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Physiological response of mature red spruce trees to partial and complete sapwood severing

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Abstract Drought frequency and severity are projected to increase in many regions of the world, yet it remains unclear how mesic forest trees will respond to these novel climate conditions. Experimentally imposing drought in forests at the stand scale is logistically difficult, however, disturbing the hydraulic functioning of individual trees can induce severe water stress and may inform how large trees respond to future droughts. In this study, we manipulated water availability of red spruce (*Picea rubens* Sarg.) trees by partially or completely severing sapwood, and measured impacts on water relations and photosynthetic efficiency over four months. Trees with total sapwood severed (TOT) experienced a rapid 96.7 % reduction in daily sap flow whereas trees with only partial sapwood severed (PAR; estimated 2–5 % sapwood remaining) and no sapwood severed (CON; phloem girdled control) experienced average reductions of 74.3 % and 4.6%, respectively. Sapwood severing in TOT trees resulted in declining midday shoot water potential compared to PAR and CON trees, but TOT trees did not surpass the water potential indicative of 50 % loss of conductivity until approximately 12 weeks post treatment. At 7 weeks post treatment, TOT trees had 6.8 times lower midday stomatal conductance than PAR and CON trees. Furthermore, branch- and crown-wood water potentials reached extreme values (below measurement threshold of − 7.7 MPa) in TOT trees by the time of tree harvest at 18 weeks but remained high and did not differ between PAR and CON trees. Our results indicate that with minimal intact sapwood, PAR trees still had sufficient hydraulic functioning to avoid water stress, while TOT trees had temporary resistance to water stress likely associated with declines in carbon sequestration and growth. These findings advance our understanding of how red spruce may physiologically respond to periods of water stress in future climates.

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1 Introduction

Climate change is expected to increase the risk of droughts during the growing season, causing rising concern regarding drought-induced forest growth declines and mortality (Choat et al. 2018; Sánchez-Pinillos et al. 2022; McDowell et al. 2022; Gazol and Camarero 2022). Drought impacts may also be amplified by projections for increased temperature and vapor pressure deficit (VPD) associated with climate change (Horton et al. 2014; Will et al. 2013), which can increase evapotranspiration rates (Hayhoe et al. 2007; Trenberth 2011) and directly reduce tree physiological functioning, growth, and survival (Choat et al. 2018). While the mesic forests of the northeastern United States have rarely experienced drought in the past (Lombard 2004), recent severe drought events (Sweet et al. 2017) and climate change projections (Liénard et al. 2016) highlight an increasing threat for local forests.

In order to better understand how forests may respond to novel future drought conditions, it is essential to investigate mature tree physiological responses to drought stress (Coble et al. 2017). There is a growing body of work addressing natural drought induced tree mortality and growth reductions (Allen et al. 2015; Anderegg et al. 2016; Martinez-Vilalta et al. 2019; Gazol and Camarero 2022), however many of these studies are retrospective, limiting our understanding of physiological responses of mature trees during the drought. The logistical difficulties in experimentally imposing drought on large trees (D'Orangeville et al. 2013; Asbjornsen et al. 2018) has led to a paucity of research on this topic, driving uncertainty about how forests will respond to these novel drought conditions. Research into plant hydraulics has attempted to overcome this problem by sampling large branches from canopy trees and monitoring elements of their physiology (embolism formation, stomatal conductance, water potential, etc.) during bench dehydration experiments in the lab (Choat et al. 2003; Brodersen et al. 2019; Blackman et al. 2019; Brodribb et al. 2021). Monitoring shoots in bench dehydrations has emerged as a new technique to improve our ability to predict how trees respond to drought (Blackman et al. 2016, 2019) but also may not adequately incorporate the role of trunk-wood in buffering daily and seasonal water demands (Čermák et al. 2007). Therefore, an approach that limits water transport to the entire tree crown but maintains hydraulic connections to the large water storage in the trunk-wood may provide further insights into how large canopy trees can resist physiological stress during water deficits. Indeed, sapwood severing studies were at the forefront of our early understanding of xylem structure and function (Greenidge 1957; Kozlowski 1961) and continue to improve our understanding of the role of trunk xylem in whole-tree water relations (Dietrich et al. 2018).

Leaves are one of the first organs to experience the negative effects of water deficit but also have adaptations to avoid water stress. For example, during periods of water deficit, trees commonly show decreased leaf and shoot water potentials (Ψ) that can lead to embolism formation and spread (Irvine et al. 1998). Some species are able to temporarily maintain fairly stable Ψ values and avoid steep drops by closing stomata to reduce water loss (Klein 2014). Importantly, however, reductions in stomatal conductance can also lead to reduced photosynthesis and growth as carbon sequestration rates decline (Drake et al. 2017). Conversely, some species maintain more open stomata during periods of water deficit in order to continue sequestering carbon, but may have other adaptations to avoid hydraulic failure (McDowell et al. 2008). During periods of extreme water limitation, leaf metabolism can be interrupted as water potentials decline, leading to reductions in chlorophyll concentration, photosynthetic capacity, and net photosynthesis (Prieto et al. 2009; Ditmarová et al. 2010; Melaouhi et al. 2021).

Hydraulic and photosynthetic physiology have evolved together as part of a coordinated strategy to maximize carbon uptake (McDowell et al. 2019) while minimizing hydraulic risk over the long-term. While the importance of avoiding carbon depletion during drought is important, most studies find that drought induced mortality is almost always associated with hydraulic failure (Adams et al. 2017). As such, leaf-level physiological responses to water deficit may be coordinated with stem and whole-tree physiological responses, including when water stress is substantial enough to induce embolism formation and spread (Mayr et al. 2002, 2003; Wason et al. 2018).

For example, both phloem (Zweifel et al. 2000; Ilek et al. 2017) and xylem in tree trunks may provide important capacitive buffers during diurnal fluctuations in water demand by the canopy (Čermák et al. 2007; Scholz et al. 2011). However, during extreme deficit conditions, embolism formation and spread in xylem can rapidly lead to persistent reductions in water storage and transport capacity (Paljakka et al. 2020). Importantly, xylem in many larger portions of woody plants, such as trunks, appear to have far more hydraulic transport capacity than is required to meet demand (Dietrich et al. 2018). This suggests that stored water reserves released from these tissues as embolisms spread could be important for maintaining hydration of other tissues such as leaves and cambia.

Red spruce (*Picea rubens* Sarg.) is a shade tolerant, slow-growing coniferous gymnosperm common in the mesic forests of the northeastern United States that is expected to face substantial reductions in suitable habitat remaining in the United States by 2100 (Iverson et al. 2008; Landscape Change Research Group 2014). Red spruce is often considered a climate-sensitive species, and regional studies have shown growth declines in years following low precipitation (Kosiba et al. 2018). However, there is some discrepancy in the drought tolerance classification for red spruce, with published classes ranging from intolerant to tolerant (Coble et al. 2017). This range in drought tolerance classes may be due to confounding impacts of higher temperature and VPD that often coincide with soil moisture deficits (White et al. 2014; Wason et al. 2019). As such, there is a need to improve our understanding of the physiological response of red spruce to periods of water deficit.

