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Combined heat and drought events reduce first-year survival of tree seedlings, especially at southern range margins

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In forests, first-year tree seedlings experience high mortality rates, yet we know relatively little about how extreme climate events contribute. In this study, we exposed over 700 containerized seedlings of eight tree species to three heat and three drought treatments, and their combinations, that represent extreme conditions currently beyond the climate typically experienced by species at the temperate-boreal ecotone. We measured the height and survival of all seedlings and compared these responses to species traits. We found that, overall, combined heat and drought reduced survival more than either stressor alone. Reductions in survival were strongest for two northern conifer species with relatively low root-to-shoot biomass ratios. In contrast, two more southerly distributed species with the largest root systems had higher survival. Treatments did not impact growth or biomass of surviving seedlings. These results establish that higher temperatures or shifting precipitation regimes may not pose a major threat to first-year seedlings separately, but combined warming and drought have the potential to cause widespread mortality, particularly at southern range margins. These findings demonstrate the importance of first-year seedling survival under combined stressors and clarify how these rare but extreme events can cause regeneration failure. Although difficult to predict, these events should be considered in adaptive management planning and forest modeling due to their potential for profound impacts.

KEYWORDS

combined stress, drought, heat, range margins, survival, tree seedlings

Introduction

In many parts of the world, changing temperature and moisture conditions are altering forest composition (Allen et al., 2010; Forzieri et al., 2022; Hammond et al., 2022). Transition zones between forest types, such as the temperate-boreal ecotone in the northern United States and southern Canada, are expected to experience the most change as many tree species in this region are at their northern or southern range margins (Boulanger et al., 2017). Northerly-distributed species, such as *Picea* spp. and *Abies balsamea*, are expected to experience significant reductions in suitable habitat as early as 2060 (Andrews et al., 2022). The regeneration layer, and especially first-year tree seedlings, are particularly sensitive to temperature and moisture conditions (Johnson et al., 2011) and changes in climate, like increased heat or drought frequency, may facilitate rapid changes

in forest composition that are manifested first in the regeneration layer (Canham and Murphy, 2017; Fisichelli et al., 2013). Climate change induced compositional shifts in the temperate-boreal forest may lead to loss of regionally unique spruce-fir forests and valuable ecosystem services (Andrews et al., 2022; Davis, 1966; Pohjanmies et al., 2017). Despite the sensitivity of trees at this early life stage, most studies have focused on responses of tree seedlings to climate after their first year, potentially missing a critical abiotic filter on tree survival in response to climate stress (for example, Balducci et al., 2015; Ziegler et al., 2024).

With projected warming and habitat loss in the temperate-boreal ecotone, many temperate deciduous species with southerly distributions relative to the ecotone (hereafter, “temperate broadleaves”) are expected to increase in abundance relative to more northerly-distributed conifer species (hereafter, “northern conifers”; Andrews et al., 2022; Prasad et al., 2020; Tang and Beckage, 2010). These changes are likely to occur as species are exposed to novel climate conditions, as first-year seedlings of temperate broadleaves are shown to have higher survival than first-year seedlings of northern conifers when exposed to heat and drought conditions (Fisichelli et al., 2014; Wright et al., 2018). Despite this, most studies investigating species-specific responses to abiotic stress are limited to experimental studies that use older seedlings (for example, Crockett and Hurteau, 2024; Putnam and Reich, 2017; Reich et al., 2015; Rodgers et al., 2018; Will et al., 2013). While this work is valuable, it ignores the critical developmental stage of newly emerged trees and limits our understanding of how climate stress impacts tree regeneration, therefore reducing the accuracy of forest simulation models in climate sensitive regions (Hanbury-Brown et al., 2022). Since first-year seedlings are likely more sensitive to climate but most regeneration data come from older seedlings, we may be underestimating the sensitivity and impacts of climate change on forest composition.

While first-year seedling survival is naturally low (De Steven, 1991; Frey et al., 2007), compared to long-term climate changes, survival of first-year seedlings is likely to be most impacted by extreme climate events, like heat, drought, and combined heat and drought events (Anderegg et al., 2019; McDowell et al., 2008; Menezes-Silva et al., 2019). First-year seedlings have a limited capacity to avoid heat and drought stress due to their small size, shallow roots, and newly developed vascular systems (Johnson et al., 2011). Though relatively few studies focus specifically on first-year seedlings, research conducted using older seedlings suggests that while both elevated temperatures and drought conditions can reduce seedling survival, responses vary by species (Crockett and Hurteau, 2024; Lalor et al., 2023; Moran et al., 2019), and we expect these effects to apply more strongly to first-year seedlings than to older seedlings. For example, warming has been shown in some cases to reduce survival for northern conifers and some, but not all, temperate broadleaves (Rank et al., 2022; Rodgers et al., 2018). However, reduced survival of northern conifers depends on the extent of warming (Kunert et al., 2022) and if it coincides with drought (Fisichelli et al., 2014; Wright et al., 2018). Although the effects of heat and drought on first-year tree seedling survival have been addressed for some species native to the temperate-boreal ecotone, there is a need to expand this work

to encompass more species and include additional measurements to characterize the extent to which heated and droughted plants experience physiological stress (Balducci et al., 2015). We have a strong understanding of how extreme climate events impact growth of saplings and canopy trees, but the lack of data on first-year seedlings limits the ability to understand what climate-driven forest compositional shifts will occur as a result of first-year seedling mortality.

Among surviving seedlings, growth responses to abiotic stress vary by species and range locations. For instance, Reich et al. (2015) and Wright et al. (2018) found that warming increases the growth of temperate broadleaves within the temperate-boreal ecotone, but not that of northern conifers (also see Fisichelli et al., 2012). Though Fisichelli et al. (2014) also notes that growth is greatest for temperate broadleaves and increases with temperature, this effect depends on the degree of warming and moisture availability. Other species-specific studies conducted with temperate broadleaves in multiple ecosystems show varying effects of warming, so the native range of seedlings has great potential to dictate growth responses as the climate continues to warm (Carón et al., 2015; Meeussen et al., 2022; Putnam and Reich, 2017). Warming is generally expected to increase growth for temperate broadleaf species provided they can avoid moisture stress. However, reduced or altered precipitation regimes associated with climate change and the small size of first-year seedlings increase the likelihood that seedlings will experience moisture stress.

