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Article

Temporary thinning shock in previously shaded red spruce

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Abstract

Silvicultural thinning can lead to rapid microclimatic changes for residual trees. Despite the benefits of decreased competition, thinning may induce "thinning shock"—temporary negative physiological responses as trees acclimate to new conditions. We examined the impact of thinning on the microclimate and physiology of residual, previously shaded red spruce (*Picea rubens* Sarg.) trees relative to non-thinned controls. Both daily maximum temperature and vapor pressure deficit increased post thinning, with larger increases observed on hotter and drier days. In response to these environmental changes, we found clear evidence of physiological declines. At 1.7 weeks post thinning, we found a 0.59 MPa reduction in average midday water potential relative to control trees, which lasted for an additional 1.4 weeks. Thus, the trees in the thinning treatment were at or beyond published estimates of needle turgor loss. Thinning decreased the photosynthetic efficiency of current-year needles by 3.8% after 2 weeks, and it declined by 1.3% per week for the remainder of the growing season. These results suggest that thinning shock occurs in red spruce, a shade-adapted, climate-sensitive species. Thinning shock may contribute to the lagged growth responses commonly observed post thinning, and these effects may be more extreme in novel future climates.

Key words: *Picea rubens*, water potential, silvicultural thinning, photosynthesis, microclimate, vapor pressure deficit

Introduction

In the northeastern United States (US), climate change is driving warming and increasing the likelihood of extreme weather events (Vose et al. 2016; Karmalkar and Horton 2021). Average annual temperatures in the northeastern US have increased more than 1.5 °C from the late 1900s to 2020 (Young and Young 2021), and additional warming of 2.5–5.5 °C is projected by 2080 (Horton et al. 2014). Indeed, the northeastern US is projected to have the fastest warming of anywhere in the continental US, warming by 3 °C at the time average global warming reaches 2 °C (Karmalkar and Bradley 2017). Higher temperature can increase vapor pressure deficit (VPD), the difference between saturated and actual vapor pressure, resulting in drier atmospheric conditions (Will et al. 2013; Yuan et al. 2019) that directly impact tree physiology (McDowell and Allen 2015). Importantly, however, many tree species in mesic forests of the northeastern US are not well adapted to hotter and drier climate conditions (Johnson et al. 2011; Will et al. 2013; Coble et al. 2017). It is unclear how forest managers may mitigate some of the adverse effects of climate stressors both now and in the future (Linder 2000; Noss 2001; Keenan 2015).

Silvicultural thinning is widely used as a strategy to improve the growing conditions of residual trees by reducing competition for resources like light and water (Chase et al. 2016). Increased resource availability following thinning can increase tree vigor and mitigate the negative impacts of some stressors such as drought, insect infestations, and wind stress (Evans and Perschel 2009; Kerr and Haufe 2011; D'Amato et al. 2013; Sohn et al. 2013). However, increased light penetration following thinning leads to increased temperature and VPD within the canopy and understory (Aussenac 2000; Rambo and North 2009; Charrier et al. 2015). Suppressed and shade-adapted trees can experience "thinning shock"—temporary negative physiological effects following the abrupt shift from low to high light and humid to dry atmospheric conditions (Weir and Hubert 1919). Although sometimes overlooked when quantifying multi-year stand-level growth responses, physiological thinning shock may be partly responsible for lagged growth responses typically observed post thinning (Harrington and Reukema 1983; Cutter et al. 1991; Pukkala et al. 2002; Mehtätalo et al. 2014).

Exposure to high-light conditions has been shown to damage the photosystems of some tree species, leading to decreased photosynthetic efficiency (Maher et al. 2005; Zazzaro

2009; Bannister et al. 2013; Costa et al. 2020). Thinning can also increase water loss through transpiration, resulting in increased daily sap flow (Lagergren et al. 2008; Park et al. 2018). In some coniferous species, stomatal closure from exposure to dry air after thinning can actually reduce transpiration to conserve water at the cost of reduced carbon gain (Brix and Mitchell 1986; Simonin et al. 2006). The short-term negative impacts of thinning on growth are often offset by the long-term positive effects of increased light availability and access to below-ground resources. However, thinning has also been implicated in residual tree mortality, especially for low-vigor trees (Powers et al. 2010). Furthermore, regional predictions for warming and increased VPD (Horton et al. 2014; Ficklin and Novick 2017), as well as canopy structure impacts on warming rates in the sub-canopy (Zellweger et al. 2020), suggest that thinning shock effects may become more severe in the future.

Thinning shock effects may be more prominent in shade-tolerant evergreen conifers grown in full or partial shade, as their shade-adapted leaves are abruptly exposed to increased light conditions post thinning. Red spruce (*Picea rubens* Sarg.) is a commonly managed shade-tolerant evergreen conifer native to the northeastern US that has significant economic importance to northeastern communities (McCaskill et al. 2016). While red spruce individuals and populations have experienced a recovery in the last two decades from environmental stress caused by acid rain (DeHayes et al. 2000), this is largely related to elevated temperatures outside the traditional growing season, coupled with declining acid depositions (Kosiba et al. 2018; Wason et al. 2019). While this recovery may persist in the near term, in the long term red spruce is expected to have substantially reduced suitable habitat in the US by 2100 due to shifting climate regimes (Andrews et al. 2022) and is often considered to be climate-sensitive due to the negative influence of warming, drought, and increases in VPD on tree function and growth (Day 2000; White et al. 2014; Wason et al. 2019). Importantly, increasing temperatures may be particularly threatening for red spruce when experienced during the growing season, as previous summer temperature is negatively correlated with current year growth (Kosiba et al. 2018; Wason et al. 2019).