The drought tolerances of other spruce species including Norway [*Picea abies* (L.) Karst], black [*Picea mariana* (Mill.) B.S.P.], white [*Picea glauca* (Moench) Voss], and silver [*Picea pungens* Engelm.] have been studied in seedlings and suggest some may exhibit resistance strategies to avoid water stress, indicated by the ability to maintain turgor after short-term periods of water deficit (Tan et al. 1992; Marshall et al. 2000). Indeed, after experiencing water stress some species are able to accumulate solutes in leaves to lower their turgor loss point (TLP) and avoid wilting (Bartlett et al. 2014). Furthermore, red spruce seedling and sapling drought studies suggest that after eight weeks of severe experimental drought, red spruce exhibits reductions in xylem Ψ and terminal growth (Roberts and Cannon Jr 1992). However, studies on smaller trees do not always translate to larger trees (McDowell et al. 2013). While large trees may have a larger root system to water (Trugman et al. 2021), they may be more vulnerable to drought effects (Bartholomew et al. 2020) due to increased rates of evaporation from larger exposed crowns, longer hydraulic pathways, and larger susceptibility to hydraulic stress (Allen et al. 2010; McDowell et al. 2013; Bennett et al. 2015). Therefore, as drought continues to drive declines in mature forest trees, studies that focus on canopy tree response to drought can improve our ability to predict drought impacts on forest composition and structure (Allen et al. 2010; Pretzsch et al. 2020; Bottero et al. 2021).

The goal of this study was to determine how mature red spruce trees respond to sapwood-severing-induced extreme water deficit. Although sapwood severing is not intended to replicate natural drought conditions, it can inform potential physiological responses employed during natural droughts. Therefore, we conducted a sapwood severing treatment similar to Dietrich et al. (2018) by cutting functional xylem, thus preventing water transport from the roots to the stem. We expected that (1) sapwood severing would rapidly reduce sap flow via stomatal closure to conserve water, (2) sapwood severed trees would gradually draw down trunk-wood water storage before reaching critical hydraulic thresholds in leaves and (3) that during this period of resistance and prior to leaf desiccation, photosynthetic efficiency would be maintained suggesting resilience to short-term droughts.

2 Material and methods

2.1 Study area and focal tree characteristics

This study was performed on a 0.12-ha forested plot within the University of Maine's Dwight B. Demeritt Forest in Old Town, Maine, USA (44° 55′ N, 68° 40′ W; see map in Fig. S1a available as Supplementary Data). Species composition was dominated by eastern hemlock [*Tsuga canadensis* (L.) Carrière] and balsam fir [*Abies balsamea* (L.) Mill], with smaller amounts of red spruce, white pine (*Pinus strobus* L.), paper birch (*Betula papyrifera* Marshall), white-cedar (*Thuja occidentalis* L.), red maple (*Acer rubrum* L.), and red oak (*Quercus rubra* L.). During the 2020 growing season, we intensively monitored the leaf and trunk-wood water content and water potential, photosynthetic efficiency, chlorophyll concentration, and stomatal conductance of eight subdominant red spruce trees in this stand (see plot layout in Fig. S1b available as Supplementary Data). All eight trees were mature (apparent age at breast height 52–70 years; ring counts from cross-sections after the experiment), similar in size [diameter at breast height (DBH) 16–26 cm, total height 11.8–19.9 m], had healthy crowns [live crown ratio (LCR) from lowest living branch 0.22–0.47; DeYoung 2016] and had no visible trunk damage (Table 1).

From June through November 12th, 2020, study site mean maximum daily temperature was 20.8 °C, and average daily maximum VPD was 1.2 kPa (average of subcanopy iButton Hygrochron temperature and humidity loggers, Maxim Integrated Products, Inc., Sunnyvale, California; deployed following (Wason et al. 2017). See Fig. S2 available as Supplementary Data). Soils were well drained silty-loam (USDA Web Soil Survey). Periodic soil moisture measurements obtained with a handheld soil moisture sensor (Model HS2, Campbell Scientific, USA) approximately 1 m from the base of study trees were consistently above 18 % volumetric water content in the top 20 cm of soil suggesting that the focal trees did not experience any substantial soil water deficit conditions during this study (Górnik et al. 2008; Ortiz and Salas-Fernandez 2022).

Crowding of focal tree crowns from neighboring trees varied (Table 1) due to a recent overstory removal study imposed on the eight focal red spruce trees. Two weeks prior to initiating the sapwood severing treatment (detailed below), we removed all competing trees (> 2.5 cm DBH) within 5 m of four focal trees (complete removal). The other four trees had no competition removed. We initially expected that the previous overstory removal would impact the results of this sapwood severing experiment, as the level of crown exposure may influence transpiration and tree water stress (Lagergren et al. 2008). Therefore, in our data analysis we initially included overstory removal treatment in all our statistical models to test for main and interactive effects. However, we did not see any evidence to suggest that increased exposure of canopies significantly impacted the results of the sapwood severing experiment, except for growing season photosynthetic efficiency (more detail in "Data analysis" section).

2.2 Sapwood severing treatment design

In order to experimentally impose a water deficit, we severed the sapwood on four red spruce trees, leaving the other four trees as controls (see images of treatments in Fig. S1c, d available as Supplementary Data). We aimed to sever 100 % of the sapwood to prevent all water transport from the soil to the canopy. We estimated sapwood depth of each tree using the translucence method as a proxy for sapwood area (DeRose and Seymour 2009) on two increment cores collected 0.6 m above the soil surface. Average sapwood depth per tree ranged from 1.4 (±0.1) to 2.9 (±0.2) cm (Table 1).

Table 1 Characteristics of focal red spruce trees

Tree #	DBH (cm)	Total height (m)	Live crown ratio	Estimated sapwood depth (cm)	Estimated sapwood area remaining (%)	Overstory removal treatment	Sapwood severing treatment
1	20.6	16.7	0.26	2.7 ± 0.1	2	No removal	PAR
2	16.8	16.1	0.22	2.3 ± 0.1	0	Complete removal	TOT
3	19.0	16.2	0.22	2.2 ± 0.1	100	Complete removal	CON
4	17.2	16.4	0.32	1.4 ± 0.1	100	No removal	CON
5	29.1	19.9	0.47	2.4 ± 0.1	5	Complete removal	PAR
6	24.9	17.8	0.44	2.9 ± 0.2	100	Complete removal	CON
7	19.2	11.8	0.32	1.9 ± 0.0	100	No removal	CON
8	25.4	15.9	0.38	2.2 ± 0.1	0	No removal	TOT

Diameter at breast height (DBH), total tree height, live crown ratio, average sapwood depth (± SE), and the sapwood severing treatment applied to each tree (CON, phloem girdled control; PAR, partial sapwood severed; TOT, total sapwood severed)

For the four sapwood-severed trees, on July 6, 2020, we used a circular saw to sever the sapwood around the entire tree circumference 0.6 m above the ground. For each tree, the blade depth was set to 1.5 × the average sapwood depth of each tree, plus the average bark width of all trees (0.28 cm). To quantify the physiological changes due to severing the xylem relative to phloem, we girdled the phloem on the four control trees. The saw blade width was 0.3 cm; we therefore removed an equivalent width of phloem from the controls using a razor blade. For sapwood-severed trees, we used plastic shims to stabilize the gap in each tree, wrapped the cut with plastic sheeting, and braced the trees with wooden supports.