Incorporating species-level traits, particularly those related to temperature- and drought- tolerance, can improve our ability to predict first-year survival and growth of trees in response to extreme climate events (Bartlett et al., 2012; McGregor et al., 2021; Münchinger et al., 2023). Because drought can induce physiological stress such as hydraulic failure, reduced net photosynthesis, and decreased leaf conductance (Hammond et al., 2019; Reich et al., 2018), seedling survival during heat and drought stress is strongly linked to hydraulic traits and growth is linked to both hydraulic- and carbon-related traits (Adams et al., 2017; Johnson et al., 2018). Hydraulic traits that may be particularly important for first-year survival in heat and drought stress include turgor loss point (TLP; the ability to maintain leaf structure and function at low water potentials) and minimum epidermal conductance (g_{min} ; the ability to reduce residual water loss during drought). Both relate to tree growth and survival (Duursma et al., 2019; Visakorpi et al., 2024; Wang et al., 2024), but at least some studies suggest that TLP, for example, may not vary among species in their first year (Beikircher et al., 2025). Other structural traits with implications for water relations, such as leaf mass per area (LMA; Sastry et al., 2018) and root-to-shoot biomass ratio (root:shoot; Pearson and D’Orangeville, 2022), have been correlated with higher stress tolerance. These data are widely available and often used to understand the growth and survival of older trees (for example, Anderegg et al., 2019; Choat et al., 2018; McDowell et al., 2008), though more data is required to understand variation in traits during the first year of tree growth (Beikircher et al., 2025). Therefore, specific sets of traits may relate to survival and growth of first-year seedlings experiencing climate extremes and could be used to generalize species-specific patterns to broader taxonomic or functional groups.

The goal of this study was to understand how heat, drought, and combined heat and drought affect the growth and survival of first-year seedlings of tree species native to eastern North America. We exposed 793 first-year seedlings of eight tree species {balsam fir [*Abies balsamea* (L.) Mill.], red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), black ash (*Fraxinus nigra* Marsh.), red spruce (*Picea rubens* Sarg.), eastern white pine (*Pinus strobus* L.), red oak (*Quercus rubra* L.), and northern white cedar (*Thuja occidentalis* L.)} to three heat and three drought treatments, and their combinations, for 90 days. We selected species based on their relative ranges in Maine, USA, which is located at the northern limit of the temperate forest and the southern limit of the boreal forest (Goldblum and Rigg, 2010). Species included a mix of northern conifers generally approaching their southern range margins and temperate broadleaves approaching their northern range margins. Additionally, these species represent a range of traits, including species and broader taxonomic groups with relatively high TLP (*Abies balsamea*) and relatively low TLP (*Acer rubrum*, *Quercus rubra*), high g_{min} (*Thuja occidentalis*, *Acer rubrum*) and low g_{min} (*Quercus rubra*), high LMA (*Picea* spp.) and low LMA (*Acer* spp.; Bartlett et al., 2014; Duursma et al., 2019). We tested how these heat and drought treatments impacted seedling survival and growth and explored potential links with physiological traits. Generally, we hypothesized that:

- I. Across all species, warming alone would not affect seedling survival, but drought alone would decrease survival, and more so when combined with heat.
- II. Temperate broadleaf species would have increased growth in warmed treatments when adequate substrate moisture is present, and northern conifer species would experience no changes to growth because of the temperature treatments, regardless of substrate moisture.
- III. Species with the highest survival would be those with the most efficient water-conserving traits, including a low TLP, low g_{min} , high LMA, and high root:shoot, for example, red maple, red oak, and eastern white cedar.

Methods

Seeds and seedlings

To determine how first-year seedlings respond to heat and drought events, we collected seed in fall 2023 from four northern conifer and four temperate broadleaf trees native to the temperate-boreal ecotone in the northeastern US (Table 1 and Supplementary Table 1). All seeds were cold-moist stratified according to recommendations in the USDA Seed Manual except for red maple which we collected in spring 2024 when they matured (Bonner and Karrfalt, 2008; Supplementary Table 2). In late April and early May of 2024, we sowed seeds of all northern conifer species in 6.4-cm-deep (250 cm³) square containers and all temperate broadleaf species in 8.9-cm-deep (500 cm³) square containers. We used two container sizes to match expected root system size of each species to container size such that all species experienced moisture stress. The angiosperm species in this study grow more quickly than the gymnosperm species, and the root growth of angiosperm species would be limited in the

TABLE 1 List of tree species by functional leaf type and where the state of Maine, USA falls within their native ranges.

Leaf type	Species	Range
Evergreen needle-leaved species	Balsam fir (<i>Abies balsamea</i>)	Southern
	Red spruce (<i>Picea rubens</i>)	Southern/central
	Eastern white pine (<i>Pinus strobus</i>)	Northern
	Northern white cedar (<i>Thuja occidentalis</i>)	Southern
Deciduous broad-leaved species	Red oak (<i>Quercus rubra</i>)	Northern
	Red maple (<i>Acer rubrum</i>)	Northern/central
	Sugar maple (<i>Acer saccharum</i>)	Northern
	Black ash (<i>Fraxinus nigra</i>)	Northern/central

smaller containers, while the root growth of the gymnosperm species would be limited to a small portion of the media in the larger containers and therefore unlikely to experience moisture stress. We collected red maple seeds in early June (when they naturally mature) and immediately sowed seeds into 6.4-cm-deep containers. Later, established seedlings of red maple were repotted into 8.9-cm-deep containers. For all species except red oak, sugar maple, and red maple, two to four seeds were sown in each container to account for low germination rates. All containers were filled with potting media (Pro-Mix BX Growing Medium with Mycorrhizae, Premier Tech Growers and Consumers Inc., Pennsylvania USA) and hand-watered regularly. This medium includes a starter charge of nutrients that provides up to 130 mgL⁻¹ nitrate, 40 mgL⁻¹ phosphate, and 130 mgL⁻¹ potassium, plus additional macro and micronutrients for an initial electrical conductivity of up to 1.8 mmhos cm⁻¹ as measured by saturated medium extract. Containers were kept in a climate-controlled greenhouse to establish until May 31, 2024. Data on establishment rates was collected when seedlings were moved outside and again on June 12, 2024 (Supplementary Table 3). Seedlings were then kept outside on the University of Maine campus (44°53'50.0"N, 68°40'08.3"W; Supplementary Figure 1, within the current extent of the temperate-boreal ecotone), to acclimate to ambient conditions in full sunlight and protected from predation with mesh wire fencing until June 20, 2024 [day-of-treatment (DOT) 0; Supplementary Table 4]. To ensure we had enough singly planted individuals, we repotted seedlings when there was more than one individual per container but a limited number of total individuals of that species (Supplementary Table 5).

