south-facing; $n = 6$ trees per species in reference plots and $n = 6$ trees per species in the snow removal plots). At both sites, sap flow sensors were left in the trees until after the end of leaf senescence.

Each sap flow sensor consisted of two fine-wire copper–constantan probes which formed a thermocouple joined at the constantan leads to determine the temperature difference (ΔT) between the thermocouples as influenced by rates of sap flow. Bark was chiseled from each sensor's location to expose the sapwood; then, sensors were installed in freshly drilled holes extending either 21 or 11 mm into the sapwood for the maple species and red oak, respectively. These depths were chosen to capture the outer and most conductive layers of the sapwood in both species. The heated sensor within each thermocouple had electrically insulated constantan heating wire coiled around its length, was coated with thermally conducting silicon grease, and was installed in the sapwood inside of an aluminum cylinder. Each heated sensor was oriented

in the sapwood approximately 10 cm above an unheated reference probe and received 200 mW power. Once installed, sap flow sensors were covered with a plastic housing affixed to the tree with acid-free silicone sealant to prevent stem flow from reaching them. To minimize temperature fluctuations due to direct solar heating, sap flow sensors were tented with Reflectix (Markleville, IN) aluminum insulated wrap. Temperatures were recorded at 30 s intervals, and 30 min averages were recorded on multichannel dataloggers (Campbell Scientific CR1000 with AM16/32 multiplexers). At Harvard Forest, power outages caused a gap in data between DOY 148 and 158.

Sap Flow Data Analysis

Sap flow per unit area sapwood per second (J_s , in $\text{g H}_2\text{O m}^{-2}$ sapwood area s^{-1} ; henceforth referred to as “sap flow”) was calculated using the following empirical calibration equation by Granier (1987):

$$J_s = 119[(\Delta T_{\max} - \Delta T)/\Delta T]^{1.23} \quad (1)$$

where J_s is the sap flow ($\text{g H}_2\text{O m}^{-2}$ sapwood area s^{-1}), $\Delta T_{\max}$ is the maximum temperature difference established between the heated and unheated probes when there is no sap flow ($J_s = 0$), and ΔT is the temperature difference between the heated and unheated probes.

Environmental factors that affect stem water content cause variation in $\Delta T_{\max}$ over time (Lu and others 2004), necessitating frequent redefinition of the zero-flow state. For periods shorter than 10 days, $\Delta T_{\max}$ was determined to have occurred when the following two conditions were met: (1) The temperature gradient between the reference and heated probes was stable for at least 2 h and (2) the ambient VPD was calculated to be less than 0.1 kPa. Sap flow rates were calculated using the empirical relationship of temperature difference between the heated and unheated sensors at any given time, ΔT_{sap} ($^{\circ}\text{C}$), and sap velocity (Eq. 1; Granier 1987) using BaseLiner software (version 3.0.10, developed by Ram Oren, Duke University).

Sap flow data were filtered to eliminate invalid data during electrical spikes and probe failure. We averaged sap flow rates across the sensors in each tree to determine the daily sums and daily maxima of sap flow for each tree across DOY 141 to 271 (May 20 through September 27, 2010) for Hubbard Brook and DOY 136 to 288 (May 14 through October 15, 2011) for Harvard Forest. The beginning and end of the growing season were selected at Harvard Forest when sap flow rates began to increase in the early growing season and began to

decrease in the late growing season, respectively (Supporting Figure 1). All Hubbard Brook data were included in analysis because trees in this study maintained transpiration throughout the entire period of data collection. To limit measurements to daytime only, we limited our statistical analysis of sap flow rates and environmental variables to the hours 0500 to 2100 for the entire growing season.

Basal Area Increment

We measured basal area increment (BAI) to determine whether previously documented changes in tree growth associated with a smaller snowpack and greater depth and duration of soil freezing could explain observed patterns of sap flow, which have previously been described in Reinmann and others (2019) and Reinmann and Templer (2016). To control for tree size effects on ring widths, raw tree-ring measurements were converted to basal area increment (BAI) following:

$$\text{BAI} = (R_n^2\pi) - (R_{n-1}^2\pi), \quad (2)$$

where R_n = the radius of the tree at the end of year n , and R_{n-1} is the radius of the tree at the end of the previous year. Tree-level BAI was calculated by averaging each year's BAI across the two cores collected from each tree. We did not find statistically significant relationships between growing season sums of sap flow and BAI for the year that sap flow was measured at each site (2010 for sugar maple at Hubbard Brook and 2011 for red maple and red oak at Harvard Forest) or BAI for the year after sap flow was measured at each site (2011 for sugar maple at Hubbard Brook and 2012 for red maple and red oak at Harvard Forest); we therefore excluded BAI as a variable in subsequent multivariate analyses.

Statistical Analysis

We used linear mixed effects models to compare relationships between mean or maximum daily air temperatures and sap flow throughout the entire growing season. For these models, temperature and treatment were fixed effects and tree nested within plot was a random effect to account for repeated sampling. We examined models as both first- and second-order linear equations and used ANOVA to determine the best line fit. Using ANOVA, we compared the slopes for the relationships between air temperature and rates of sap flow on both typical and heat stress days between reference and snow removal plots for each tree species. For all

linear models, we examined residuals plotted against predictors and confirmed there were no patterns that indicated autocorrelation.