Like many other evergreen conifers, red spruce growth has longer lags (2–5 years) before reaching peak growth rates post thinning compared to some deciduous species that take 1–2 years (Cutter et al. 1991; Shifley 2004; Kuehne et al. 2016). Indeed, in a mechanical thinning treatment of a mixed-conifer forest, forest growth peaked 6–10 years post thinning when compared to pretreatment growth rates (Zald et al. 2022). These lagged growth responses may be partly driven by substantial thinning shock effects on physiology due to retention of multiple cohorts of shade-grown needles (Dumais and Prévost 2007). The physiology of red spruce saplings grown in gaps suggests that intermediate exposure is ideal for red spruce growth and physiology rather than high exposure from large canopy gaps (Dumais and Prévost 2014). However, it is still unclear how mature shade-adapted trees may be impacted by thinning shock.

As such, the goals of this study were to investigate the immediate physiological effects of thinning on mature red spruce trees and to generate better management guidelines that account for climate change. In this study, we quantified thinning shock in previously shaded, intermediate-crown-class red spruce trees that were fully released from crown crowding. We expected to find (1) altered microclimate post thinning, with increased maximum daily temperature and VPD, and (2) temporary physiological evidence of thinning shock exhibited through increased daily sap flow, lowered water potential, and decreased photosynthetic efficiency.

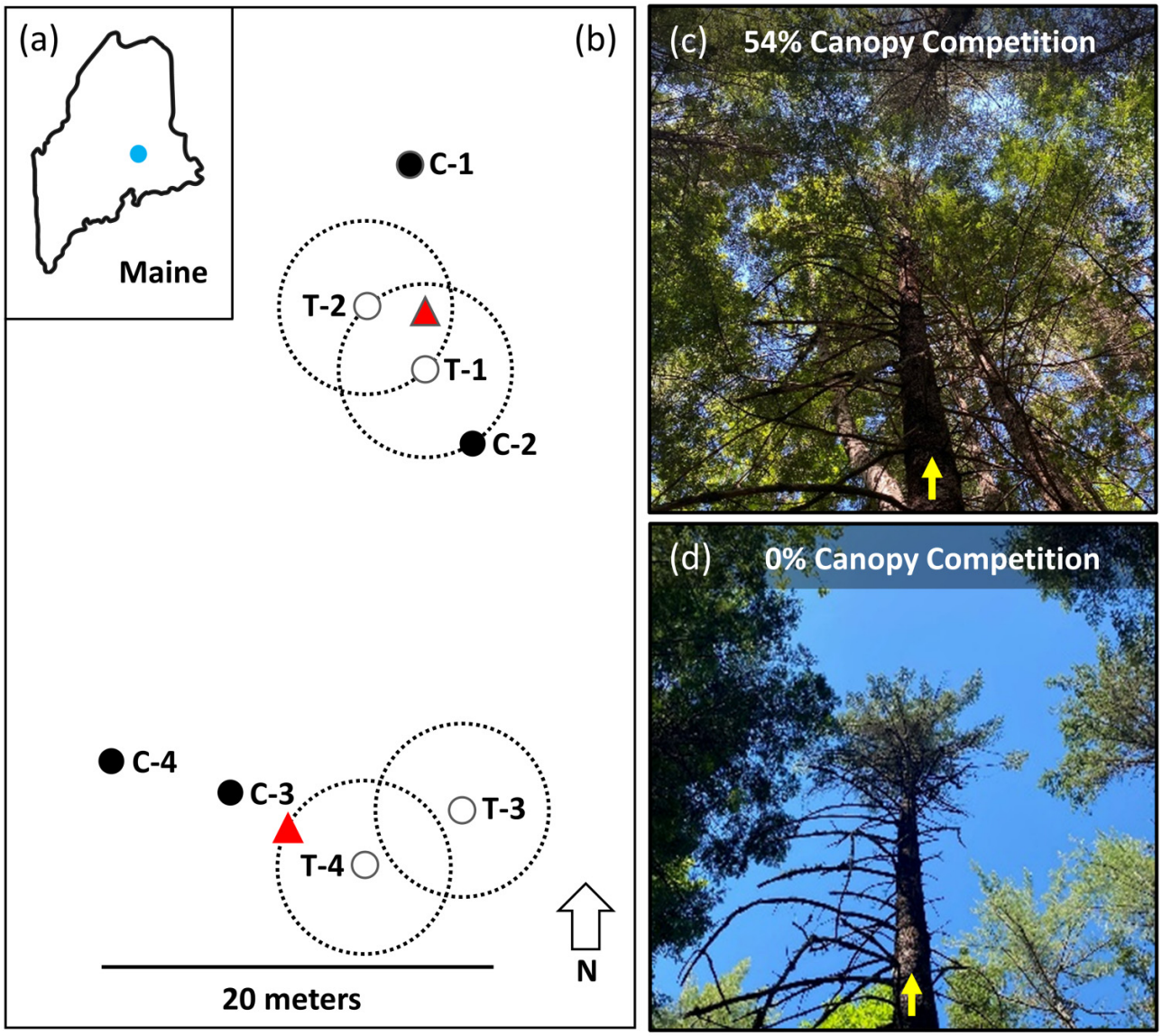
Materials and methods

Study area and thinning treatment design

This study was conducted on a 0.12 ha plot of land within the University of Maine's Dwight B. Demeritt Forest in Old Town, ME (44°55′N, 68°40′W) (Fig. 1*a*). This region's climate is classified as warm-summer humid continental (1991–2020 climate averages found in Table 1). The forest was dominated by balsam fir (*Abies balsamea* (L.) Mill) and eastern hemlock (*Tsuga canadensis* (L.) Carrière), with lesser amounts of red spruce, northern white-cedar (*Thuja occidentalis* L.), red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.), paper birch (*Betula papyrifera* Marshall), and white pine (*Pinus strobus* L.). We identified eight shaded, intermediate-crown-class (Smith et al. 1997) mature red spruce trees in this stand for intensive physiological monitoring during the 2020 growing season. These trees were placed into two groups of four based on proximity. To determine the effect of thinning on tree physiology, we selected treatment pairs (control or thinned) randomly within each group (Fig. 1*b*). Focal trees were intermediate crown class (diameter at breast height (DBH) 16–26 cm, total height 11.8–19.9 m) mature (apparent age at breast height 52–70 years; ring counts from cross-sections were collected at breast height at the end of the experiment), had vigorous crowns (live crown ratio (LCR) from lowest living branch 0.22–0.47; DeYoung 2016) and no visible stem damage (Table 2).