Experimental design

To simulate heat and drought conditions, we created 27 custom chambers from inverted 62.5-liter clear plastic storage containers (Supplementary Figure 2). Chambers were evenly divided into

three blocks (A, B, or C) of 9 chambers each (Figure 1A). Within each block, each chamber was randomly assigned to one unique combination of heat (ambient, moderate, extreme) and drought (irrigated, extended, repeated; Figure 1B). Due to limitations in the number of established seedlings and predation during the establishment phase for some species (Supplementary Table 3), the number of seedlings within a chamber was not always consistent among species. Specifically, we placed two or three individuals of angiosperm species in all chambers, except for black ash, which had overall low establishment and was limited to one individual in seven chambers in block three, and red oak, which was limited to one individual in one chamber of block three. A minimum of five individuals of each gymnosperm species, except for red spruce, was placed in each chamber. For the gymnosperm species with the highest overall establishment (eastern white pine, balsam fir, and northern white cedar), up to 13 individuals were placed in some chambers, and a subset of these extra gymnosperms (107 total seedlings) were multiply-sown (2–4 individuals per container) to guarantee sufficient individuals for destructive measurements like water potential and g_{min} . Due to limited seed stock for red spruce, three seedlings were placed in each chamber in blocks one and two, and one seedling was placed in seven chambers in block three (Supplementary Table 1; 793 total seedlings; Figure 1C). We randomized placement of seedlings within each chamber to ensure that the effect of shading was not confounded with treatment. All chambers were fitted with an automated spray irrigation system (Vibronet Mister, Netafim, Israel). Misterters were placed in the center of the chamber about 30.5-cm from the base and watered seedlings to saturation three times per week except during drought treatments.

Heat and drought treatments

Treatment timeline

All seedlings (except red maple that were added on DOT 13; Supplementary Table 4) were placed in chambers on DOT 0 (onset of experimentation) and remained in chambers until the end of September (DOT 97–106). Once in chambers, all seedlings were fully irrigated until DOT 13. Extreme warming began on DOT 12 and continued through DOT 90, but due to electrical issues, was intermittent until DOT 26. Drought treatments were applied from DOT 13 to DOT 49.

Heat treatments

The chambers used for the ambient temperature treatment had large, rectangular (645-cm² on the longer sides and 338-cm² on the shorter sides) ventilation holes cut into all four sides of the chamber to limit heat and moisture buildup (Supplementary Figure 2). We used the chamber plastic in the upper 5-cm of each ventilation hole as an angled overhang to help exclude precipitation. Chambers used for the moderate heat and extreme heat treatments had smaller (37-cm by 0.5-cm) ventilation slits on two sides, but each extreme heat chamber also had a heat mat (Heat Mat and Heat Mat Temperature Controller, Vivosun, Ontario Canada) underneath the chamber

that turned on if air temperature in the chamber dropped below 37 °C. Heat mats were used to increase air temperatures by elevating all seedlings approximately 5cm above the heat mats on a plastic platform with air holes. To partially reduce insolation, all chambers were wrapped in 30% polyethylene shade cloth (Green-Tek, Wisconsin USA), with two layers on the top of each chamber (Supplementary Figure 2).

Drought treatments

To apply drought treatments, the irrigated chambers were watered to saturation (1 h) every 2–3 days, the extended drought chambers received half of the amount of water as the irrigated chambers every 2–3 days (limited to 20 min of water 1 day a week on DOT 22 and unirrigated after DOT 38), and the repeated drought chambers experienced no watering for the duration of drought treatments (DOT 13–29 and DOT 30–49). Repeated drought chambers were watered to saturation on DOT 29 before the drought was repeated. Extended drought chambers received one third of saturation-level irrigation on DOT 30 in addition to their 1 day of water for the week.

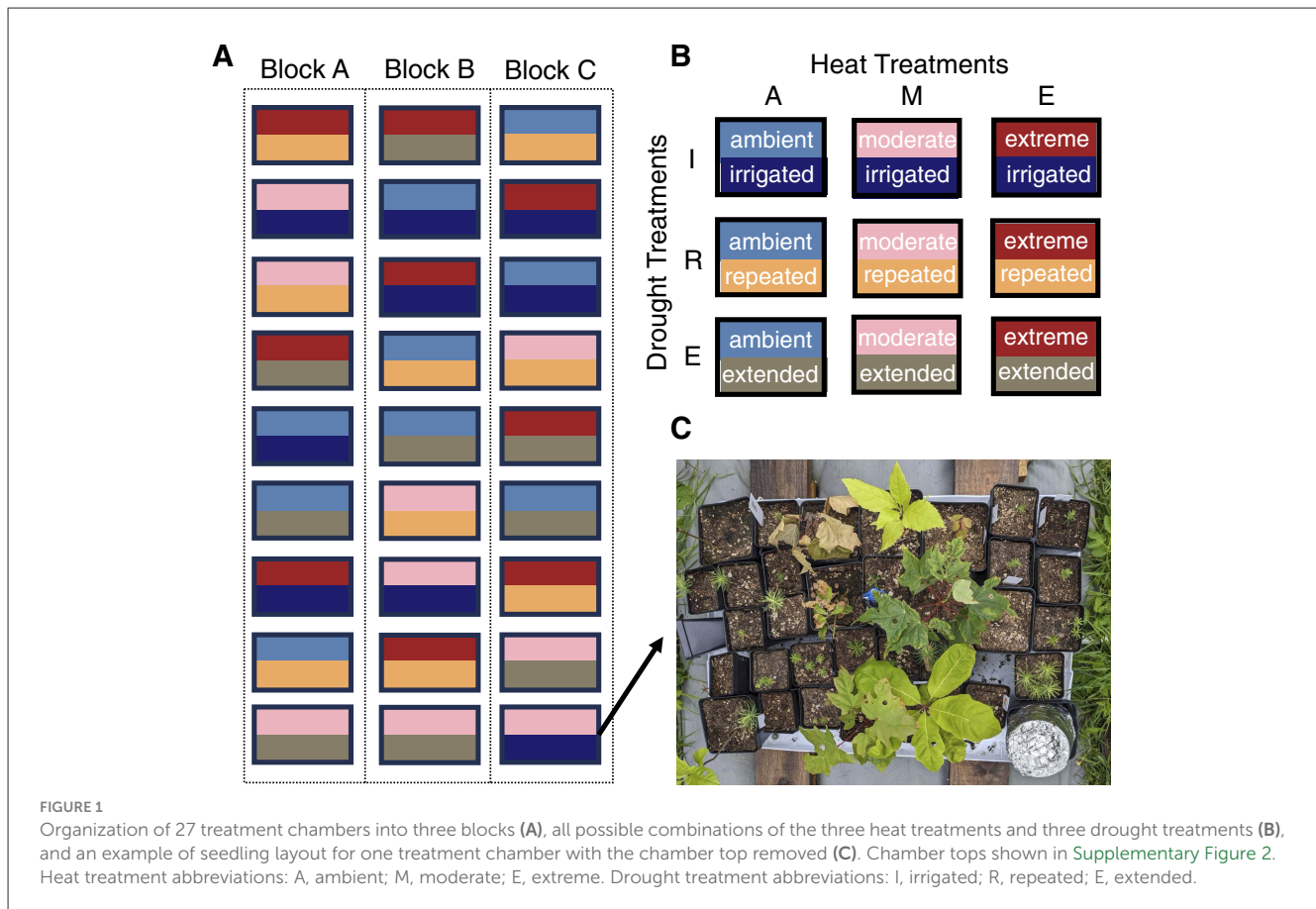
The drought treatments were designed to include two short and intense droughts (the Repeated treatment) and a more gradual and prolonged drought (the Extended treatment). We adjusted the watering to achieve these outcomes based on continuously monitored substrate moisture data.