In order to verify the percent of sapwood severed in each tree, at the end of the experiment we obtained cross sections of the trunk that encompassed the cut. We measured the depth of the cut on eight radii for each tree and quantified the amount of estimated intact sapwood relative to our initial estimates of sapwood depth. Due to larger-than-anticipated variations in bark thickness and/or potential inaccuracies in our original estimates based on translucence, two of the four trees in the sapwood severing treatment had partial sapwood remaining (Fig. 1a). Therefore, our results are split into three groups: total sapwood severed (TOT; n = 2), partial sapwood severed (PAR; n = 2), and control (CON: n = 4). Although these represent small samples sizes in each treatment group, we found clear and consistent patterns between groups that are in-line with our expectations. Furthermore, as with other studies on detailed tree physiology (Choat et al. 2005; Čermák et al. 2007; Falcão et al. 2017), the intensity of the related and repeated measurements on these trees would be logistically difficult on more trees and is instead able to provide a window into the physiology of the matures trees that has clear implications for future studies.

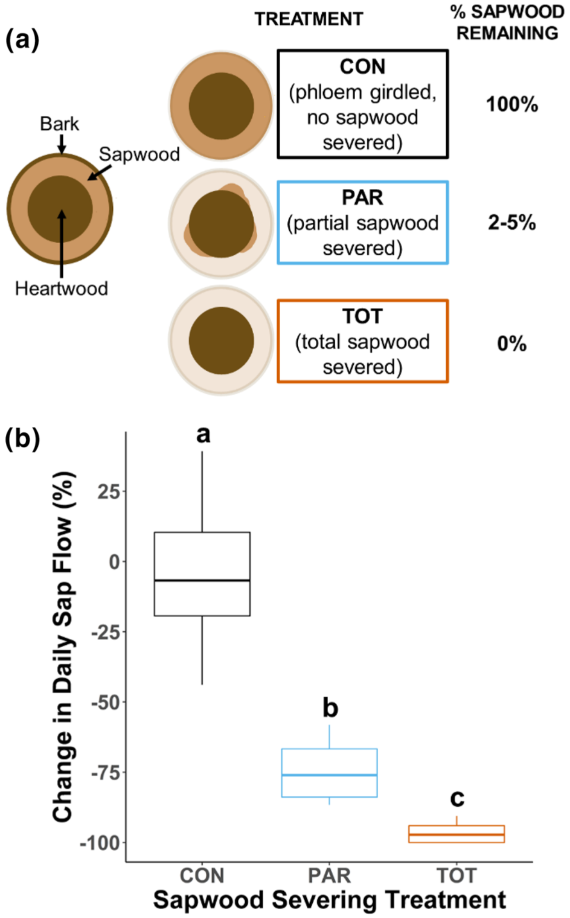

Fig. 1 **a** Representative illustrations of the three sapwood severing treatments: phloem girdled control (CON), partial sapwood severed (PAR), and total sapwood severed (TOT). **b** Box and whisker plots of % change in daily sap flow of CON, PAR, and TOT trees after treatment initiation. Percent change was calculated for five consecutive days in a period 24 days post-severing, compared to the average sap flow of each tree five days pre-severing. Differences between treatments with different letters are statistically significant ($p < 0.05$, determined by Tukey's HSD)

2.3 Impact of sapwood severing on water transport

To quantify whole-tree water use pre and post sapwood severing, custom heat ratio method (HRM) sap flow sensors (Burgess et al. 2001; Vandegehuchte and Steppe 2013) were installed in all eight focal trees 4 weeks prior to study initiation, following the methods of McIntire et al. (2021). Briefly, for each tree we removed a small section of bark at breast height on the south-facing side of the trunk and installed three steel probes (2.5 cm long, 1.0 mm diameter) spaced 5 mm apart vertically. The middle probe contained a nichrome line heater, whereas the top and bottom probes contained three Type T (copper/constantan) thermocouple temperature sensors that recorded at depths of 0.5, 1.0, and 1.5 cm. Sap flow sensors were shielded and connected to two separate data-logging stations (see Fig. S1b available as Supplementary Data). To capture high-resolution data that accurately depict the daily fluctuations in sap flow, we programmed the heater probe to release a heat pulse every 15 min throughout the growing season. The change in temperature on the upstream and downstream probes was subsequently recorded on the datalogger. Equipment malfunctions resulted in several periods of missing data; therefore, we only included days with no missing data for any trees in this analysis. Using the equations described in McIntire et al. (2021), we converted heat-pulse velocity to daily water use based on sapwood cross-sectional area.

2.4 Impacts of sapwood severing on water potential and relative water content

To determine if sapwood severing reduced shoot water potential (Ψ) at midday, multiple canopy shoot samples were collected per tree from the top half of the crown from all eight focal trees. Ψ sampling was conducted eight times throughout the growing season (June through October 2020), and three separate shoots were collected from every tree each time. Samples were collected between 12:00 and 15:00 h (midday) with a Notch Big Shot throw launcher. A 0.9 kg bag was tied to paracord and launched into the canopy, where it draped over a branch and the bag returned to the forest floor. Upon having both ends of the paracord, a hand chain saw was tied to the paracord and strung up into the tree, where it was used to saw off a branch. Within 30 s of branch severing, branches were bagged in foil-lined plastic bags containing moistened paper towels, placed in a cooler, and transported to the lab within 2 h of sample collection (Rodriguez-Dominguez et al. 2022). In the lab, we cut 2-year-old shoots (containing the full current-year and a segment of prior-year growth) from larger branches using a razor blade, and measured shoot Ψ Ψ using a pressure chamber (Model 1000, PMS Instrument Company, USA). One measurement per shoot was conducted for each of the three shoots per tree and the three values were averaged for each tree to estimate midday shoot water potential ($\Psi_{MD,S}$). From the remaining material not used for $\Psi_{MD,S}$, we also estimated leaf water content ($WC_{dry,L}$) by removing all leaves from a 2.5-cm terminal portion of a current-year shoot and obtained fresh mass and dry mass on an analytical balance (Sartorius Practum 224-1S, ± 0.0001 g) after oven drying at 60 °C for at least 48 h. $WC_{dry,L}$ was calculated as (fresh mass − dry mass)/dry mass × 100.

In order to quantify how sapwood severing impacted water relations in the trunk, we measured pre-dawn trunk-wood Ψ ($\Psi_{PD,T}$) in the focal trees seven times between June and November 2020. During each sampling event, two samples per tree were collected at breast height using a Trephor micro-borer (University of Padua, Italy) between the hours of 3:00 and 4:00 AM (pre-dawn). Microcores were extracted from the corer, the bark was removed, and xylem samples were placed directly into sealed thermocouple psychrometer chambers (Wason et al. 2018). Psychrometers were returned to the lab and left to equilibrate in a water bath for a minimum of 8 h before the final Ψ values were obtained. The psychrometers were calibrated using solutions of known Ψ (Brown and Bartos 1982). To obtain tree trunk water content ($WC_{dry,T}$), we removed the pre-dawn microcores from the chambers after equilibration, immediately measured fresh mass, then oven dried and calculated water content as described above.