To investigate how thinning impacts tree function, we conducted a thinning prescription on the four trees in the thinning treatment group on 18 June 2020. To minimize potential site and residual tree damage, trees were felled with a chainsaw and left in place throughout the remainder of the experiment. Current-year needles were already developed by the treatment initiation, allowing us to quantify the response of shade-grown needles to increased light post thinning. During the thinning treatment, we removed all competing trees (>1 cm DBH) within a 5 m radius of the four focal trees in the thinning treatment group and removed any additional crown-touching competing trees outside of that radius (Figs. 1*c*–1*d*; Fig. S1). This treatment resulted in the removal of all competition, including canopy dominant and co-dominant trees in favor of the selected intermediate-crown-class red spruce, and thus mimics a selection thinning (Helms 1998; Nyland 2016). This thinning prescription is highly relevant to spruce-fir stands, as faster-growing and shorter-lived balsam fir are often removed to release crowded but longer-lived spruce (Frank and Bjorkbom 1973).

Fig. 1. Location of study site and focal trees. (*a*) Location of the Demeritt Forest (blue circle) within ME, USA. (*b*) Schematic showing the location of individual focal trees within a 0.12 ha plot. Solid circles represent the location of each focal tree (open grey circles represent thinning treatment trees; closed black circles represent control trees). Tree identifiers are shown next to each tree, indicating pair number, and treatment (C, control; T, thinned). The dashed circles represent the 5 m radius where all trees were removed. Red triangles represent the location of the data-logging stations. Representative image of focal tree T-2 (yellow arrow) pre- (*c*) and post (*d*) thinning. Photos taken by Kelly L. French.



For 3.5 weeks post thinning, all eight focal trees were subject to intensive measurements. After that point, four focal trees (two from each treatment group) were randomly selected for use in a separate but related study that manipulated water availability (French et al. 2023). Therefore, after four weeks, those four trees were no longer included in the analysis for this study, and the remaining four trees in the original treatment were monitored until November 2020.

Quantifying crowding reduction

To calculate the crowding reduction achieved by our thinning treatment, we first quantified the degree of localized competition (trees > 1 cm DBH) within the 5 m radius of our focal trees before and after thinning, using Hegyi's competition index (Hegyi 1974):

$$\text{(1)}\qquad \mathrm{CI}_{\mathrm{focal}} = \sum_{n=1}^{N}\left(\frac{D_{\mathrm{n}}/D_{\mathrm{f}}}{\mathrm{Distance}_{\mathrm{nf}}}\right)$$

where $\mathrm{CI}_{\mathrm{focal}}$ is the crowding index for the focal tree, N is the number of competing trees, D_{n} and D_{f} are the diameters at breast height of the neighbor tree and focal tree, respectively, and $\mathrm{Distance}_{\mathrm{nf}}$ is the distance (m) between the neighbor tree and the focal tree. Thus, we take the difference between post and pre-thinning indices as a direct measure of stem-crowding reduction. Indices did not differ significantly

Table 1. Climate means of the last 30 years for Old Town, ME.

Date	PPT (mm)	T_{min} (°C)	T_{mean} (°C)	T_{max} (°C)	VPD_{min} (kPa)	VPD_{max} (kPa)
January	85.98	−13.9	−8.1	−2.4	0.028	0.221
February	64.53	−13.1	−6.9	−0.8	0.032	0.295
March	83.52	−6.9	−1.4	4	0.053	0.468
April	85.9	−0.5	5.3	11.1	0.072	0.823
May	81.79	5.3	11.7	18.1	0.07	1.234
June	94.14	10.4	16.8	23.2	0.064	1.501
July	80.11	13.9	20.1	26.3	0.067	1.701
August	78.92	12.8	19.2	25.7	0.068	1.675
September	87.66	8.4	14.8	21.2	0.039	1.234
October	113.14	2.5	8.2	13.8	0.038	0.759
November	97.21	−2.4	2.4	7.2	0.041	0.446
December	111.19	−8.8	−3.9	1.1	0.028	0.256
Annual	*1064.1*	*0.7*	*6.5*	*12.4*	*0.05*	*0.884*

Note: Data for monthly and annual climate averages for precipitation (PPT), minimum temperature (T_{min}), mean temperature (T_{mean}), maximum temperature (T_{max}), minimum vapor pressure deficit (VPD_{min}), and maximum vapor pressure deficit (VPD_{max}) based on data from 1991 to 2020 (Prism Climate Group 2020).

Table 2. Characteristics of red spruce trees in the thinning and control treatments.