To compare the relationships between VPD and daily averaged sap flow rates in reference and snow removal plots, we conducted linear mixed effects models with VPD, treatment, and their interaction as fixed effects and tree within plot as the random effect to account for repeated sampling. Slopes were considered to be zero if their 95% bootstrapped confidence intervals overlapped with zero. We examined relationships between sap flow and VPD during three time periods separately: during leaf expansion in the early growing season (first 2 weeks of sap flow measurements at each site; DOY 141–155 at Hubbard Brook and DOY 136–148 at Harvard Forest), the entire growing season, and on heat stress days. Heat stress days were determined as dates that were above the long-term average daily maximum air temperatures in July for a given site, which was 23.6 and 26.5°C for Hubbard Brook and Harvard Forest, respectively. We determined the long-term average maximum air temperature for July at the Fisher Meteorological Station at Harvard Forest for the years available: 2001 through 2017 (harvardforest.fas.harvard.edu:8080/exist/apps/datasets/showData.html?id=hf001). In order to utilize the same years for Hubbard Brook, we also determined the average daily maximum air temperature for July between the years 2001 and 2017. We utilized air temperature data from seven stations throughout Hubbard Brook (data.hubbardbrook.org/data/dataset.php?id=59). For our purposes, remaining growing season days that were below these long-term average daily maximum temperatures (or temperatures on heat stress days) were categorized as “typical” days.

All statistical analyses were conducted with R (version 3.0.3; R Core Team 2013). For all linear mixed effects models analyzed using the package “nlme” in R (Pinheiro and others 2012), we calculated the marginal R^2 values to describe the proportion of variance explained by the fixed effects using the R package “piecewiseSEM” (Lefcheck 2016).

Projected Changes in Sap Flow

We used the relationships we found between maximum daily air temperature and sap flow to project how increases in growing season air temperature may alter sap flow rates in these forests in the future because there are no expected changes in growing season VPD for this region (Ficklin and Novick 2017). We calculated the number of heat

stress days within the growing season during the long-term average (years 2001 through 2017) and those projected under low and high emissions scenarios for the years 2080–2099. Historical records of maximum daily air temperature were obtained from the SCAN site at Hubbard Brook and from the Fisher Meteorological Station at Harvard Forest between the years 2001 and 2017 and were limited to the same growing season dates used to measure sap flow (DOY 141–272 at Hubbard Brook and DOY 136–288 at Harvard Forest). We used downscaled climate projections for both Hubbard Brook and Harvard Forest using 1/16° grid cells from Phase 5 of the Coupled Model Intercomparison Project (CMIP5; complete list of models can be found in Reinmann and Hutyra 2017) to estimate projected maximum daily air temperatures (using the same growing season dates as sap flow) for the years 2080–2099 under the Intergovernmental Panel on Climate Change (IPCC) Representative Concentration Pathway (RCP) for low (RCP 4.5) and high emission (RCP 8.5) scenarios.

We also calculated the average daily instant rates of sap flow, limited to daylight hours 0500 to 2100, for each tree species within reference and snow removal plots, for typical and heat stress days separately. These values were then multiplied by the number of typical and heat stress days under historic conditions (from 2001 to 2017) and under the two projected scenarios (see Table 1) and summed for the growing season using the following equation:

$$\begin{aligned} &\text{Total growing season sap flow} \\ &= \left(\text{Daily sap flow}_{\text{typical}} \times \text{Number of days}_{\text{typical}} \right) \\ &+ \left(\text{Daily sap flow}_{\text{heat stress}} \times \text{Number of days}_{\text{heat stress}} \right) \end{aligned} \quad (3)$$

Table 1. Number of typical days and heat stress days (when air temperatures exceeded 23.6 and 26.5°C at Hubbard Brook and Harvard Forest, respectively) under historic (2005–2018) and low (RCP 4.5) and high (RCP 8.5) emissions scenarios (2080–2099) at Hubbard Brook and Harvard Forest

	Hubbard Brook		Harvard Forest	
	Typical	Heat stress	Typical	Heat stress
Historical	131	2	115	38
RCP 4.5	19	114	52	101
RCP 8.5	3	130	23	130

This calculation provides an estimate of the total rates of sap flow across the growing season scaled by the expected number of typical and heat stress days in past and future growing seasons (Table 1). Finally, total growing season rates of sap flow were divided by the total number of days in each growing season (133 for Hubbard Brook and 153 for Harvard Forest) to calculate daily rates and for comparison across sites (Figure 6). We recognize that the growing season is projected to lengthen at both sites by the end of the century, but for purposes of comparison, we kept the growing season length the same for both time periods (2001–2017 and 2080–2099).

RESULTS

Winter and Growing Season Climate

Comerford and others (2013) and Campbell and others (2014) previously described the effects of snow removal on soil frost and temperature at Hubbard Brook. Reinmann and Templer (2016) and Sorensen and others (2016) previously described the effects of snow removal on snow depth, soil frost, and soil temperature at Harvard Forest. Briefly, snow removal at both sites significantly increased the depth and duration of soil frost (Figure 1) and decreased mean winter soil temperatures (at 5 cm depth) compared to the reference plots in the 2009/2010 and 2010/2011 winters at each respective site ($P = 0.0001$ for soil temperatures at both sites). Reinmann and others (2019) and Sorensen and others (2016) previously described that there were no significant differences in soil moisture between reference and snow removal plots at either site for the growing season prior and during our sap flow measurements.