2.5 Leaf-level responses to sapwood severing during the growing season

In addition to the sap flow measurements in the trunk, we investigated how sapwood severing impacted midday stomatal conductance (g_s) and photosynthesis (A) at one point during the growing season (7 weeks post sapwood severing). Midday g_s and A were measured at ambient light, temperature, humidity, and CO_2 concentration using a LI-6400XT Portable Photosynthesis System (LI-COR, Lincoln, Nebraska, USA). On August 26, 2020, two canopy samples were retrieved at midday from the upper crown of each of the eight focal trees. Immediately upon retrieving the samples, survey measurements were made on two current-year shoot per sample per tree under ambient light conditions, in the same location in the understory. The portion of the needles that were enclosed in the chamber were bagged, and fresh leaf area was determined using a flatbed scanner.

In order to determine if sapwood severing influenced photosynthetic efficiency of needles, we used a FluorPen (Model FP 110, Photon Systems Instruments, CZ) to quantify quantum yield (F_v/F_m) of current-year leaves. Quantum yield is a measure of chloroplast photosystem II light-use efficiency and can indicate damage due to external stressors such as drought (Ben-Gal et al. 2010). Shoot samples were collected midday from the upper crown of all eight focal trees four times throughout the growing season. The shoots were immediately dark-adapted by placing them in foil-lined plastic bags and transporting them to the lab for measuring within 2 h. On each shoot (three shoots per tree), we conducted one F_v/F_m measurement on current year needles.

To determine if sapwood severing impacted leaf chlorophyll, we measured an index of chlorophyll concentration in all eight focal trees at 18 weeks post sapwood severing. We obtained and bagged three current-year shoots per tree, returned them to the lab, and used a chlorophyll meter (Model CCM-300, Opti-Sciences, USA) to estimate the chlorophyll concentration (mg m^{-2}) relative to control trees.

2.6 End-of-season measurements of water stress, storage pools, and leaf physiology

To quantify the long-term effects of the sapwood severing treatment on tree water relations, all eight focal trees were harvested on November 12, 2020 (18 weeks post sapwood severing). During harvesting, we measured crown-wood water potential ($\Psi_{MD,CW}$) and water content ($WC_{sat,CW}$) using microcores as described above, but from the trunk just below the base of the live crown. We also measured branch water potential ($\Psi_{MD,B}$) and water content ($WC_{sat,B}$). Two branches containing 7 years of growth from the upper half of the crown were collected from each tree, placed in black plastic bags containing damp paper towels, and left to equilibrate in the lab for an hour. Afterwards, 1-cm segments of 3- and 4-year branches were removed and debarked, and Ψ was measured using the same methods as with the microcores. Water content was quantified as (fresh mass/saturated mass) × 100. Expressing water content relative to saturated mass helps remove any effect of varying wood densities.

Lastly, to quantify the impact of sapwood severing on radial growth, we calculated basal area increment (BAI) for all eight focal trees using two separate radii on breast-height trunk cross-sections collected after harvesting. Cross sections were scanned and measured in CooRecorder (Cybis.se), and the average ring width was calculated for each tree and converted to BAI using the 'dplR' package in R (Bunn 2010; RStudio Team 2020). For each tree, we calculated percent change in BAI for 2020 relative to the average BAI from the 5 years prior.

2.7 Data analysis

To determine if sapwood severing impacted daily sap flow, we compared average total daily sap flow for the 5 days pre-severing, with the total daily sap flow in a 5-day period starting 24 days after sapwood severing (earliest period with complete data for all trees). We used a logit transformation on the proportions of post- to pre-treatment averages of daily sap flow, and then used a linear mixed-effects model to determine if sap flow change differed as a function of treatment (TOT, PAR, CON), with a random effect for tree nested within day. To assess physiological responses to these treatments throughout the growing season, we generated linear mixed-effects models for $\Psi_{MD,S}$, $\Psi_{PD,T}$, $WC_{dry,L}$ and $WC_{dry,T}$. All models included fixed effects for sapwood severing treatment and time since the sapwood was severed, an interaction between these effects, a random effect for tree, and a first-order autocorrelation term to account for temporal autocorrelation.

To determine if sapwood severing impacted F_v/F_m throughout the growing season, we generated linear mixed-effects models with sapwood severing treatment, overstory removal treatment, and day of year as fixed effects. This model also included an interaction between overstory removal treatment and day of year, a random effect for tree, and a first-order autocorrelation term to account for temporal autocorrelation. For g_s, A, and for the end-of-season measurements of F_v/F_m and chlorophyll concentration, we used linear mixed-effects models with a fixed effect for sapwood severing treatment, and a random effect for sample nested within tree. The F_v/F_m and chlorophyll concentration models also included a fixed effect for overstory removal treatment.

For end-of-season measurements of branch Ψ and water content, we tested for a significant effect of the sapwood-severing treatment using linear mixed-effects models with sapwood-severing treatment as a fixed effect and sample nested within tree as a random effect. After checking that ANOVA assumptions were met, one-way ANOVAs with Tukey's honest significant difference (HSD) tests were used to test for sapwood-severing treatment effects on Ψ and water contents of crown-wood samples. To test for significant differences between treatments in percent change in BAI, we used a one-way ANOVA.

All data were analyzed, organized, and visualized using R and the packages “nlme,” “lme4,” “ggeffects,” “ggpubr,” “lsmeans,” “multcomp,” and “ggplot2” (Hothorn et al. 2008; Bates et al. 2015; Lenth 2016; Wickham 2016; Lüdecke 2018; Kassambara 2020; RStudio Team 2020; Pinheiro et al. 2021).

3 Results

The sapwood severing treatment reduced estimated sapwood area of PAR trees to 2 % or 5 % and TOT trees to 0 % (Fig. 1a). Severing sapwood caused a 74.3 % (±3.5, 58.1–86.6; mean, standard error, and range) reduction in sap flow in PAR trees, and a 96.7% (±1.1, 90.6–100.0 %; mean, standard error, and range) reduction in TOT trees over a 5-day period starting 24 days post-sapwood severing ($p<0.01$; Fig. 1b). CON trees did not experience significant changes in sap flow (average reduction of 4.6 %, ±5.2, 43.9% reduction to 39.2 % increase; mean, standard error, and range). Although we only have data for one PAR and one TOT tree immediately post-sapwood severing, they displayed a 68.5 % and 99.9 % immediate reduction in sap flow 1 day after sapwood severing, respectively, compared to CON trees (average 8.8 % reduction). Those data suggest that changes in sap flow occurred quickly and were similar to the effects observed on day 24.