Chamber temperature and humidity

Unfortunately, we are unable to report temperature and humidity data due to data loss after three days of data collection. However, we reconstructed one of each warming chamber type the following summer and recorded hourly temperature and relative humidity for 31 days in July and August to better understand how environmental conditions varied among treatments without seedlings in the chambers (HOBO MX2302A External Temperature/RH Sensor Data Logger, Onset, Bourne, MA). We found that, compared to the ambient chamber, average daily temperature was 3.0 ± 1.6 °C (mean ± 2 standard deviations) warmer in the moderate heat chamber and 7.7 ± 1.8 °C warmer in the extreme heat chamber. Average daily vapor pressure deficit was 0.9 ± 0.7 and 1.8 ± 0.9 kPa higher in moderate and extreme heat chambers, respectively, than in ambient chambers (Supplementary Figure 3).

Substrate moisture

To quantify the effect of the drought treatments on water availability, one individual per species per chamber was weighed in its pot twice a week to approximate changes in substrate moisture. Mass was converted to approximate substrate moisture based on earlier measurements of the dry mass of the corresponding container size filled with media. To estimate substrate moisture, we subtracted dry mass from current mass and divided the difference by substrate volume.



Survival and growth

To assess the effects of heat and drought treatments on growth and survival, we measured the height (length of stem) at the start of heat treatments (DOT 0) and the end of the season (EOS; DOT 90–92). Survival (live or dead; based on the presence of any green foliage) was measured on those dates and twice more during the drought treatments to capture progressive declines (DOT 36 and 53). We also quantified the final biomass for 417 living seedlings from blocks A and B after EOS height and vigor assessments. To obtain biomass, seedlings were carefully removed from containers, roots were rinsed in water, and all living tissue was placed in paper envelopes and dried at 70 °C for a minimum of 1 week. Roots, stems, and live leaves were measured separately.

Water relations

To better understand the extent to which drought treatments may have caused drought stress, we measured midday (between 11:00 and 14:00) leaf water potential (Ψ_{leaf}) twice. Although we were limited in our ability to sample for water potential by the number of sensors and limiting destructive measurements on seedlings, we were able to conduct a total of four sampling rounds across two different time periods. We first sampled partway through the drought on DOT 27 and 28 to determine how extended drought differed from irrigated (ambient temperature) and how repeated drought differed from irrigated (extreme heat). At the end of the drought on DOT 48 and 49, we then sampled

two more times to assess how extended drought differed from irrigated (ambient temperature) and how extreme heat differed from ambient heat (extended drought). We used thermocouple psychrometers calibrated using sodium chloride solutions of known water potentials (TCP; JRD Merrill Specialty Equipment, Logan, UT, USA) to estimate Ψ_{leaf} . Due to a limited number of TCP chambers for estimating Ψ_{leaf} , we could only sample one individual per species from each of four treatment chambers, divided evenly among two treatment combinations each day.

To measure Ψ_{leaf} , we followed the protocol outlined in Barry et al. (2024). Briefly, we collected two to four needles (depending on their size) per northern conifer species and one leaf disc per temperate broadleaf species for each seedling and immediately placed them in a TCP chamber and stored them in a cooler for the duration of sampling. Red maple seedlings were not large enough to be sampled on DOT 27 and 28. TCP chambers were transported to the lab after sample collection, connected to a datalogger, placed in a temperature-controlled water bath, and allowed to equilibrate for at least 6 h. Once measurements were stable, a minimum of three values were averaged to obtain Ψ_{leaf} .

Species-level traits

To explore potential species-level traits, we estimated the leaf minimum epidermal conductance (g_{min}), leaf turgor loss point (TLP), and leaf mass-per-area (LMA) in late August (DOT 67, 65, 67 respectively) for all species. To determine g_{min} , we followed

the protocol outlined in Sack and Scoffoni (2010). Seedlings were watered to saturation and covered in a black bag for at least 1 h to stop transpiration and achieve full turgor before sampling one leaf (temperate broadleaves) or whole shoot (1.1–5 cm; northern conifers) from six individuals of each species taken from three ambient \times irrigated chambers and three ambient \times extended drought chambers. Cut ends of samples were sealed with petroleum jelly, and samples were hung in a dark box with constant air circulation, and weighed at regular intervals (Barry et al., 2024). Temperature and relative humidity were monitored and recorded throughout the dry downs (HOBO MX2302A External Temperature/RH Sensor Data Logger, Onset, Bourne, MA). Each sample was weighed a minimum of five times, and g_{\min} was calculated using the g_{\min} Analysis Spreadsheet Tool from the slope of the dry-down curve (Sack, 2010).

To estimate the leaf-mass-per-area (LMA), we used the same leaf samples used in the g_{\min} analyses. All leaves from temperate broadleaf species were scanned (Epson V600 Photo Scanner model B11B198011) before and after g_{\min} measurements. For northern conifer species, we stripped the needles from each shoot and scanned them after g_{\min} measurements. We calculated the area of leaves and needles using ImageJ (Schindelin et al., 2012). We then used the oven-dry mass (dried at 70 °C > 48 h) to calculate the LMA of each sample, using the formula: $LMA = \text{dry leaf mass}/\text{leaf area}$.

To estimate TLP, we followed the rapid osmometer method (Bartlett et al., 2012), substituting the osmometer with TCPs (Barry et al., 2024). We sampled eight individuals per species, two from each of four treatment chambers (two ambient \times irrigated chambers and two ambient \times extended drought chambers). Seedlings were watered to saturation and covered in a black bag for at least 1 h to stop transpiration and achieve full turgor. A leaf disc was collected from each temperate broadleaf, and 3–5 needles were removed from each northern conifer. Samples were wrapped in aluminum foil, flash frozen in liquid nitrogen for 2 min, removed from the foil, and placed in a TCP chamber. Once all samples were in TCP chambers, the same protocol described for Ψ_{leaf} was followed to estimate osmotic potential at full turgor. We then applied the established regression equation from Bartlett et al. (2012) to predict turgor loss point from the estimates of osmotic potential at full turgor.

Statistical analyses

To analyze substrate moisture, we modeled approximate substrate moisture as a response in a linear mixed effects model using the lowest observed substrate moisture for each given container throughout the study. Our initial model included fixed effects for species, heat treatment, and drought treatment, all possible interactions, and chamber as a random effect. If the three-way interaction was significant, we followed up with separate models for each species testing for effects of heat, drought, and their interaction. If the three-way interaction was not significant, it was removed, and we further reduced model complexity by progressively removing non-significant two-way interactions and rerunning the model each time until the final model included only significant interactions (if any) and all three predictors as main effects.