Compared to historic air temperatures, a greater frequency of warmer maximum daily air temperatures is projected for the years 2080–2099 under the low (RCP 4.5) and high (RCP 8.5) emissions scenarios for growing seasons at both sites (Figure 2). Mean historic maximum daily temperature throughout the growing season at Hubbard Brook was 22.4°C and is expected to increase between 26.1 and 29.2°C, whereas the mean growing season maximum air temperature at Harvard Forest was 23.5°C and is expected to increase to between 27.2 and 30.1°C by the year 2099. With these increases in temperatures, the number of heat stress days will increase at both Hubbard Brook and Harvard Forest to between 112 and 128 or 63 and 92 days, respectively (Table 1).

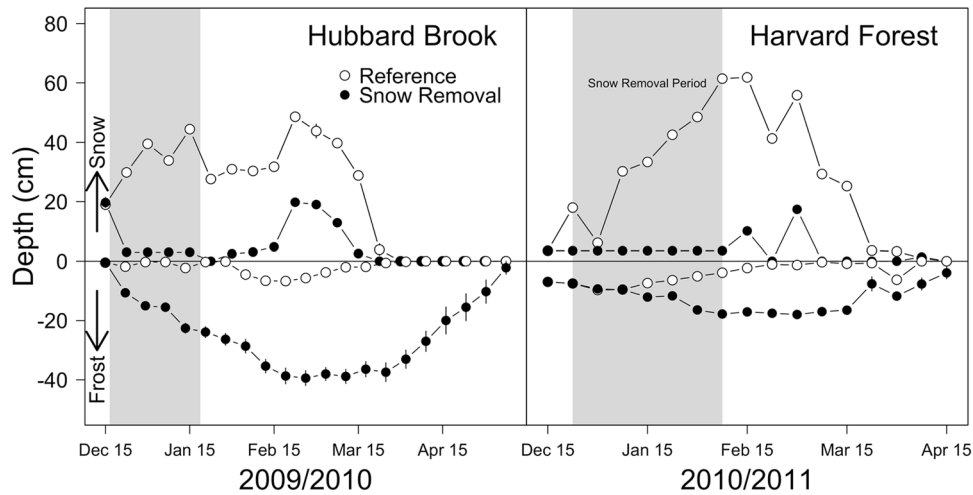


Figure 1. Snow (≥ 0 cm) and soil frost (≤ 0 cm) depth in reference and snow removal plots for the 2009/2010 winter at Hubbard Brook and 2010/2011 winter at Harvard Forest. Error bars represent standard error of the mean. Some error bars are not visible because of the low amount of variability across plots.

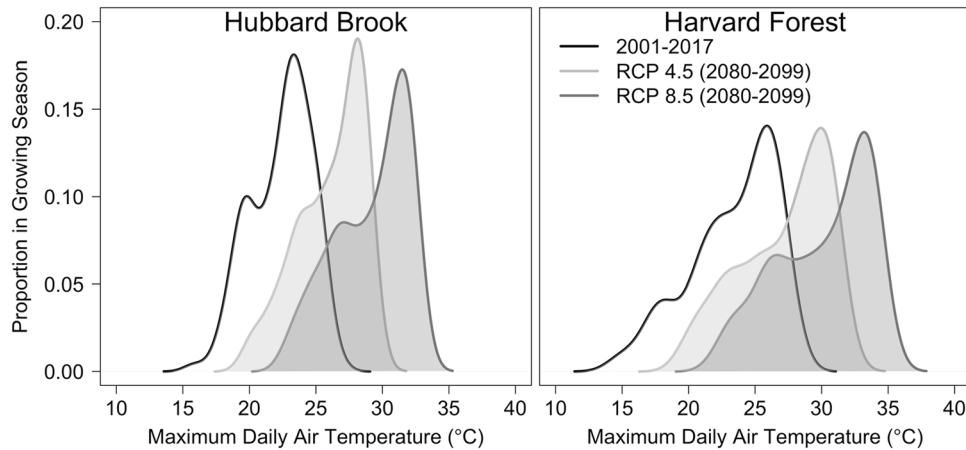


Figure 2. Frequency of maximum daily air temperatures observed at Hubbard Brook and Harvard Forest for the growing season using kernel density plots. Historic averages for air temperature between the years 2005 and 2018 were calculated from the SCAN site at Hubbard Brook and the Fisher Meteorological Station at Harvard Forest, with low (RCP 4.5) and high (RCP 8.5) emissions scenarios calculated based on CMIP5 data for each region.

Water Uptake by Trees

Sap flow rates did not vary significantly with basal area increment ($P = 0.09$, 0.38 , and 0.22 for sugar maple, red maple, and red oak, respectively), but were correlated positively with VPD for all three tree species ($P < 0.001$ for all three tree species; Figures 3, 4). All tree species had increased rates of sap flow with increased mean (Figure 5A) and maximum (Figure 5B) daily air temperatures. Under both RCP 4.5 and 8.5 emissions scenarios predicting increased frequency of heat stress days over the next century, sap flow rates of all three tree species are projected to increase compared to current conditions (Figure 6).