Tree ID	DBH (cm)	Total height (m)	Live crown ratio	Sapwood radial depth (cm)
C-1	20.6	16.7	0.26	2.7 ± 0.1
C-2	17.2	16.4	0.32	1.4 ± 0.1
C-3	19.2	11.8	0.32	1.9 ± 0
C-4	25.4	15.9	0.38	2.2 ± 0.1
T-1	19.0	16.2	0.22	2.2 ± 0
T-2	16.8	16.1	0.22	2.3 ± 0.1
T-3	29.1	19.9	0.47	2.4 ± 0.1
T-4	24.9	17.8	0.44	2.9 ± 0.2
Average ± SE	*21.5 ± 1.6*	*16.33 ± 0.80*	*0.33 ± 0.03*	*2.3 ± 0.2*

Note: Tree identifier (ID) indicates the pair number and the treatment assigned; C, control; T, thinned. Diameter at breast height (DBH), total height, and live crown ratio were measured after trees were harvested in November 2020. Sapwood radius was obtained visually from two increment cores taken 0.6 m above the ground, and the average is reported in cm ± standard error (SE).

between treatments prior to thinning (paired t test, $p = 0.70$; Fig. S1; Table 3).

We anticipated that any rapid changes in tree physiological responses to thinning would be primarily driven by exposing shade-adapted needles to full sunlight. Therefore, we also quantified the increase in crown exposure achieved by the thinning with a custom crown crowding index (Table 3) calculated pre- and post thinning. The crown of each tree was visually divided into three sections (upper, middle, lower) and assigned a number based on the degree of crown crowding (0 = no crowding; 1 = partial crowding; 2 = full crowding, fully blocked/shaded by other foliage) on all four sides (N, E, S, and W). To express an overall crown crowding index for a given tree, we summed the three values and expressed the result as a percentage relative to full crowding. Crown crowding did not differ between treatments prior to thinning (paired t test, $p = 0.88$; Table 3).

Thinning influences on microclimate

To determine how thinning influenced local microclimate conditions, we measured temperature and humidity starting two weeks prior to the thinning. Temperature and humidity loggers (iButton Thermochron and Hygrochon models, Maxim Integrated Products, Inc., Sunnyvale, California) were deployed 1 m above the ground at the center of the white plastic radiation shields on the north side of all eight focal trees (Wason et al. 2017). We paired trees of different treatments based on location and placed the same type of iButton within each pair. On four trees (two in control and two in thinning treatments), we measured temperature and humidity every hour (Hygrochron model DS1923, resolution 0.0625 °C and 0.04%); on the remaining four trees, we measured temperature every two hours (Thermochron model DS1921H, resolution 0.5 °C). We used these data to calculate VPD (Gotsch et al. 2017).

Impact of thinning on tree water use

To quantify whole-tree water use pre-thinning and post thinning, custom Heat Ratio Method sap flow sensors were installed two weeks before the thinning treatment in all eight focal trees following the methods of Burgess et al. (2001). On the south-facing side of the stems, we removed a small section of bark at breast height, used a guide and a #54 drill bit to drill three holes into the xylem 0.5 cm apart vertically and

Table 3. Pre-thinning to post thinning changes in crowding for focal red spruce trees.

	Hegyi's crowding index		Crown crowding index (%)	
Tree ID	Pre-thinning	Post thinning	Pre-thinning	Post thinning
C-1	4.05	4.05	54	54
C-2	4.40	4.07	63	54
C-3	2.55	2.55	100	100
C-4	1.66	1.66	71	71
T-1	3.61	0.20	92	0
T-2	4.61	0.00	54	0
T-3	1.89	0.00	83	0
T-4	3.54	0.00	50	0

Note: Unique tree ID, crown competition (pre- and post thinning), and Hegyi's crowding index (pre- and post thinning) listed for each focal tree. Tree ID indicates the pair number and the treatment assigned; C, control; T, thinned. Crown crowding represents crowding as a percentage relative to a fully suppressed crown according to our index. Hegyi's crowding index was calculated based on all trees >1 cm DBH within a 5 m radius of the focal tree.

3 cm deep, and inserted three steel probes (2.5 cm long, approximately 1.25 mm diameter). The middle probe contained the nichrome heater, and probes containing three Type T thermocouple sensors at depths of 0.5, 1.0, and 1.5 cm were installed 0.5 cm above and below this heater.

A 3-s heat pulse was generated every 15 min throughout the duration of the study, and temperature changes detected by the probes were recorded on the CR1000 and CR1000X dataloggers. Heat-pulse velocity was calculated based on the ratio of temperature changes above vs. below the middle needle (Burgess et al. 2001). Due to thermocouple and heater failures several data gaps occurred; these were removed from the water-use analysis. We only included data in analysis for days with no missing data for any of the eight trees. We converted heat-pulse velocity to daily water use (McIntire et al. 2021) based on sapwood cross-sectional area estimates. We obtained these estimates using the translucence method (DeRose and Seymour 2009) conducted on two radial increment cores collected 0.6 m above the ground on all eight trees prior to treatment initiation. Sapwood radial depth ranged from 1.4 to 2.9 cm (Table 2).

To determine whether thinning reduced shoot water potential during peak transpiration, crown shoot samples were collected from the middle or upper crown of focal trees with a Notch Big Shot throw weight launcher and rope chain saw between 12:00 and 15:00 h (midday). To capture immediate thinning shock effects, we conducted an intensive period of measurements on all trees for 3.5 weeks post thinning, with less-frequent measurements carried out throughout the remainder of the growing season. During each sampling event, three branches were collected per tree and immediately bagged in foil-lined plastic bags with damp paper towels inside. These branches were subsequently placed in a cooler with an ice pack and transported to the lab for analysis within 2 h of sample collection. Due to the small size of current-year shoots, two-year-old shoots (current-year and a portion of prior-year growth) were severed from the larger branches with a razor blade, and water potential was measured on these shoots using a pressure chamber (Model 1000, PMS Instrument Company, USA). One measurement per shoot was conducted for each of the three shoots per tree, averaged to give us midday shoot water potential values (Ψ_{MD}) per tree per sampling date.