To quantify differences in Ψ_{leaf} , we calculated one average Ψ_{leaf} for each species and treatment combination on a given sampling day. Then, we used those values to calculate the difference in Ψ_{leaf} between our control treatment and test treatment on a given day (ΔWP_{leaf}) and ran one sample *t*-tests on each comparison.

To determine the effects of species, heat, and drought on seedling survival, we modeled EOS survival as a binomial response variable in a generalized linear mixed effects model using the same model selection process described for substrate moisture.

To determine the effects of species, heat, and drought on growth, we estimated growth as absolute EOS height, relative height growth (relative to start-of-treatment height), total biomass, and root:shoot biomass ratio (root:shoot). We used each of these growth metrics as response variables in linear mixed effects models using the same predictors and selection process described for substrate moisture, above. After fitting models, we checked model assumptions including normality of residuals and Q-Q plots. These tests lead us to log-transform absolute EOS height, total biomass, and root:shoot before rerunning the model reduction process.

In all mixed-effects models, we included a random intercept for chamber to account for variation in sample size. To test for pairwise comparisons for significant main effects or interactions in all models, we conducted *post-hoc* pairwise comparisons of estimated marginal means, applying a Sidak adjustment to account for multiple comparisons (Šidák, 1967). Compact letter displays were used to group treatments with statistically similar means, with different letters indicating significant differences. For all models, we tested if the repotting of some individuals (Supplementary Table 5) impacted the results by rerunning the model selection process excluding individuals that were repotted. We found that our results and conclusions were not impacted by the repotting and we report only the combined results here. Additionally, we tested if the inclusion of multiply-sown seedlings (13% of total individuals used in survival, height, and biomass analyses) impacted results and found that our conclusions were not impacted if these individuals were removed.

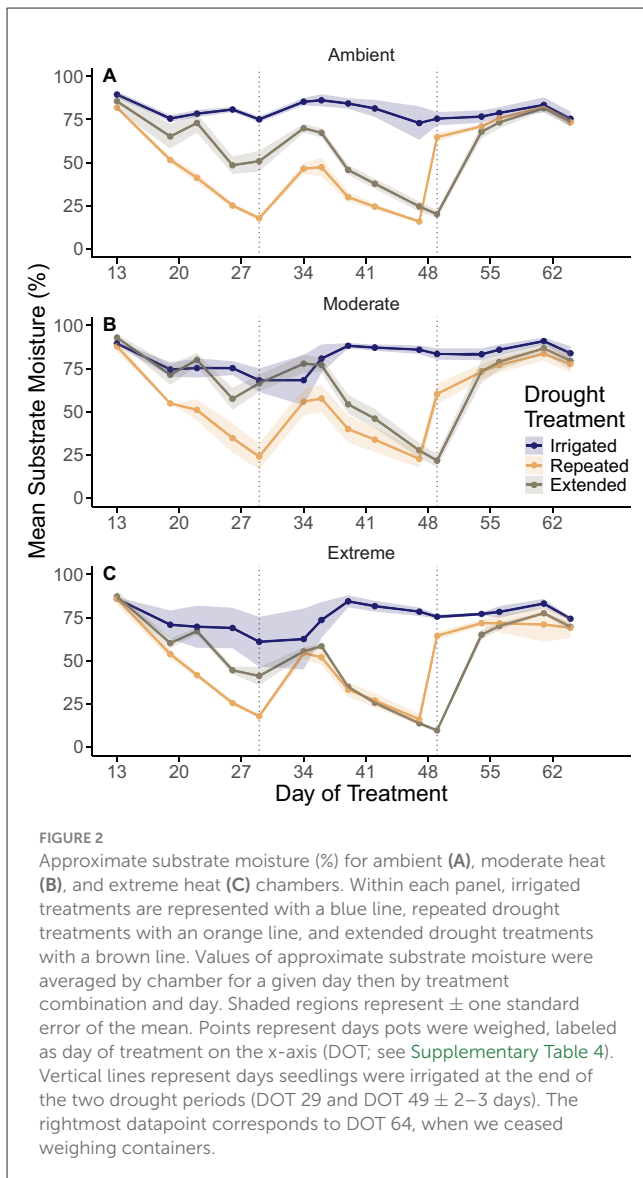
To determine how species traits may drive patterns in survival, we tested how species mean g_{\min} , LMA, and root:shoot each separately predict species mean survival (across all treatments) using linear regressions. We also tested for correlations among traits using Pearson correlation coefficients to investigate the relationship between g_{\min} , LMA, and root:shoot. To analyze TLP, we tested for differences in TLP by species and drought treatment.

All analyses were run in R using RStudio (ver. 4.4.1, R Core Team, 2024) and using packages “stats,” “lme4,” “car,” “emmeans,” and “multcomp” (Bates et al., 2015; Fox et al., 2024; Hothorn et al., 2008; Lenth et al., 2025; R Core Team, 2024).

Results

Heat and drought treatments

We found no significant interactions in our models of minimum substrate moisture. Drought treatments significantly reduced minimum substrate moisture (p -value < 0.001), with the repeated drought experiencing two successive declines in substrate moisture and the extended drought experiencing one gradual



decline (Figures 2A–C). However, minimum substrate moisture did not differ significantly between repeated and extended drought treatments ($p = 0.992$) nor among heat treatments ($p = 0.213$), though the chambers experiencing extreme warming and the extended drought reached the lowest recorded substrate moisture (Figure 2C). We found that during three of our sampling events for ψ_{leaf} , the ψ_{leaf} of drought treated plants was not significantly lower than controls. However, near the end of the drought treatments we did find that, on average, seedlings experiencing extreme heat and extended drought had ψ_{leaf} 1.1 MPa lower than seedlings experiencing ambient heat and extended drought (p -value = 0.003; Table 2).

Survival

We found that overall, survival declined most in response to combined heat and drought (final model included a drought \times

heat interaction; p -value = 0.038; Figure 3; Supplementary Table 6). However, survival also differed by species (final model included a species main effect; p -value < 0.001). Two northern conifers, red spruce (Figure 4A) and balsam fir (Figure 4B), had the lowest survival and were most impacted by combined heat and drought treatments. In contrast, two temperate broadleaf species, black ash (Figure 4G) and red oak (Figure 4H), had the highest survival and were not impacted by combined heat and drought treatments. The remaining species (Figures 4C–F) demonstrated intermediate reductions in survival to combined heat and drought.

Height

EOS height was not impacted by drought ($p = 0.261$) or heat ($p = 0.256$), but the final model did include a significant effect of species ($p < 0.001$; Supplementary Table 6). Our initial model of EOS height included a significant interaction between species and drought treatment ($p = 0.027$). Despite the interaction, pairwise comparisons showed no differences among drought treatments for any species, suggesting that this interaction was minor and instead that species was the major factor determining EOS height (Supplementary Figure 4). Therefore, we removed this interaction and used an additive model. Generally, we found that all northern conifers were shorter than all temperate broadleaves (Figure 5A), and results from our model of relative height growth over the treatment period found only a significant effect of species ($p < 0.001$). Red maple and northern white cedar had the highest relative height growth, whereas red spruce had intermediate relative height growth, and all other species had low relative height growth over the course of our treatments (Figure 5B).