Sugar Maple

Sap flow by sugar maple trees was not significantly different between typical and heat stress days within reference or snow removal plots ($P = 0.81$ and $P = 0.20$ for reference and snow removal plots, respectively; Figure 5). Similarly, snow removal did not affect the relationship between rates of sap flow and daily mean or maximum air temperatures ($P = 0.65$ and $P = 0.68$ for mean and maximum air temperatures, respectively) for sugar maple trees. In the early growing season (DOY 141–155), rates of sap flow in sugar maple trees were $42 \pm 1.7\%$ less sensitive to changes in VPD in the snow removal compared to reference plots (4.03 ± 0.77

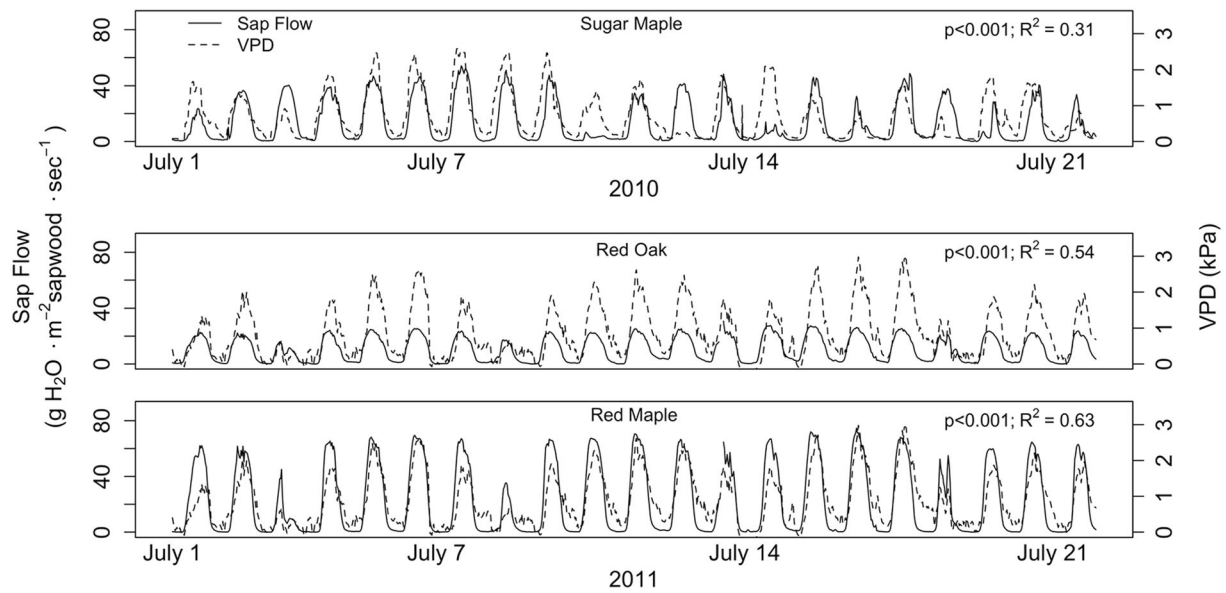


Figure 3. Relationships between instantaneous rates of sap flow and vapor pressure deficit (VPD) during 3 weeks of the peak growing season at each site (Hubbard Brook and Harvard Forest) to make viewing the data easier than the entire growing season. Figures show averages across reference plots only. The R^2 and P values provided are for the line of best fit between sap flow and VPD during the 3 weeks of data shown.

and $6.9 \pm 1.1 \text{ g H}_2\text{O m}^{-2} \text{ sapwood s}^{-1}$ per kPa VPD in snow removal and reference plots, respectively; $P = 0.003$; Figure 4A). Across the heat stress days, rates of sap flow in sugar maple trees appeared insensitive to changes in VPD in both reference and snow removal plots (-1.6 ± 5.5 and $-1.5 \pm 3.3 \text{ g H}_2\text{O m}^{-2} \text{ sapwood s}^{-1}$ per kPa VPD in reference and snow removal plots, respectively; Figure 4G). Of the three tree species examined, sugar maples are projected to experience the smallest increase in sap flow with warmer air temperatures, increasing between 8 and 11% for reference and snow removal conditions, respectively (Figure 6).

Red Maple

There was a significant increase in sap flow rates by red maples with increased mean and maximum daily air temperatures on heat stress days compared to typical days ($P < 0.001$ for both reference and snow removal plots, respectively). In addition, there was a trend of decreased sap flow rates by red maples in the snow removal plots compared to reference plots for both mean and maximum daily air temperatures ($P = 0.09$ and $P = 0.05$, respectively; Figure 5A, B). Although rates of red maple sap flow across the growing season and on heat stress days did not differ, they were $24 \pm 2.7\%$ and $19 \pm 0.091\%$ less sensitive to changes in VPD in snow removal compared to reference plots

(14.8 ± 1.05 and $19.5 \pm 1.1 \text{ g H}_2\text{O m}^{-2} \text{ sapwood s}^{-1}$ per kPa VPD in snow removal and reference plots, respectively, during the growing season, $P < 0.001$, Figure 4E; 16.42 ± 1.49 and $19.88 \pm 1.78 \text{ g H}_2\text{O m}^{-2} \text{ sapwood s}^{-1}$ per kPa VPD in snow removal and reference plots, respectively, on heat stress days, $P < 0.001$, Figure 4H). Red maples are projected experience increased rates of sap flow by 29–38% and 26–35% under reference and smaller snow conditions, respectively, and are projected to have the overall highest rates of sap flow of the three tree species studied (Figure 6).