In addition to reduced sap flow, $\Psi_{MD,S}$ declined 0.13 MPa week^{-1} in TOT trees and diverged from CON (non-overlapping 95 % confidence intervals) 2.4 weeks after sapwood severing (significant treatment × day interaction: $p<0.01$, Fig. 2a). By the end of the growing season (October 15, 14.5 weeks after initiating treatments), TOT trees had reached $\Psi_{MD,S}$ values of −3.50 MPa (±0.37) compared to PAR and CON that had not declined and were at −1.50 MPa

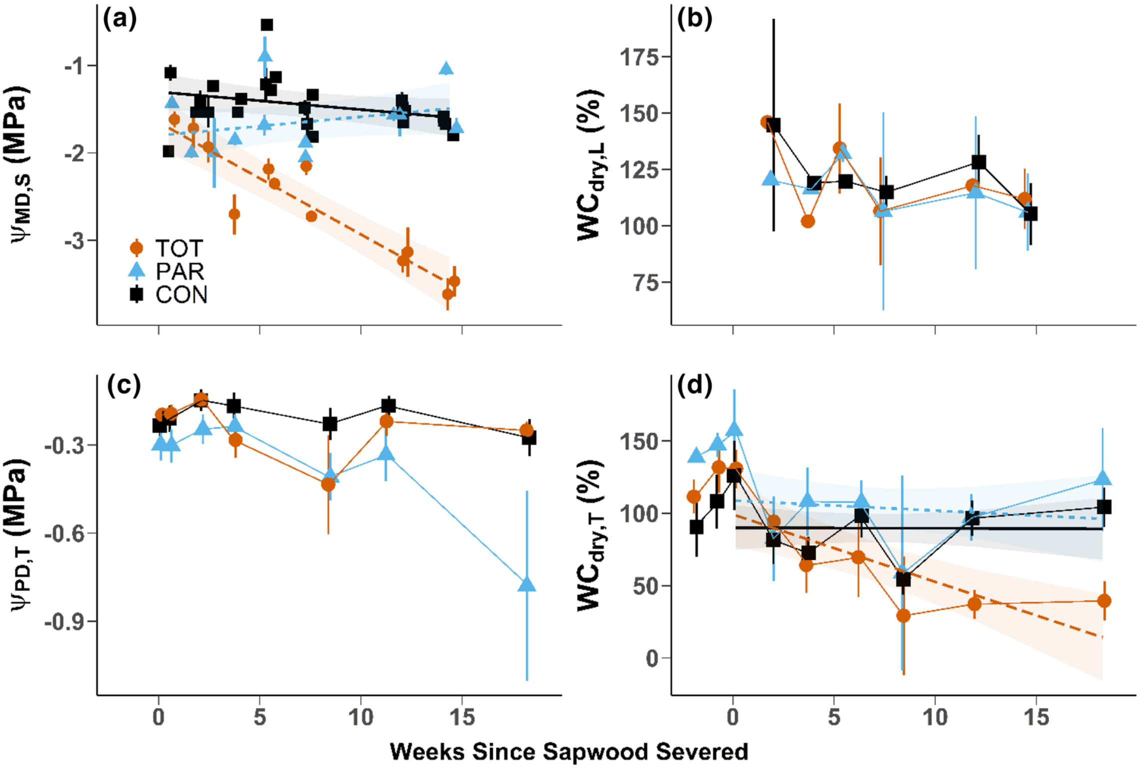

Fig. 2 **a** Shoot midday water potential ($\Psi_{MD,S}$) for each individual focal tree, **b** average water content of leaves ($WC_{dry,L}$), **c** trunk-wood pre-dawn water potentials ($\Psi_{PD,T}$), and **d** average water content of trunk-wood ($WC_{dry,T}$) (±2 SEs). Statistically significant linear mixed-effects models are overlayed with 95% confidence intervals shown as the shaded region

and − 1.59 MPa, respectively. Despite the decline in $\Psi_{MD,S}$ for TOT, we did not see a corresponding decline in $WC_{dry,L}$ in any of the treatments ($p = 0.904$, Fig. 2b).

While there were no statistically significant reductions in $\Psi_{PD,T}$ based on time since treatment initiation ($p = 0.05$), trunk-wood pre-dawn water potentials ($\Psi_{PD,T}$) were not reduced by the sapwood severing treatment ($p = 0.25$, Fig. 2c). However, we did find that $WC_{dry,T}$ declined significantly in TOT trees (4.65 % $week^{-1}$) and diverged from CON trees (non-overlapping 95 % confidence intervals) at 7.0 weeks post sapwood severing (Fig. 2d; significant interaction between treatment and day; $p = 0.01$). Although $WC_{dry,T}$ did initially vary slightly between treatment groups in the two measurements prior to the treatment initiation (Fig. 2d; $p < 0.01$), these differences were absent 1 day after the start of the treatment ($p = 0.30$).

We found that midday stomatal conductance (g_s) was significantly reduced in TOT trees ($p < 0.01$, Fig. 3) when measured at 7 weeks post sapwood severing. TOT tree g_s (13.4 mmol m^{-2} s^{-1}) was, on average, only 14.5 % of PAR g_s (92.7 mmol m^{-2} s^{-1}), and 15 % of CON g_s (89.4 mmol m^{-2} s^{-1}). Despite this decline, g_s in the TOT treatment group was still 4.1 times larger than lab measurements of g_{min} (3.3 mmol m^{-2} s^{-1}; range = 1.9–5.5, Methods available as Supplementary Data) suggesting only partial stomatal closure in the field. We found that A was not significantly impacted by sapwood severing treatment ($p = 0.65$) or overstory removal treatment ($p = 0.96$) when assessed once at 7 weeks post treatment.

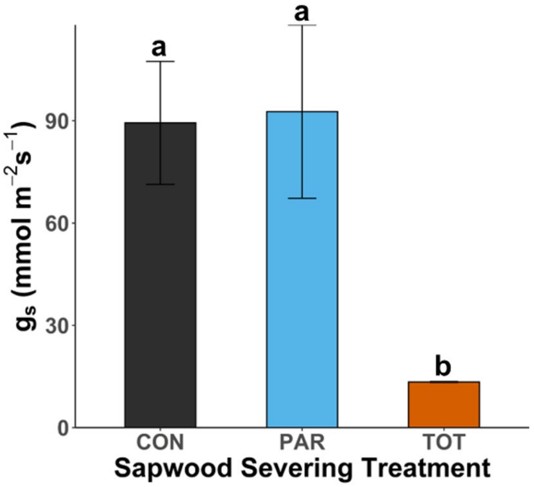

Fig. 3 Average stomatal conductance values (g_s, mmol m^{-2} $s.^{-1}$, ± SE) per treatment for control (CON), partially severed (PAR), and totally severed (TOT) trees, obtained from two individual leaf samples per tree at 7 weeks post sapwood severing. Treatment means with different letters are statistically significant ($p < 0.05$, determined by Tukey's HSD)

We found the recent overstory removal study only significantly impacted growing season photosynthetic efficiency (F_v/F_m) in focal trees. Throughout the growing season, photosynthetic efficiency was reduced by the complete overstory removal treatment, and the interactive effect of time × overstory removal treatment ($p < 0.01$) indicated this effect increased as time progressed. F_v/F_m was not reduced by sapwood severing during the growing season ($p = 0.17$; data not shown).

By the end-of-season measurements in November (18 weeks post-treatment), there was no significant difference in photosynthetic efficiency due to overstory removal treatment ($p = 0.60$). However, at 18 weeks photosynthetic efficiency was significantly reduced by sapwood severing ($p < 0.01$, Fig. 4a), with TOT trees displaying 80.2 % and 79.5 % lower F_v/F_m compared to CON and PAR trees, respectively. We also found that during end-of-season measurements, chlorophyll concentration had declined in both TOT (36.5 % reduction) and PAR (25.4 % reduction) trees ($p = 0.03$, Fig. 4b).