Thinning impacts on photosynthesis

To determine whether the thinning treatment influenced photosynthesis, a FluorPen FP 110 (Photon Systems Instruments, CZ) was used to quantify quantum yield of photosynthesis. Quantum yield, quantified as F_v/F_m (variable fluorescence/maximum fluorescence), is a measure of photosystem II efficiency in chloroplasts and can indicate damage to leaves exposed to excessive light or other stressors (Robakowski 2005). Starting 1.5 weeks after the thinning, we removed three shoots per tree from our collected branches (detailed above) and conducted one F_v/F_m measurement per shoot on current-year needles on each sampling date.

Impact of thinning on radial growth

To quantify the impact of thinning on tree growth, we calculated basal area increment (BAI) for the four trees still in the original treatment design at the end of the study period (21 weeks post thinning). Stem cross-sections were collected from breast height after harvesting the focal trees in November 2020. Cross-sections were sanded with progressively finer sandpaper and scanned, and ring width was measured in CooRecorder (Cybis.se) for two distinct radii per cross-section. Ring width was converted to BAI using the dlpR package in R (Bunn 2010; RStudio Team 2020). We calculated % change in BAI for 2020 (the year of the thinning) compared to the average BAI for five years prior.

Statistical analysis

To test whether our thinning treatment had a significant impact on microclimate, we generated linear mixed-effects models for testing differences in daily maximum temperature (T_{diff}) and daily maximum VPD (VPD_{diff}) between paired control and thinning treatment trees. We modeled T_{diff} and VPD_{diff} as a function of time period (pre- vs. post thinning),

maximum daily temperature (T_{max}) or VPD (VPD_{max}) from control trees as fixed effects with an interaction, and the date of measurement as a random effect. The interaction between time period and T_{max} or VPD_{max} allowed us to test whether hotter or drier days tended to show larger differences between treatments. The random effect for date accounted for repeated measurements and temporal autocorrelation. As we had only 14 days of microclimate data pre-thinning, we focused on the 14 days pre-thinning and 14 days post thinning in our microclimate analysis.

To assess whether thinning impacted total daily tree water use, we averaged the total daily water use ($mL \cdot day^{-1}$) for each tree for 5 days pre-thinning and 5 days post thinning (longer periods not available due to sensor malfunctions). For each tree, we calculated the % change in daily water use after the thinning and used a paired t test to test for consistent changes in water use between treatments.

To determine whether thinning impacted Ψ_{MD} in the first few weeks immediately post thinning and the remainder of the experiment, we generated linear mixed-effects models predicting Ψ_{MD} (MPa) with fixed effects for treatment (thinned vs. control) and tree and date as crossed random effects. When testing whether the thinning treatment impacted photosynthesis over the duration of the experiment, we modeled F_v/F_m as a function of the fixed-effects treatment and days since the thinning, including an interaction effect and a first-order autocorrelation term to account for temporal autocorrelation. All data were analyzed, organized, and visualized using R and the packages "nlme" and "ggplot2" (Wickham 2016; RStudio Team 2020; Pinheiro et al. 2021).

Results

The thinning treatment reduced both the CI_{focal} and the crown crowding index to 0 (Table 3). The thinning also significantly increased maximum daily temperature (Figs. 2*a*–2*b*) and VPD (Figs. 2*c*–2*d*) in the understory. Importantly, in the post thinning period, we found that the difference in microclimate between control and thinning treatment trees was more extreme on hot and dry days (T_{diff} model: T_{max} × period interaction $p < 0.01$, conditional $R^2 = 0.66$, Fig. 2*b*; VPD_{diff} model: VPD_{max} × period interaction $p < 0.01$, $R^2 = 0.68$, Fig. 2*d*). For example, on the first day post thinning, control trees experienced relatively hot (T_{max} of 33.7 °C; Fig. 2*a*) and dry conditions (VPD_{max} of 4.0 kPa; Fig. 2*c*). Our models predict that on a day with these conditions, trees in the thinned treatment would experience even hotter (+2.6 °C in T_{max}; Fig. 2*b*) and drier (+0.78 kPa increase in VPD_{max}; Fig. 2*d*) conditions than controls. On days with lower T_{max} and VPD_{max}, differences were less extreme or not evident.

We did not find evidence that thinning changed daily sap flow. On average, sap flow of all eight trees increased in the five days post thinning by 21% (−16% to 39%), but treatments did not differ significantly (paired t test, $p = 0.35$; Fig. 3*a*). Despite no change in sap flow, we found that Ψ_{MD} of thinning treatment trees was on average 0.59 MPa lower than control trees during the 3.1 weeks following thinning (significant treatment effect, $p < 0.01$; Fig. 3*b*). Ψ_{MD} levels of trees in the thinned treatment were the lowest 2.4 weeks post thinning (range −2.07 to −2.15 MPa). For the remainder of the growing season, the effect of treatment diminished, with thinning treatment trees being on average only 0.18 MPa lower than controls ($p = 0.03$; Fig. S3).

We found that thinning reduced photosynthetic efficiency of needles (quantified by F_v/F_m) throughout the entire growing season (Fig. 4). A significant treatment × days since thinning interaction ($p = 0.02$) indicated that this effect increased as time progressed. According to our model, thinning treatment tree photosynthetic efficiency was 3.8% lower than controls 2 weeks post thinning and lower than controls by 33.5% 17 weeks post thinning. Control trees maintained F_v/F_m levels close to healthy levels (0.83) (Kitajima and Butler 1975) throughout the duration of the experiment.

For the four trees that were maintained in this treatment combination for the duration of the growing season (see Methods), thinning may have caused a decline in current year BAI compared to the average BAI from the five previous years. Trees in the thinning treatment had reductions in relative BAI (−28.7 and −27.0%), but there was no consistent growth pattern in the two remaining control treatment trees (−21.7% and 58.0%).