Biomass

The final model for total biomass included a significant interaction between species and drought treatment ($p = 0.02$; Supplementary Table 6). However, pairwise comparisons revealed only one minor difference among treatments for one species (Supplementary Figure 5). Therefore, we removed this interaction and the only remaining predictor for total biomass was species ($p < 0.001$). Generally, northern conifers had lower total biomass than temperate broadleaves, with red spruce having the lowest total biomass and red oak having the highest total biomass (Figure 6A). Similarly, the final model for root:shoot included no interactions (Supplementary Figure 6) and only a significant effect of species ($p < 0.001$). Differences in root:shoot were less pronounced, but we generally found that northern conifers had lower root:shoot than temperate broadleaf species (Figure 6B).

Water relations and species-level traits

Although we found general patterns separating northern conifers and temperate broadleaf species in regard to survival and growth, we found that LMA (Figure 7A; p -value = 0.08), g_{min} (Figure 7B; p -value = 0.26), and root:shoot (Figure 7C; p -value =

TABLE 2 Day of water potential sampling (day of treatment; DOT); treatments sampled that day with the number of species for which species-level average water potential fell below cross-species average turgor loss point (-1.47 ; 95% CI = -1.57 to -1.36) in parentheses; cross-species average difference in water potential (Δ WP; group 1–group 2) with standard error in parentheses; and the p -value from a one-sample t -test used to determine if Δ WP was, on average, below 0.

DOT	Group 1	Group 2	Δ WP	p -value
27, 28	Ambient \times extended (2)	Ambient \times irrigated (1)	-0.20 (0.16)	0.124
27, 28	Extreme \times repeated (5)	Extreme \times irrigated (5)	-0.34 (0.23)	0.093
48	Ambient \times extended (1)	Ambient \times irrigated (0)	-0.40 (0.38)	0.167
49	Extreme \times extended (4)	Ambient \times extended (0)	-1.07 (0.27)	0.003

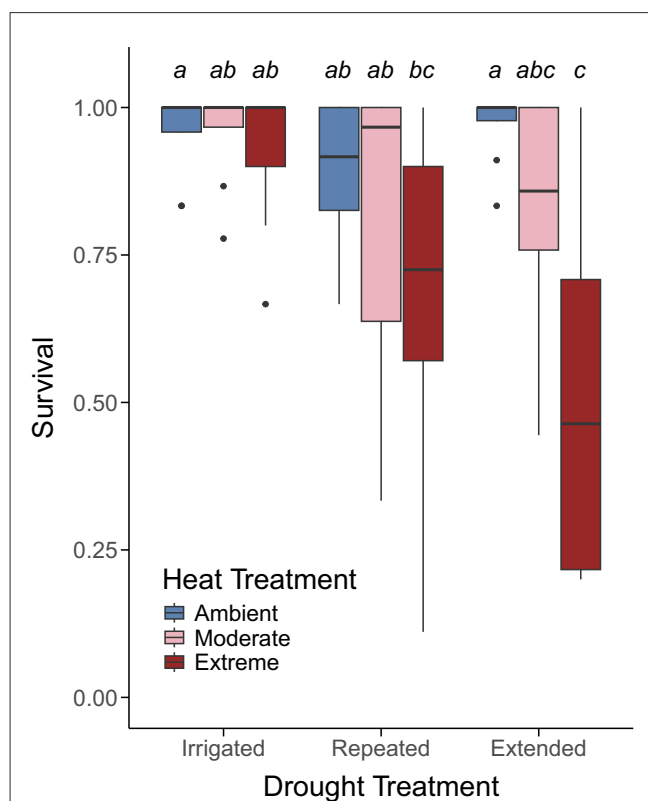


FIGURE 3

Survival (as a proportion of living individuals) within a chamber averaged across all species and treatment combinations. Boxes represent the middle 50% of data and the horizontal line represents the median survival within a treatment combination. Whiskers extend to $1.5 \times$ the interquartile range and any data points beyond that range are represented as separate dots. Annotations above bars indicate significant differences in survival among treatment combinations from a Sidak *post-hoc* test if boxes do not share a letter. Sample size for each species is as follows: red spruce ($n = 66$), balsam fir ($n = 136$), eastern white pine ($n = 171$), northern white cedar ($n = 179$), red maple ($n = 56$), sugar maple ($n = 64$), black ash ($n = 47$), and red oak ($n = 67$).

0.09) were not linearly related to species-level survival. Although there were not consistent linear relationships, we did find that the two species with the lowest survival (balsam fir and red spruce) had the largest LMA and lowest root:shoot. We also found that the two species with the highest survival (red oak and black ash) had the highest root:shoot (Table 3). We did not find correlations

between LMA and g_{min} (p -value = 0.46), LMA and root:shoot (p -value = 0.07), or g_{min} and root:shoot (p -value = 0.90). We found no differences in TLP by species or treatment combination, leading us to average all values to obtain one TLP for all species. However, we did find that midday Ψ_{leaf} of seedlings occasionally exceeded (was lower than) the mean TLP (-1.47 ± 0.052 MPa), particularly in the extreme heat treatments that were also experiencing a drought (Supplementary Figures 7A, D).

Discussion

Our study revealed how extreme environmental conditions can reduce the survival of first-year seedlings native to the northeastern USA. We found that northern conifers at the southern edge of their range margin, red spruce and balsam fir, have overall lower survival than other conifers and temperate broadleaf species. Furthermore, survival of northern conifers responded more negatively to extreme conditions (heat and drought) than other species. The species with the highest survival had the highest root-to-shoot biomass ratio, suggesting this may be a critical factor for seedling survival in extreme conditions. Despite impacts to survival, for seedlings that survived the treatments, heat and drought did not cause reductions in height or biomass growth in this first year. These data expand our understanding of the sensitivity of first-year seedlings to extreme climate conditions and suggest that combined extremes may dramatically impact regeneration in the regional temperate-boreal ecotone.