During the end-of-season measurements, we also found that total sapwood severing had significantly decreased crown-wood ($p < 0.01$) and branch ($p < 0.01$) Ψ_{MD} values, with TOT trees reaching extremely low values below − 7.7 MPa, surpassing the measurement range of our sensors (Fig. 5a, b). Additionally, $WC_{sat,CW}$ was significantly impacted by treatment, with TOT trees showing reduced $WC_{sat,CW}$ ($p = 0.04$, see Fig. S3a available as Supplementary Data). Despite the significant main effect of treatment on $WC_{sat,CW}$, we found only marginally lower $WC_{sat,CW}$ in the TOT treatment (Tukey's HSD; $p = 0.0583$). Tree $WC_{sat,B}$ was not impacted by drought treatment ($p = 0.12$, see Fig. S3b available as Supplementary Data).

We quantified percent change in BAI in the current year compared to the average BAI from the five previous years and found that there was no statistically significant difference between sapwood severing treatments (presumably due to some variability in the controls). TOT trees showed reductions

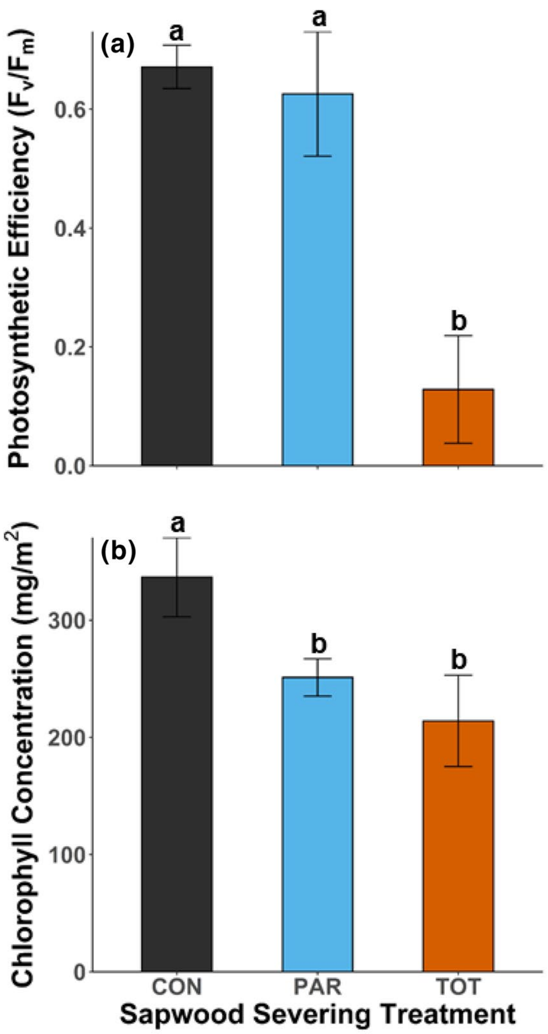

Fig. 4 **a** Photosynthetic efficiency (F_v/F_m) and **b** chlorophyll concentration (mg m^{-2}) for each sapwood severing treatment 18 weeks post treatment—control (CON), partial sapwood severed (PAR), and total sapwood severed (TOT) (±2 SEs). Treatment means with different letters are statistically significant ($p < 0.05$, determined by Tukey's HSD)

in BAI (−62.9 % and −35.2 %), whereas PAR and CON trees showed positive and negative changes. PAR trees showed only minor changes (−14.8 % and 4.0 %), and CON trees showed a larger range of changes (−28.7, −26.9 %, −21.7 %, 57.9 %; see Fig. S4 available as Supplementary Data).

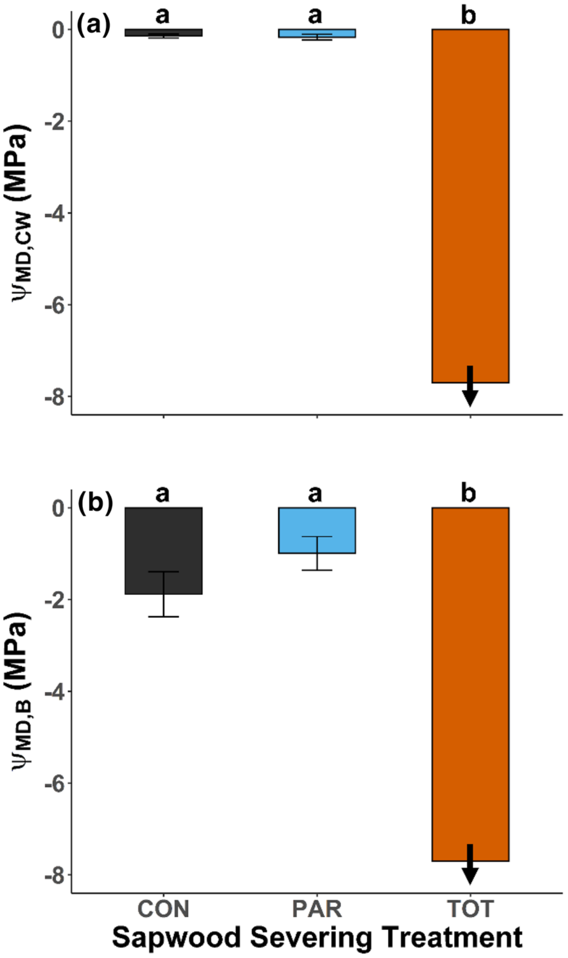

Fig. 5 Average end-of-season **a** midday crown-wood water potentials ($\Psi_{MD,CW}$) and **b** midday branch water potentials ($\Psi_{MD,B}$) in each of the sapwood severing treatments: control (CON), partial sapwood severed (PAR), and total sapwood severed (TOT, ±) (±2 SEs). Black arrows indicate Ψ is below the range of our sensors (−7.7 MPa). Statistical significance ($p < 0.05$) between treatment means as determined by Tukey's HSD is indicated with lowercase letters

4 Discussion

4.1 Sapwood severing and tree water status

Although our estimates indicate we successfully severed 100 % of the sapwood in TOT trees, effectively cutting off all water transport from the roots to the canopy of the tree, we saw a relatively slow decline in Ψ of TOT trees. Lower Ψ values are commonly associated with increased dehydration in leaves (Parkash and Singh 2020), but there are several critical thresholds that can indicate water stress in trees, including TLP and the stem Ψ at which a tree loses 50 % of its hydraulic conductivity (P_{50}). Shoot Ψ at which red spruce reaches its TLP has been reported as − 1.3 to − 1.5 MPa during the growing season (Andersen and McLaughlin 1991). All focal trees in our study surpassed − 1.5 MPa at some point during the growing season, however TOT trees continued to decline by 0.13 MPa week^{-1} for the duration of the growing season.

Although we did not quantify TLP directly in this study, we expect that TOT trees may have lowered their TLP as much as − 0.5 MPa in response to the experimental water deficit, a plastic response that has previously been quantified in drought-stressed plants including spruce (Bartlett et al. 2014). Embolism formation and spread often begins after turgor loss and the P_{50} value for red spruce has been reported around − 3.5 MPa (Sperry and Tyree 1990), and many trees can survive up to as much as 80 % loss of conductivity (Hammond et al. 2019). In this study, TOT trees did not surpass $\Psi_{MD,S}$ values of − 3.0 MPa until 12 weeks after sapwood severing, despite receiving no additional water from the soil. Importantly, this conveys that sapwood severing at the trunk base is not a proxy for percent loss of conductivity in the whole tree, and suggests that red spruce may have avoided extensive embolism formation for much of the growing season and may be initially resilient to short-term periods of water deficit.