Red Oak

There were significantly greater sap flow rates for red oak trees in snow removal plots than reference plots ($P < 0.01$) and on heat stress days compared to typical days ($P < 0.001$ for both reference and snow removal plots). In contrast, rates of sap flow in red oak trees were 190% more sensitive to changes in VPD in snow removal than reference plots on the heat stress days ($P = 0.005$; 14.63 ± 1.19 and $5.21 \pm 0.84 \text{ g H}_2\text{O m}^{-2} \text{ sapwood s}^{-1}$ per kPa VPD in snow removal and reference plots, respectively; Figure 4I). The largest increases in sap flow rates of all three species due to rising air temperatures are observed for red oaks under reference snow conditions (61–70% increase from current rates under low and high emissions scenarios, respectively; Figure 6).

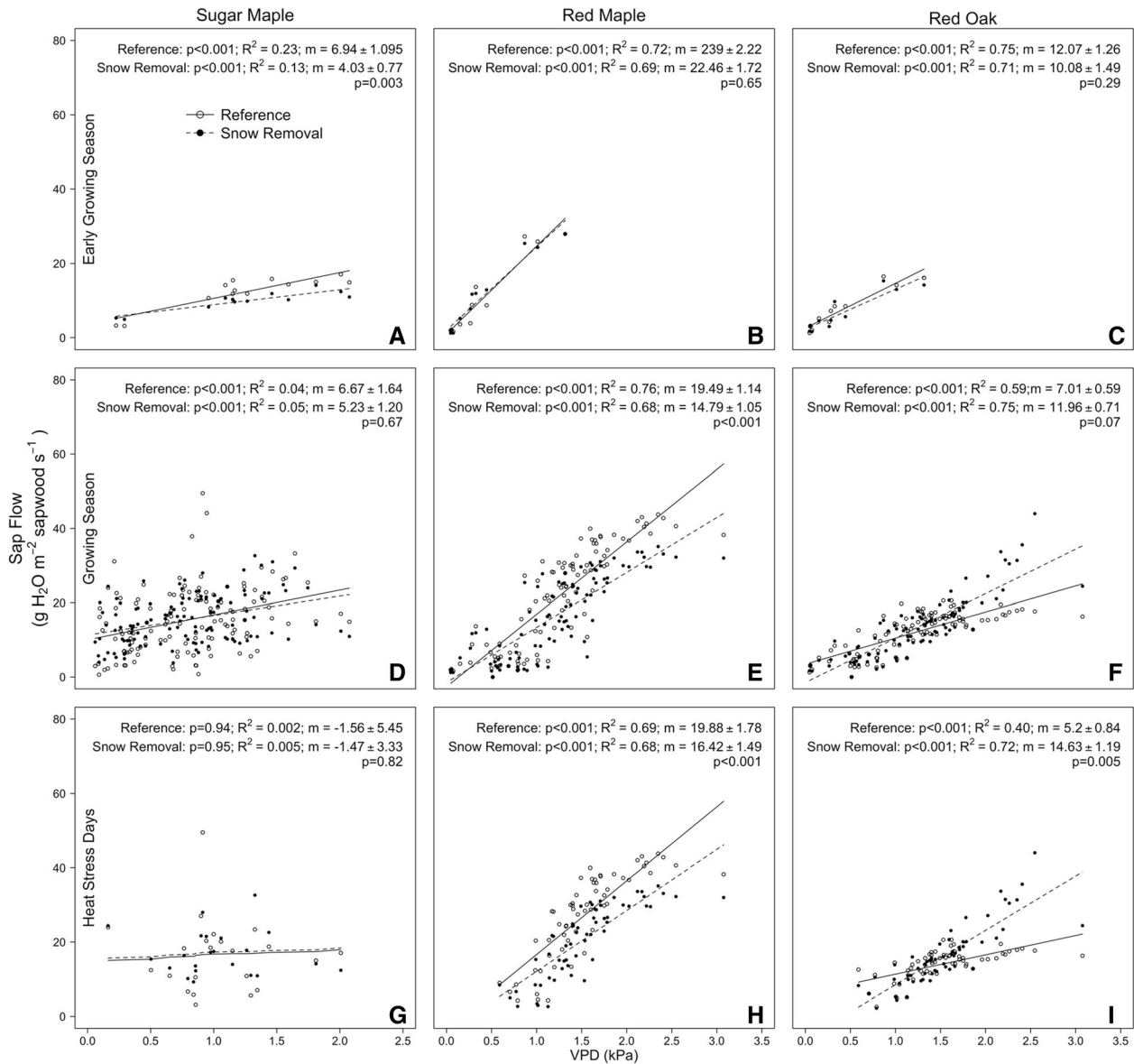


Figure 4. Relationships between rates of sap flow and VPD (kPa) for the three tree species during three time periods: early growing season (Hubbard Brook DOY 141–155 in 2010 and Harvard Forest DOY 136–148 in 2011; panels **A–C**), entire growing season (panels **D–F**), and heat stress days (when air temperatures were > 23.6 and > 26.5°C at Hubbard Brook and Harvard Forest, respectively; panels **G–I**). Each dot represents the daily average rate of sap flow and VPD for daylight hours for individual trees in reference or snow removal plots. *P* values are included comparing the slopes between reference and snow removal plots.