Discussion

Our finding that both temperature and VPD increased in the thinned treatment relative to the control treatment is consistent with evidence from other studies assessing the impact of thinning on microclimate (Aussenac 2000; Charrier et al. 2015). Our results also show that the thinning-induced increases in temperature and VPD were more extreme on days with higher absolute values of temperature and VPD, a situation that may occur more frequently with global warming (Yuan et al. 2019). These results are in line with data suggesting that the loss of canopy cover significantly reduces the temperature buffering that occurs between the macroclimate and sub-canopy microclimate, thus accelerating rates of sub-canopy warming (Zellweger et al. 2020). Red spruce experiences declines in net photosynthesis and stomatal conductance at air temperatures above 32 °C and VPD values above 2 kPa (Day 2000). Therefore, projected regional increases in temperature and VPD may have more extreme negative impacts on shaded red spruce, especially if the adjacent canopy is suddenly removed. This suggests that in future climates, management strategies or natural disturbances that greatly reduce canopy cover may have more pronounced effects on sub-canopy microclimate.

Contrary to other studies (Bréda et al. 1995; Park et al. 2018), we did not see significant changes in daily sap flow between thinning treatment and control trees within five days post thinning. Increased VPD is known to increase water use in some conifers (Kunert et al. 2010; Børja et al. 2016); however, other *Picea* A. Dietr. species are known to maintain constant midday water potential in periods of climatic stress by reducing stomatal conductance (Sade et al. 2012; Sullivan et al. 2017). In another study, red spruce stomatal conductance declined by 43% and net photosynthesis declined by 26% between VPD values of 2 and 3.5 kPa (Day 2000). In the three days post thinning, the VPD in the understory of our

Fig. 2. Thinning influences tree microclimate. Average maximum daily temperature (Temp) (*a*) and vapor pressure deficit (VPD) (*b*) obtained from iButton temperature and humidity loggers for thinning treatment (thinned, open circles) and control treatment (control, filled circles) trees (±S.E., $n = 7$). Microclimate data encompasses 14 days pre- and post thinning, with the grey shaded area representing the pre-thinning period. Mixed-effects models for difference between treatments in (*c*) temperature (T_{diff}) and (*d*) VPD (VPD_{diff}) built using 28 days of temperature data, 14 days pre-thinning and 14 days post thinning. Data for the entire growing season are presented in Figs. S2*a* and S2*b*.

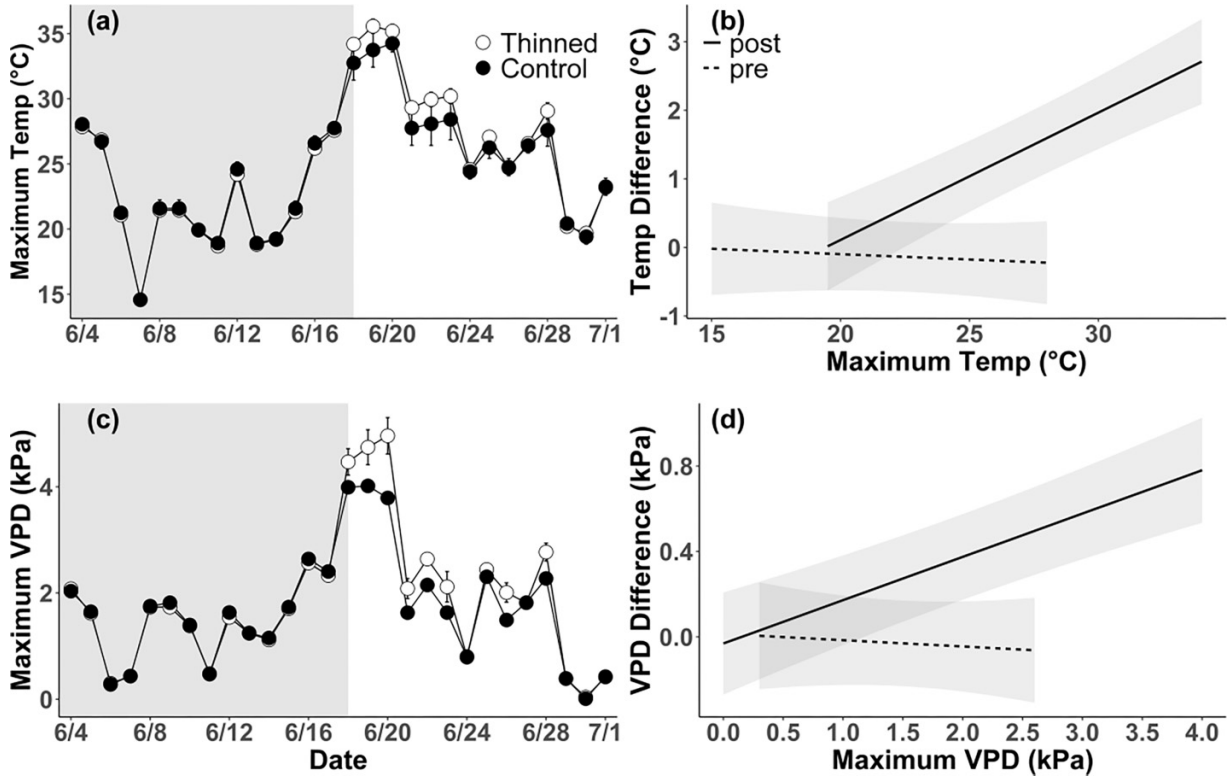


Fig. 3. Thinning influences on tree water use. (*a*) Percent change in average sap flow between the 5 days pre-thinning and post thinning for the thinning treatment (thinned) and control treatment (control) (±2 SEs). (*b*) Treatment-level average midday shoot water potentials (Ψ_{MD}) of thinning treatment (open circles) and control (closed circles) trees for 3.5 weeks post thinning (±2 SEs; data points jittered along the horizontal axis).