We did not witness any decline in tree $\Psi_{PD,T}$ of TOT or PAR relative to CON trees throughout this experiment. The Ψ gradients in trees typically results in relatively high Ψ in trunk-wood, even during relatively dry periods (Wason et al. 2018). However, the trunk-wood can serve as a large capacitor that may supply leaves during periods of drought. Indeed, other studies of xylem capacitance in gymnosperms find that trunk-wood is able to release much larger amounts of water than branches before experiencing declining Ψ (McCulloh et al. 2014). The apparently high trunk wood capacitance in our trees, coupled with the significant decline in $WC_{dry,T}$ of TOT trees throughout the growing season, suggest that the trunk may release water to the transpiration stream in order to maintain leaf water status without associated declines in $\Psi_{PD,T}$.

TOT trees did not experience associated declines in $WC_{dry,L}$, suggesting they indeed may have resisted losing substantial volumes of water until November, when we witnessed widespread leaf drop. This resistance likely depends largely on capacitance and water storage, within the xylem itself (Borchert and Pockman 2005), along with the parenchyma (Jupa et al. 2016) and phloem (Pfautsch et al. 2015). The large declines in trunk wood water content suggest that xylem water stores were depleted throughout the growing season. Importantly, future studies quantifying and comparing these responses of competing species within an ecosystem will yield a more holistic view of the drivers of current and projected shifts in species populations.

The fact that g_s was significantly reduced in our TOT trees relative to PAR and CON trees suggests that during water deficit, red spruce close stomata partially and avoid excess water loss, similar to some other conifers (Lu et al. 1995; Irvine et al. 1998). This could explain the relatively gradual decline in $\Psi_{MD,S}$ throughout the growing season, and consistent $WC_{dry,L}$. Furthermore, there is evidence that leaf water content remained consistent and high even at the TLP (Bartlett et al. 2012) supporting the hypothesis that water stores in leaves may remain constant during periods of water stress compared to other measures of hydraulic status such as Ψ (Martinez-Vilalta et al. 2019). Interestingly, severing 100 % of sapwood in Douglas fir [Pseudotsuga meziesii (Mirb.) Franco] caused rapid leaf Ψ declines of from − 1.5 to − 2.3 MPa within one day (Brix and Mitchell 1985), while here we witnessed a decline over several weeks in our TOT trees. However, g_s of our TOT trees, although far lower than CON and PAR trees, was still 4.1 times greater than our measured and other published (Borer et al. 2005) g_{min} values, indicating stomatal closure was not complete and that some transpiration was still occurring.

Although TOT trees did show temporary resistance to water stress throughout the growing season, our November measurements showed that TOT trees surpassed important hydraulic thresholds by the end of the season. During the end of season measurements at 18 weeks after sapwood severing, TOT tree $\Psi_{MD,CW}$ and $\Psi_{MD,B}$ both reached extremely low values below − 7.7 MPa. While embolism refilling and recovery from seasonal winter drought stress has been witnessed in mature Norway spruce, this has only been quantified in trees with shoot and stem Ψ that have not yet surpassed − 2 MPa (Mayr et al. 2014).

This indicates that our TOT trees, if they were experiencing similar water-stress conditions due to a natural drought instead of permanent sapwood severing and hydraulic failure, may have been able to recover earlier in the growing season but may not have recovered after 18 weeks. The widespread leaf mortality witnessed in TOT trees at the end of the experiment coupled with the extremely negative values of Ψ in the branches, correlates with the vulnerability segmentation hypothesis (Tyree and Ewers 1991). Indeed, low investment organs such as leaves and branches are often more likely to experience embolism, as a means of protecting high investment organs such as the trunk and roots during periods of stress (Wason et al. 2018; Song et al. 2022). However, the extremely low values of crown wood Ψ indicate that this protection mechanism was only temporary within TOT trees.

4.2 Sapwood severing impacts on gas exchange and photosynthetic efficiency

Alongside water status, climate impacts on tree gas exchange and photosynthesis have important implications for tree growth and survival during drought (McDowell et al. 2022). We detected an 85.0 % decline in g_s in TOT trees compared to CON trees when assessed at week seven, suggesting that completely severing sapwood and reducing sap flow causes stomatal closure that would also limit CO_2 uptake. Stomatal closure in response to water deficit is widely observed, including for other *Picea* spp. (Bigras 2005; Ditmarová et al. 2010). Although we saw clear patterns in g_s that matched our expectations, we found more variation than expected in A for CON (4.23 ± 1.8 µmol m^{-2} s^{-1}) and PAR (3.24 ± 3.7 µmol m^{-2} s^{-1}) trees when assessed during the seventh week post sapwood severing. Since photosynthetic efficiency (F_v/F_m) remained high for these trees (Fig. 4a), this variation in A may be driven by a metabolic disruption such as feedback inhabitation driven by the phloem girdling within some of the sampled shoots (Urban et al. 2017). Regardless, A for all TOT trees was strongly reduced and consistently low, averaging 0.78 ± 0.40 µmol m^{-2} s^{-1}, which is 8.3 % of the maximum A we measured on CON trees. For the TOT trees, this suggests that stomatal closure may have driven some declines in photosynthesis that would be expected to impact longer-term carbon relations of the trees.

We also did not see a significant decline in photosynthetic efficiency throughout the growing season, this was perhaps due to the overshadowing effect of the overstory removal treatment which impacted light environment. Similar results have been detected in other evergreen species subjected to water and light manipulation treatments (Pardos and Calama 2022), with increased light driving temporary declines in F_v/F_m. However, over longer time frames (18 weeks post sapwood severing), we did observe reductions in TOT F_v/F_m by 80.9 % compared to CON trees, suggesting that the chronic drought stress eventually drove declines in maximum potential photosynthesis. Supporting this result, in PAR and TOT trees, we also found significant declines in chlorophyll concentration by end of season, of 25.4 % and 36.5 %, respectively. Declines in chlorophyll concentration have been quantified in Norway spruce seedlings subjected to severe drought (Ditmarová et al. 2010), which supports our findings in TOT trees. Chlorophyll fluorescence continuously declines during periods of drought stress and may act as an indicator of tree mortality (Guadagno et al. 2017). However, based on our results for PAR trees that experienced some declines in chlorophyll concentration by week 18, slight but prolonged drought conditions can also negatively impact these trees. Indeed, declines in chlorophyll concentration have been detected in conifer seedlings grown in solution, in response to an induced reduction of only -0.15 to -0.60 MPa in osmotic potential (Dubos et al. 2003), aligning with our results.

Finally, our results align with our expectation that although red spruce may have strong resistance to water stress, this resistance strategy may reduce growth. Although our results for percent change in BAI were not statistically significant for current year growth, both TOT trees did exhibit substantial growth reductions of 35.2 and 62.9 %. Other studies suggest that eastern US temperate forests have strong current-year seasonal drought sensitivity, exhibiting large growth reductions when droughts occur during periods of peak growth (D'Orangeville et al. 2018; Asbjornsen et al. 2021). Additionally, droughts often have strong lagged effects in growth that persist multiple years after the water deficit has alleviated (Kannenberg et al. 2019; Asbjornsen et al. 2021). Therefore, if the reduced water supply experienced by TOT trees had indeed been a severe natural drought that ended prior to the trees' mortality, the trees likely would have had significant growth reductions in the following year.