Survival was reduced for most species in response to heat and drought

Overall, we found that survival responded strongly to the treatments, particularly the extreme heat treatment combined with either the repeated or extended drought. This reduction in survival was strongest for the northern conifer species red spruce and balsam fir. Although many other studies have highlighted the importance of moisture for the persistence of red spruce and balsam fir (Collier et al., 2022; Greenwood et al., 2008; Roberts and Cannon, 1992), these were the only two species in our study to also experience substantial declines in survival in response to heat alone. Though, the temperatures in the extreme heat treatment were likely greater than current and projected future temperatures in these species' ranges and therefore more representative of potential future extreme heat waves. These results confirm a growing

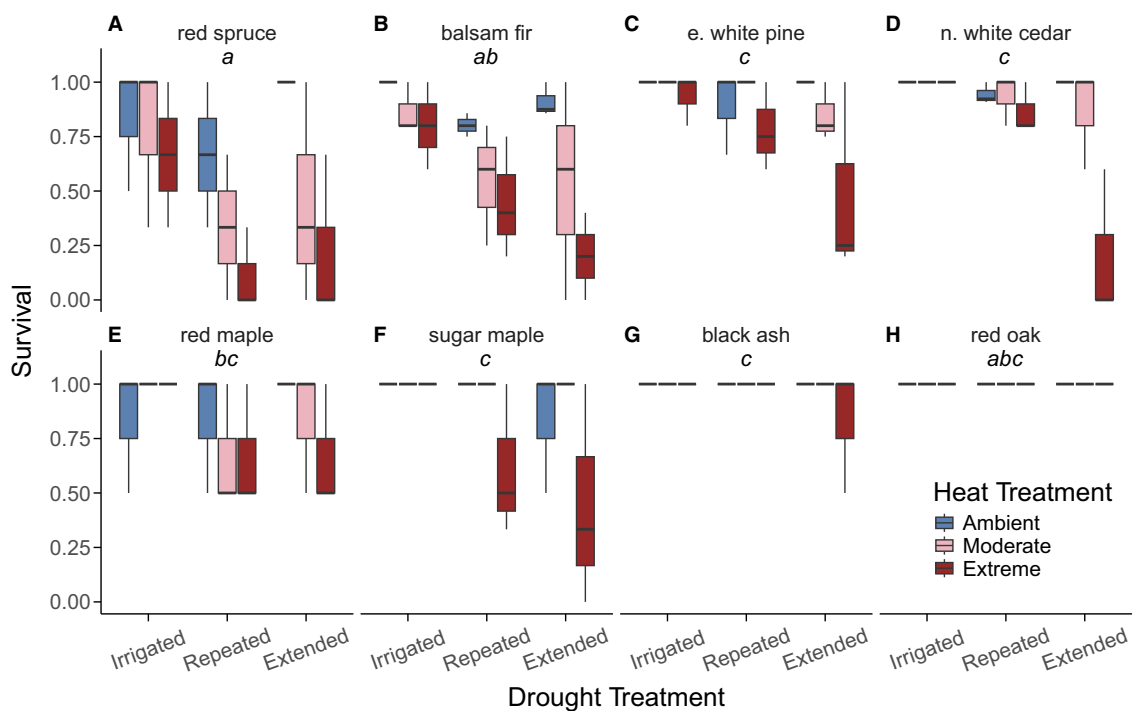


FIGURE 4 Survival (as a proportion of living individuals) within a chamber at the end of the growing season for each species: (A) red spruce (*Picea rubens*) (B) balsam fir (*Abies balsamea*) (C) eastern white pine (*Pinus strobus*) (D) northern white cedar (*Thuja occidentalis*) (E) red maple (*Acer rubrum*) (F) sugar maple (*Acer saccharum*) (G) black ash (*Fraxinus nigra*) (H) red oak (*Quercus rubra*). Boxes represent the middle 50% of data and the horizontal line represents the median survival within a treatment combination. Whiskers extend to 1.5 × the interquartile range and any data points beyond that range are represented as separate dots. Annotations at the top of each panel indicate significant differences in survival among species from a Sidak *post-hoc* test if boxes do not share a letter. Sample size for each species is as follows: red spruce ($n = 66$), balsam fir ($n = 136$), eastern white pine ($n = 171$), northern white cedar ($n = 179$), red maple ($n = 56$), sugar maple ($n = 64$), black ash ($n = 47$), and red oak ($n = 67$).

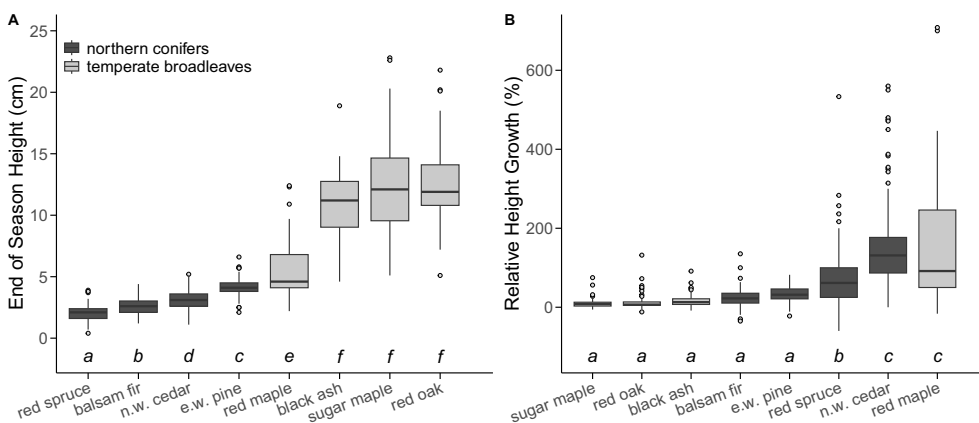
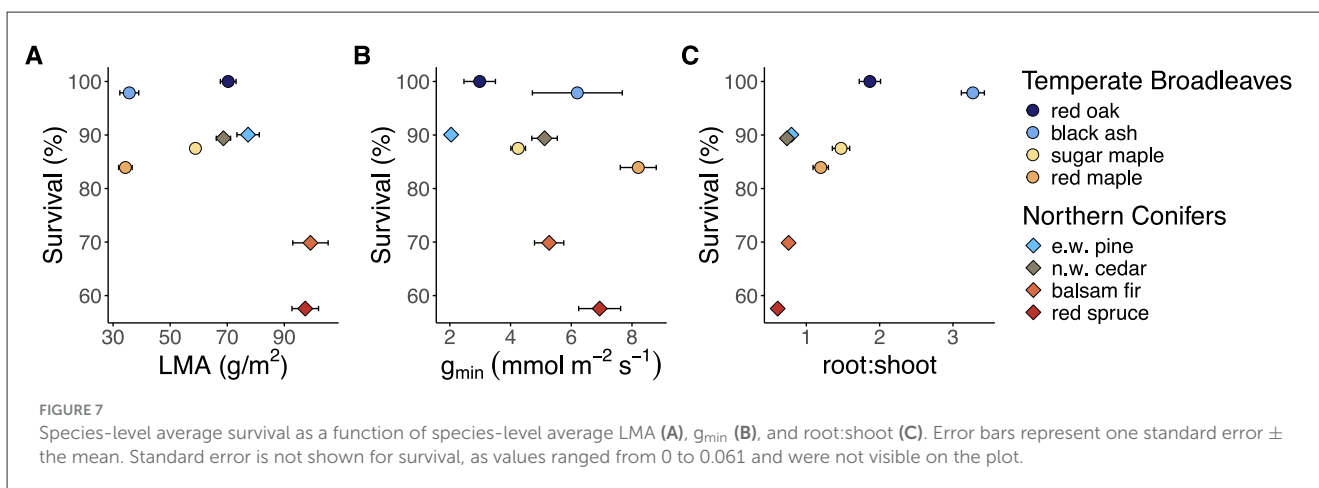
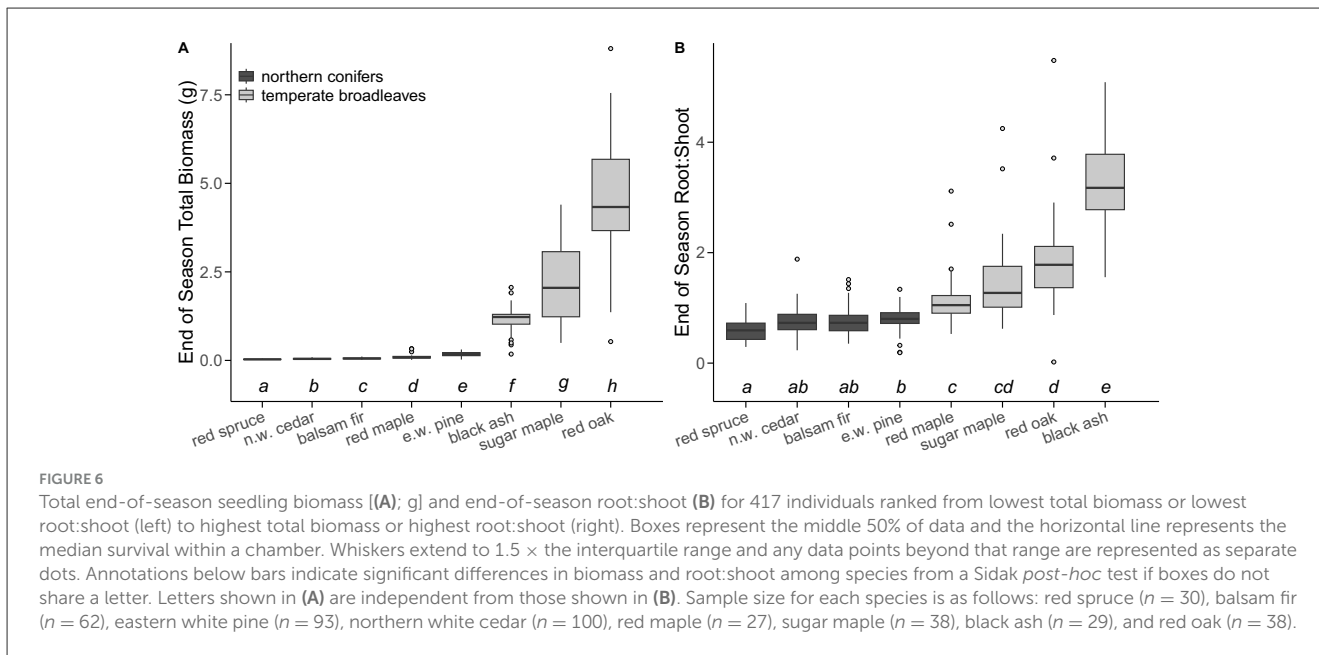