DISCUSSION

Our results demonstrate that the projected rise in both growing season air temperatures (Hayhoe and others 2007; IPCC 2014) and number of heat stress days (Figure 2; Table 1) over the next century is likely to increase rates of transpiration by temperate forest trees, but the magnitude of responses will vary among tree species (Figure 6). Also, the increased rates of transpiration with air temperatures

will be offset for red maples and heightened in red oaks by a smaller winter snowpack. Rates of sap flow measured in this study were within the range reported previously for temperate deciduous forest trees (Bovard and others 2005; Daley and Phillips 2006; Juice and others 2016), and like previous studies, sap flow rates were positively correlated with air temperature and VPD (Granier and others 1996; Sun and others 2000; Lu and others 2004;

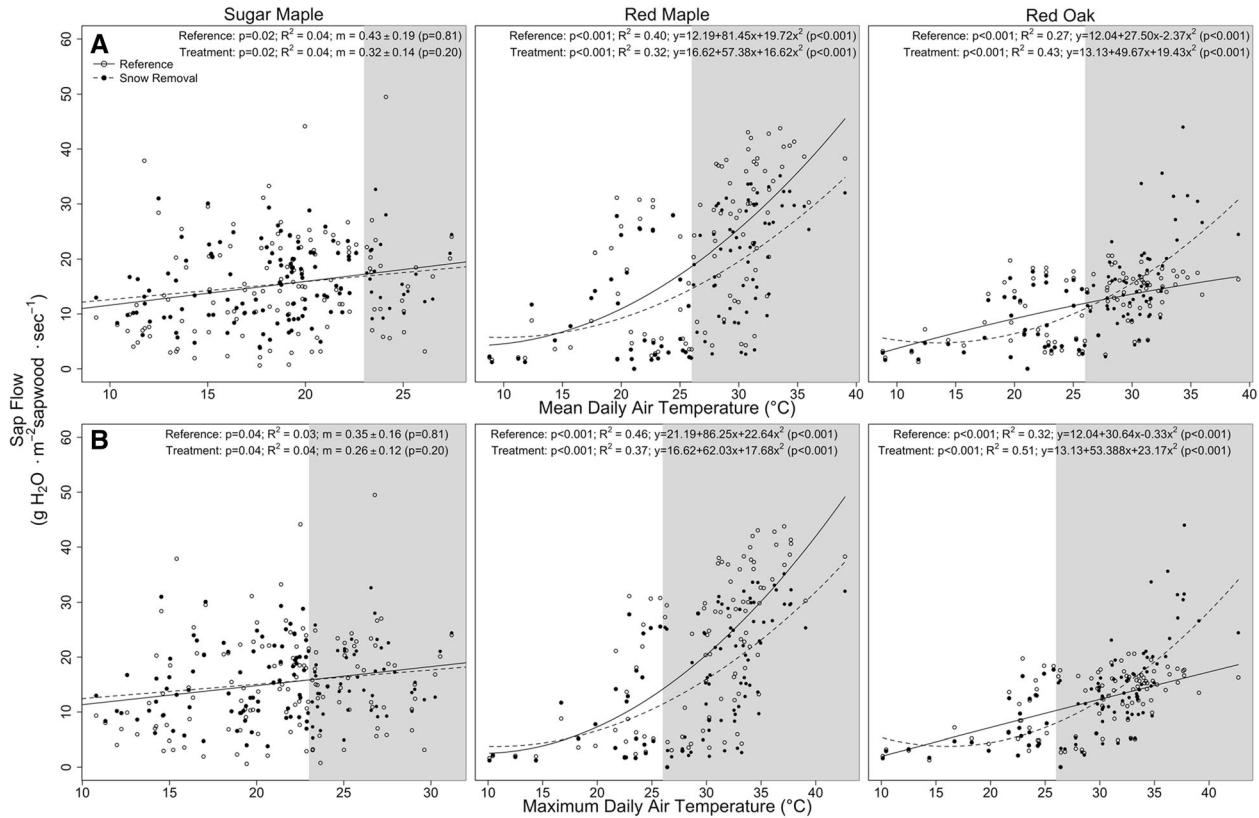


Figure 5. Relationships between rates of sap flow and **A** mean and **B** maximum daily air temperatures (°C) for the three tree species throughout the entire growing season. Each dot represents the daily average rate of sap flow for individual trees in the reference (solid lines) or snow removal (dashed lines) plots during daylight hours (0500 to 2100). First-order linear models are shown for sugar maples and second-order models for red maples and red oaks. *P* values are shown in parentheses comparing slopes between the typical and heat stress days, within reference or snow removal plots for each tree species. *R*², slopes, and equations before the parentheses are for best fit lines that include all days (both typical and heat stress days). Shaded region represents days that are considered heat stress days (when air temperatures were > 23.6 and > 26.5°C at Hubbard Brook and Harvard Forest, respectively). *P* values for the effects of treatment on the relationship between mean and maximum air temperatures and sap flow, respectively, are as follows: *P* = 0.65, *P* = 0.68 for sugar maples; *P* = 0.09, *P* = 0.05 for red maples; *P* < 0.01, *P* < 0.01 for red oaks.

Bovard and others 2005; Juhász and others 2013). We assume no significant changes in VPD (based on lack of projected change; Ficklin and Novick 2017), water limitation (based on conflicting reports; Ollinger and others 1998; Martin-Benito and Pederson 2015), or growing season length (for sake of comparison) over the next century throughout our interpretation of results.