4.3 Partially severing sapwood did not induce extreme water deficit

We found that severing 95 to 98 % of functional sapwood in PAR trees did not cause reductions in hydraulic status of canopy trees over one growing season, despite a 74 % reduction in sap flow. Previous studies have shown that interrupting 50–69 % of sapwood conduits in mature Norway spruce and Douglas fir trees did not negatively impact crown water status when measured continuously for 4.5–6 weeks (Brix and Mitchell 1985; Dietrich et al. 2018). While we did not directly measure sap flow re-routing around the cut, Dietrich et al. (2018) quantified that residual xylem adjacent to the cut edge had 40 % higher flow rates. Our work expands these results by demonstrating that, despite PAR trees only having an estimated 2–5 % remaining sapwood, they still maintained 25.7 % of their pre-severing daily sap flow values with higher flow rates in the intact sapwood. While our estimates of sapwood area were obtained using the translucence method and may deviate slightly from absolute values, these results indicate that some conifers may have a much greater volume of functional sapwood than needed to meet canopy water requirements. This is perhaps as a byproduct of the dual role of xylem tracheids as both a support and transport tissue. However, the large amount of sapwood may also serve as strategy to avoid reaching low Ψ values during periods of drought or injury that induce embolism formation, and furthermore as a potential insurance mechanism in case of loss of hydraulic conductivity due to formation of these embolisms (Hacke and Sperry 2001; Sperry and Robson 2001; Pittermann and Sperry 2006).

Interestingly, while the PAR treatment did not induce extreme water deficit, it significantly reduced chlorophyll concentration in current year leaves by 25.4 %. One possible explanation for this response is that while PAR trees did not experience significant water stress, severing the sapwood limited nitrogen uptake from the soil, inducing a physiological response. Nitrogen is required for the production of chlorophyll in plants (Bassi et al. 2018), and studies of several northeastern tree species have shown increased leaf nitrogen concentration is correlated with increased leaf chlorophyll concentration (Croft et al. 2017). As such, a combination of drought stress and nitrogen deficiency may have induced the stronger reduction in chlorophyll concentration witnessed in TOT trees.

4.4 Using sapwood severing to understand how trees respond to natural drought

It is important to note that although our sapwood severing treatment to induce water deficit differs in several key ways from a natural drought, it is a straightforward and easily implemented approach that bypasses many of the logistical constraints when trying to manipulate water availability to canopy trees (Asbjornsen et al. 2018). However, sapwood severing rapidly imposes water deficit, whereas in a natural drought soils would dry more slowly, potentially allowing time for trees to adjust important hydraulic thresholds to promote drought resistance (Bartlett et al. 2014). Although our sapwood severing treatment does not attempt to simulate a natural drought, the partial or complete cessation of water transport through the xylem does mimic inaccessibility to soil moisture and thus may provide new insight into large canopy tree drought responses in typically mesic forests that are otherwise difficult to estimate. Furthermore, this methodology could be used in future studies to compare the responses of different species in the same environment, and in association with a more holistic view of other aspects of tree carbon and water relations to inform species- and community-level responses to climate change stressors.

Periods of natural drought may be associated with additional physiological stressors not experienced by our sapwood-severed trees during this study. For example, tree water stress during natural soil droughts may be exacerbated by increased VPD, with drier air driving increased tree water loss through transpiration (Will et al. 2013). While the results of our experiment suggest red spruce may have an initial resistance to water deficit stress, indicated by the relatively slow decline in TOT tree Ψ and maintenance of high photosynthetic efficiency for most of the growing season, we only assessed this over one growing season and the stress was unaccompanied by other stressors that typically occur with drought. Coble et al. (2017) highlighted the variety of drought tolerance classifications that have been assigned to red spruce, ranging from intolerant to somewhat tolerant. Much of this variation in these classifications is based on the different metrics and time scales studied, as there is often a tradeoff between short term sensitivity and long-term tolerance. Based on our results, we suggest that mature red spruce may be sensitive to short term drought, closing stomata to conserve water and resist initial water stress. While red spruce may be able to survive these short-term droughts at the expense of carbon gain, it may still be intolerant of exposure to longer-term severe water deficits, which is important when considering the impacts of climate change more broadly. Indeed, red maple seedlings exhibit greater absolute growth and survival than red spruce in response to environmental warming and drought (Vaughn et al. 2021). This evidence suggests that in future climates, simultaneous water deficits and warming may lead to the exclusion of red spruce from previous habitats due to its intolerance, and underperformance relative to other species.

4.5 Experimental approach

To sever the sapwood of canopy trees, it is necessary to also sever the phloem. This is often accounted for by severing the phloem in control trees. In this study, disrupting the phloem in the CON trees did not cause any noticeable physiological responses such as stomatal closure, which can be induced in response to the loss of the belowground carbohydrate sink and consequent sugar accumulation in leaves (Kottapalli et al. 2018). Furthermore, the lack of a phloem-girdling response in this study could be due to the short time span of this project, or may be similar to other studies on Norway spruce that show phloem girdling does not result in carbohydrate accumulation above the girdle, potentially due to induced increases in radial growth above the girdle (Oberhuber et al. 2017) or increased maintenance respiration (Domec and Pruyn 2008).

Although our experimentally-imposed extreme drought focused on sapwood severing, some studies find foliar water uptake may reduce water stress (Schreel and Steppe 2019; Berry et al. 2019). Importantly, regional total precipitation for the growing season (July–September) of 2020 was only 204 mm, while the average from 10 years prior was 284 mm (± 24 mm) (NOAA National Centers for Environmental Information 2021), suggesting foliar water uptake was not an important source of water. Additionally, we minimized the possibility of any water uptake occurring through the cut made during sapwood severing by thoroughly wrapping that section of the trunk with plastic sheeting. As such, any effects of foliar water uptake or absorption through the cut trunk should be minimal.

5 Conclusions

In conclusion, considering the study's environmental conditions, our results suggest that red spruce can avoid physiological water stress throughout the growing season with relatively little (estimated 2–5 %) sapwood left intact. In trees with no sapwood remaining, red spruce reduced water loss during this period of extreme water deficit, likely at the expense of carbon gain. Despite conserving water and drawing down stored water reserves in trunk-wood, trees with no intact sapwood succumbed to water stress, showing almost total needle loss 18 weeks after treatments were implemented. These results suggest that red spruce may be more tolerant to extreme water deficit than some previous classifications may suggest (Coble et al. 2017), but that this tolerance may also come with important growth tradeoffs due to stomatal closure and reductions in photosynthetic efficiency. As such, although red spruce may be able to initially survive periods of extreme water limitation, the potential growth reductions and lagged effects that may persist into subsequent years could make red spruce less competitive in future drier climates.

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Author contributions All authors participated in conceptualization and study design. KF and JW collected the data. KF, DM, MV, and JW analyzed the data. All authors contributed to writing the manuscript.

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Data availability Data associated with this study are available at: https://doi.org/10.5061/dryad.4b8gthth7.

Declarations

Competing interests None declared.

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