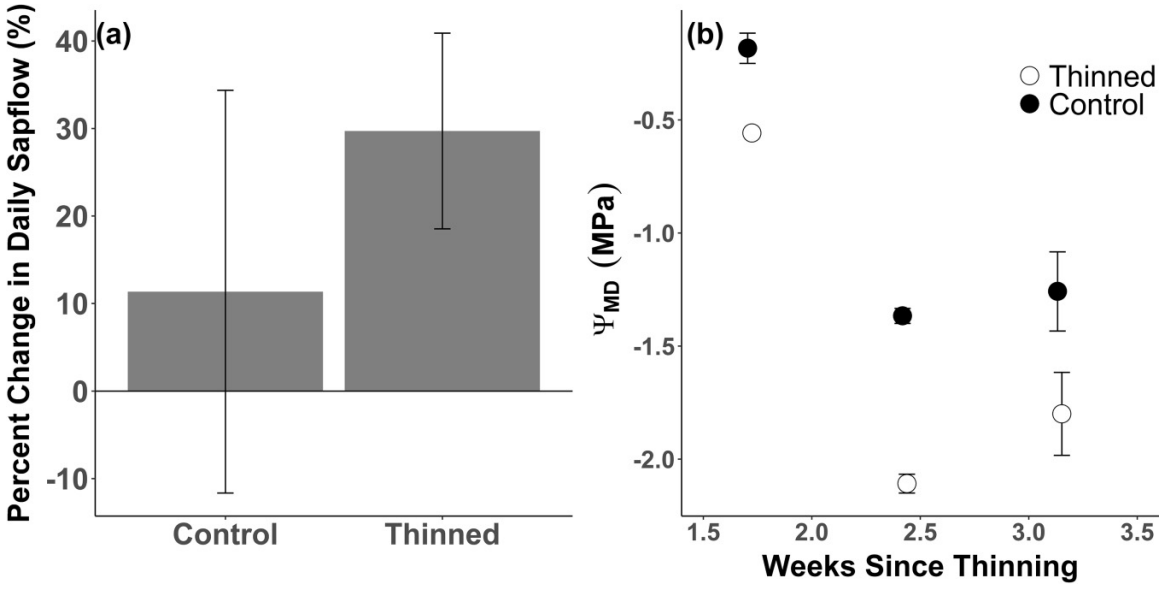
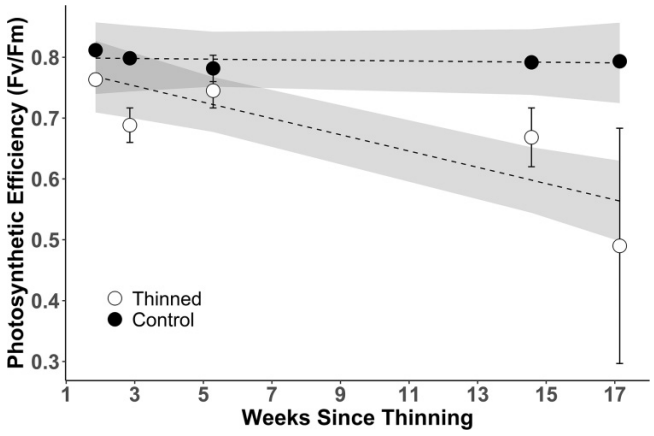


Fig. 4. Thinning decreases tree photosynthetic efficiency. Average photosynthetic efficiency values (F_v/F_m) of thinning treatment (open circles) and control treatment trees (filled circles) for 17 weeks post thinning (±S.E.). Linear-mixed-effects models are represented by dashed lines. 95% confidence intervals from the linear mixed-effects model are represented by the grey shaded area.



thinning treatment trees was of 4.4–5.0 kPa. Therefore, we may not have observed a change in daily sap flow due to the possibility that trees in the thinned treatment closed stomata to conserve water in response to the locally increased VPD. Although we did not quantify this directly, stomatal closure would likely come at the cost of decreased photosynthesis, and this potential effect should be quantified in future thinning shock studies.

Trees in the thinning treatment had temporarily lowered Ψ_{MD} values, which is consistent with studies showing that increased temperature and VPD lead to lowered Ψ_{MD} values (Eamus et al. 2013). Though we did not measure turgor loss point (TLP) in our study, previous studies report that the TLP for red spruce is between −1.3 and −1.5 MPa (Andersen and McLaughlin 1991). Although these values may not directly apply to our focal trees, this suggests that the trees in the thinning treatment are more likely than control trees to approach critical hydraulic thresholds such as the TLP and that trees in the thinning treatment may have approached or surpassed their TLP when experiencing thinning shock. However, with time to acclimate, trees may also lower their TLP during periods of water stress (Bartlett et al. 2014). Future studies should examine TLP pre-thinning and post thinning to determine the influence of sudden crown exposure.

The decline in Ψ_{MD} we measured likely initiated partial stomatal closure that, in addition to increased VPD, could explain the lack of an effect on whole-tree water use discussed previously. Our Ψ_{MD} results thus provide important new data on negative effects on water status immediately following thinning. These results appear to contradict previous findings that reduced competition for water leads to increased Ψ_{MD} values in thinned stands (Skov et al. 2004; Eamus et al. 2013; Gleason et al. 2017), at least for previously shaded, suddenly released trees like those in the present study. However, many studies focus on long-term benefits that may take months or years to occur and may not capture the immediate, short-term negative impacts of thinning shock on Ψ_{MD} that we report here. Furthermore, as heat and drought increase in future years (Hayhoe et al. 2007; Fernandez et al. 2020), these temporary negative impacts of thinning shock may become more pronounced.