Tree Species-Specific Responses

Sugar Maple

In support of our first hypothesis, we found that rates of sap flow per kPa VPD in the early growing season were reduced in trees experiencing soil freezing compared to those that experienced a substantial snowpack and little to no soil freezing in the previous winter. Companion studies have

found that soil freezing injures roots of sugar maple trees (Campbell and others 2014; Sanders-DeMott and others 2018), which could explain the reduction in transpiration by this tree species in the early growing season. However, we found no effect of soil freezing on transpiration later in the growing season. It is possible that later in the growing season, root damage caused by soil freezing is ameliorated due to fine root turnover (Tierney and others 2001), leading to no difference in rates of sap flow after the early growing season. Despite potential root damage from the previous winter, sugar maple trees maintained a positive relationship between temperature and sap flow regardless of snow removal treatment. Thus, even with the possible diminished ability to take up water in the early growing season, we still expect marginal in-

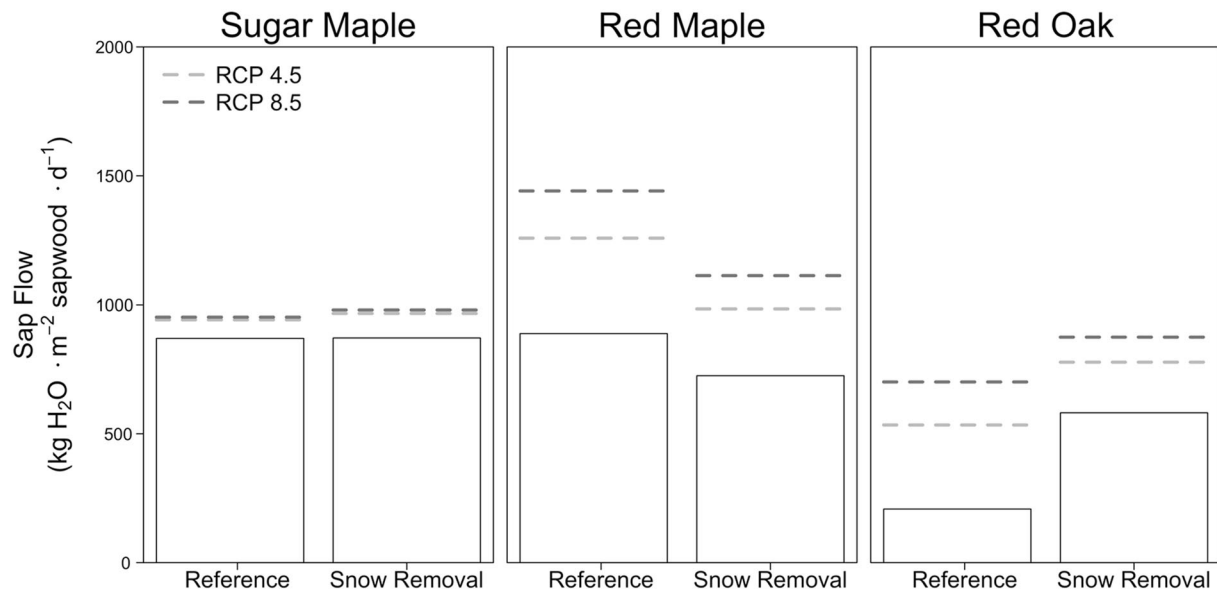


Figure 6. Current and projected average daily rates of sap flow for the growing season under historic (2005–2018; bars) and projected maximum daily air temperatures with low (RCP4.5; dashed light gray) and high (RCP 8.5; dashed dark gray) emissions scenarios for the years 2080–2099.

creases in sap flow with projected increases in heat stress days over the next century.

In addition, during the 2010 growing season, an early leaf-out followed by late spring frost (DOY 129–131) in the northeastern USA led many hardwood trees to drop their initial flush of leaves and produce a second flush of leaves, including sugar maples at Hubbard Brook (Hufkens and others 2012). We observed reduced leaf litterfall mass in fall 2010 compared to prior years (Supporting Figure 2), as well as reduced litterfall in snow removal plots compared to reference plots. Our litterfall results from fall 2008–2010 suggest that there may have been a reduction in above-ground productivity in 2010 due to this late spring frost, which is similar to observed reductions in net primary productivity across the region due to the late spring frost (Hufkens and others 2012). However, because we did not measure the mass of litterfall from the first flush of leaves in spring 2010, we cannot conclude definitively whether total annual litterfall was reduced in 2010 in response to the late soil frost. The loss of the initial flush of leaves in 2010 could have led to a reduction in the overall rates of sap flow rates for sugar maple trees in both reference and snow removal plots at Hubbard Brook that year. Despite the larger reduction in aboveground productivity in snow removal compared to reference plots in 2010 (Reinmann and others 2019), we were surprised that we did not observe differences in sap flow throughout the

growing season for sugar maples with snow removal compared to reference plots, as we would have expected a decrease in sap flow to parallel the decreases in net primary productivity.

Red Maple

Despite the positive relationship between red maple sap flow, temperature, and VPD, we found that the effects of a smaller winter snowpack and increased depth and duration of soil freezing extend throughout the growing season and reduce rates of sap flow (both with temperature and kPa VPD) for this tree species. The fact that a reduced winter snowpack and increased soil freezing decreased rates of sap flow per kPa VPD on both typical and heat stress days suggests red maple trees may have decreased stomatal conductance in response to stressful conditions (that is, root damage and high temperatures). Despite the decreased rates of sap flow due to soil freezing, our findings still suggest that red maples, compared to sugar maples and red oaks, will continue to have the highest average daily rates of sap flow per unit sap wood by the end of the century.

Red Oak

In contrast to both maple species, rates of sap flow by red oaks increased (both with temperature and kPa VPD) in response to a smaller winter snowpack and greater depth and duration of soil freezing. Red oak's anisohydric physiology may explain why

they continued to take up water on heat stress days and in response to snow removal, while other tree species like sugar and red maples, when exposed to heat stress days or soil freezing, reduce their transpiration in the early growing season. Further, reduced transpiration by co-occurring red maples may increase soil water availability for red oak trees in the long term, which may contribute to the observed increase in transpiration by red oaks in response to a smaller snow pack and soil freezing.

IMPLICATIONS AND CONCLUSIONS

Among the three tree species, sugar maple trees responded as we expected to increased soil freezing by reducing rates of transpiration in the early growing season, possibly due to root damage that was later ameliorated by fine root turnover. Given that red maples responded to a smaller snowpack to a lesser degree than sugar maples in past studies (Sanders-DeMott and others 2018), we were surprised to observe decreased transpiration throughout the growing season and on heat stress days in response to a smaller snowpack and greater soil freezing for this tree species. We were also surprised to observe increased rates of transpiration in red oak trees in response to soil freezing, though it may be due to larger water availability caused by reduced transpiration in co-occurring red maples as we did not see any differences in soil moisture with soil freezing. Previously published data from our group indicate that while there were no pre-treatment differences in DBH or growth rates between reference and snow removal plots, we observed trends of decreased growth rates in red oak and red maple, and increased growth rates in red maple trees, with increased soil freezing. The reduced net primary productivity we observed with snow removal parallels our findings of reduced sap flow in the early growing season in sugar maple trees. However, the reduced productivity observed in red oak trees in response to soil freezing does not explain the increases in sap flow we observed in that tree species, and increased productivity in red maple trees (Reinmann and Templer 2016; Reinmann and others 2019) does not explain the decreases in sap flow we observed in that tree species. These results leave us wondering: (1) Do red maple trees decrease transpiration in response to soil freezing because roots are damaged and/or because they close their stomata? (2) Do red oak trees increase transpiration in response to soil freezing because the reduction in transpiration by co-occurring red maples increases water availability or because root damage impairs stomatal regulation? As mentioned

previously, it is unclear whether water is a limiting resource in mixed temperate forests (Ollinger and others 1998; Martin-Benito and Pederson 2015); therefore, we cannot conclude whether or not reduced transpiration by red maples led to increased transpiration by red oaks.

In our previous research, we found that the aboveground woody biomass of sugar maple trees decreased, red oaks did not change, and red maples increased, in response to a smaller winter snowpack and greater depth and duration of soil freezing (Reinmann and Templer 2016; Reinmann and others 2019). The findings that red oaks experiencing a smaller snowpack and increased soil freezing have no change in aboveground biomass and increased rates of water uptake compared to reference trees suggest that this species may have decreased water use efficiency (WUE; greater uptake of carbon relative to water uptake) under these conditions. In contrast, WUE in red maples may have increased in response to soil freezing, as evidenced by their greater aboveground biomass increment (Reinmann and Templer 2016), and decreased transpiration compared to reference plots.

Throughout the northeastern USA, the relative abundance and range of red maples have been increasing (Fei and Steiner 2007), whereas the relative abundance of red oak (Fei and Steiner 2007) and sugar maple (Horsley and others 2002) has declined. It has long been questioned why red maple trees outcompete other co-occurring hardwood tree species, and the answer is in part due to their ability to grow under a wide range of environmental conditions (Abrams 1998). Our results further indicate the resilience of this species to soil freezing may contribute to their competitiveness; despite soil freezing decreasing rates of transpiration, red maple trees appeared to increase WUE. Red oaks, which experienced an increase in transpiration rates and decreases in WUE, risk cavitation in the future with warmer temperatures and greater soil freezing. These results suggest that between these two species, red maple trees might have a competitive advantage.

Our results demonstrate that reduced snowpack and increased soil freezing have negative impacts on the transpiration dynamics of some tree species, which is consistent with the already documented negative effects of reduced snow pack and increased soil freezing on root health (Tierney and others 2001; Cleavitt and others 2008; Comerford and others 2013), nutrient uptake (Campbell and others 2014), and aboveground growth (Reinmann and others 2019). In contrast, sugar maple was only

impacted early in the growing season and red maple, despite reduced rates of sap flow in response to a smaller winter snowpack throughout the growing season, had higher rates of transpiration compared to red oak and sugar maples. Building on the understanding that temperate tree species vary in their effects on biogeochemical cycling (Lovett and Mitchell 2004; Templer and others 2005; Sanders-DeMott and others 2018) and water balance (Daley and others 2008), our results further demonstrate that winter climate change and increases in growing season heat stress days can have variable impacts on transpiration among species. Understanding the species-specific responses by temperate forest trees to a changing climate suggests we might continue to see widespread expansion of red maple trees, with possible declines in red oak trees, thus altering forest composition and, possibly, water cycling.

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