In addition to temporary declines in Ψ_{MD}, we also found immediate declines in photosynthetic efficiency in trees in the thinned treatment. While our sample size was reduced for the last few measurements, our data suggest these declines continued for the remainder of the growing season. To our knowledge, impacts of thinning on photosynthesis have not been quantified in mature conifers, but our results imply these are likely similar to the reduced photosynthetic efficiency shown in conifer saplings grown in high-light conditions (Maher et al. 2005; Zazzaro 2009; Bannister et al. 2013). Many shade-adapted tree species reach peak photosynthesis at relatively low-light levels, and additional light can cause damage to photochemistry. For example, excess light can inhibit Photosystem II repair cycles, causing long-lasting damage to leaves (Melis 1999; Murata et al. 2007). Rapidly changing the light environment also requires time for the trees to acclimate to new conditions and produce new leaves. Dumais and Prévost (2014) found that advanced red spruce regeneration shows either a small decline or no change in maximum photosynthesis (A_{max}) until five years after thinning.

Importantly, this acclimation to new high-light levels results from the change from shade-grown leaves to sun-grown leaves takes multiple years in conifers (Dumais and Prévost 2007). Indeed, red spruce leaves can live to a maximal age of 8.6 years (Kayama et al. 2007). Thus, these thinning shock effects on photosynthesis in addition to stomatal responses to water status in shade leaves may drive the multi-year lag in maximum growth response that occurs post thinning (Cutter et al. 1991; Pukkala et al. 2002; Mehtätalo et al. 2014). We found that when trees were harvested in November, the two trees in the original thinning treatment experienced reductions in BAI by −28.7% and −27.0% compared to their average growth from the previous five years, whereas control treatment trees showed more variation (−21.7% and 58.0% changes). While we could not test for a significant effect in our trees due to the limited sample size, in theory the negative physiological effects detected may lead to temporary negative growth effects post thinning, although these effects, like those from other climate stressors, may be even stronger in the year following stress (Kosiba et al. 2018; Kannenberg et al. 2019). Importantly, post thinning growth responses may be negatively impacted not only by both abiotic climate factors but also below-ground biotic relationships, including the presence of root grafts between residual trees and stumps (Tarroux et al. 2010). Thus, future studies should incorporate a holistic approach to consider the negative interactive effects of multiple physiological stressors post management.

Management implications

Our results suggest that the negative effects of thinning around partially shaded, intermediate-crown-class red spruce may worsen in future climates and that alternative management strategies may be needed to mitigate thinning

shock. Removing upper crown classes during thinning has been shown to cause greater microclimate variability and increase extremes more than thinning methods removing lower crown classes (Rambo and North 2009), likely due to the large changes in canopy cover and formation of gaps. This indicates that thinning methods that remove upper crown classes may induce more thinning shock effects in residual shade-grown trees of shade tolerant, climate-sensitive species. Thinning methods that remove lower crown classes may successfully reduce stand density while maintaining canopy closure, preventing extreme and abrupt changes in light and microclimate (Rambo and North 2009) that drive these short-term negative effects. However, this comes with the tradeoff of maintaining pre-thinning levels of aboveground competition for light, which may weaken growth responses in the long term. Multi-aged management systems (i.e., selection cutting, irregular shelterwood, etc.) have also been recommended as methods that may mitigate the effects of climate stress while simultaneously maintaining structural diversity, which can be decreased by heavy thinning of upper or lower crown classes exclusively (Dumais and Prévost 2007; D'Amato et al. 2011; Kuehne et al. 2018). These multi-aged systems may promote some canopy gap formation, increasing light availability for residual trees but not as severely or abruptly as other systems. Future thinning shock studies should investigate physiological responses of residual, mature trees of all crown classes exposed to a gradient of management strategies to understand how various systems may respond in future projected climates.

Importantly, our thinning treatment removed all neighboring trees, including those in dominant and co-dominant crown classes, to benefit trees in lower classes. As such, this thinning may have effects similar to those of a diameter-limit cut. Diameter-limit cutting (i.e., removing all trees above a specified diameter) is rarely recommended due to the demonstrated poorer growth potential of lower crown class trees (Kelty and D'Amato 2006). However, in spruce-fir stands, faster-growing and shorter-lived balsam fir are often removed to release crowded but longer-lived spruce (Frank and Bjorkbom 1973). This selection cutting can lead unintentionally to a diameter-limit cut, making this thinning treatment imposed here highly relevant to the forest type. The negative effects of diameter-limit cutting on tree volume, growth, and value in spruce-fir have been documented (Kenefic et al. 2005), but the potential for increased thinning shock has not been previously addressed in this context of this practice. The negative thinning shock effects revealed in our study provide further evidence of the potential negative outcomes of diameter-limit cutting, especially during periods of climate stress, which are more likely in the future. Instead, pre-commercial thinning could be used to improve the competitive position of the desired red spruce, potentially preventing them from falling into vulnerable lower crown classes.

Conclusions

Our findings suggest that exposing shade-adapted, mature red spruce trees by thinning causes significant changes in microclimate, which may drive temporary physiological thinning shock effects. We found that a substantial decline in Ψ_{MD} occurred temporarily from 1.7 to 3.1 weeks in trees in the thinning treatment (despite no changes in sap flow), but this effect diminished over time. However, the thinning treatment immediately reduced photosynthetic efficiency of needles, and this effect worsened throughout the growing season. In projected future climates, the changes in microclimate induced by thinning may be more severe, which may exacerbate thinning shock effects in red spruce and other shade-adapted and climate-sensitive species. However, monitoring how these physiological effects directly impact carbon sequestration and growth, as well as whether these physiological effects persist into subsequent growing seasons, will be important in understanding the full-impact thinning has on residual trees. Lastly, additional studies investigating tree physiological responses to alternative thinning methods are needed to understand whether these thinning shock effects can be mitigated, especially in the face of warmer, more variable climates.

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Competing interests

The authors declare there are no competing interests.

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Supplementary material

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