FIGURE 5 Absolute end-of-season (EOS) height [cm; (A)] and relative height growth as a percentage of height at the start of the treatments [%; (B)] of all seedlings by individuals for each of our study species. Species are ranked from lowest EOS height or lowest relative height growth (left) to highest EOS height or highest relative height growth (right). Boxes represent the middle 50% of data and the horizontal line represents the median height or height growth for each species. Whiskers extend to 1.5 × the interquartile range and any data points beyond that range are represented as separate dots. Annotations below bars indicate significant differences in height and height growth among species from a Sidak *post-hoc* test if boxes do not share a letter. Letters shown in (A) are independent from those shown in (B). Sample size for each species is as follows: red spruce ($n = 65$), balsam fir ($n = 136$), eastern white pine ($n = 171$), northern white cedar ($n = 178$), red maple ($n = 56$), sugar maple ($n = 63$), black ash ($n = 46$), and red oak ($n = 65$).



understanding that these species and other species are vulnerable to changes in climate, particularly at their southern range margins, and provide new context into how these climate changes may interact to impact forest regeneration (Canham and Murphy, 2017; Vaughn et al., 2021).

Generally, when combined with heat, the extended drought treatment led to greater reductions in survival than the repeated drought treatment. Despite only finding significantly low water potential for seedlings in the extreme heat and extended drought treatment, we suspect that at the observed substrate moisture values, very minor changes in moisture did not capture the known large differences in water potential that can occur (van Kampen et al., 2022). However, low survival in the combined heat and extended drought treatments provide indirect evidence that the seedlings in this treatment experienced physiological stress. These results are further supported by the overall lower minimum substrate moisture in the extreme heat and extended drought treatment. Collectively, these results point to the importance

of hydraulic stress dictating survival and the strong degree to which this depends upon both soil moisture and atmospheric dryness (vapor pressure deficit) that generally increases with warming (Berry and Smith, 2013; Day, 2000; Grossiord et al., 2020), and future first-year seedling studies may consider including more repeated measurements of hydraulic stress during drought treatments. Indeed, the small size of seedlings and small root systems may reduce their ability to buffer changes in water potential from rapidly changing environmental conditions (Scholz et al., 2011), leading to catastrophic hydraulic failure and mortality.

Growth of surviving seedlings did not decline in response to heat and drought

Although treatments strongly impacted survival, we found no effect of any treatment on height or biomass growth of seedlings in this first year. This lack of response may be attributed to

TABLE 3 Species-level average leaf-mass-per-area (LMA), minimum epidermal conductance (g_{\min}), and root-to-shoot biomass ratio (root:shoot) \pm one standard error in parentheses.

Species	LMA (g/m ²)	g_{\min} (mmol m ⁻² s ⁻¹)	root:shoot
Red spruce (<i>Picea rubens</i>)	^a 97.34 (4.65)	^b 6.93 (0.69)	^d 0.61 (0.04)
Balsam fir (<i>Abies balsamea</i>)	^a 97.34 (4.65)	^b 5.27 (0.48)	^d 0.76 (0.04)
E. white pine (<i>Pinus strobus</i>)	^b 77.30 (3.92)	^d 2.04 (0.14)	^c 0.80 (0.02)
N. white cedar (<i>Thuja occidentalis</i>)	^b 77.30 (3.92)	^{cd} 5.12 (0.42)	^{bc} 0.72 (0.03)
Red maple (<i>Acer rubrum</i>)	^b 77.30 (3.92)	^a 8.21 (0.59)	^a 1.17 (0.12)
Sugar maple (<i>Acer saccharum</i>)	^c 58.85 (1.63)	^c 4.25 (0.24)	^b 1.44 (0.10)
Black ask (<i>Fraxinus nigra</i>)	^c 58.85 (1.63)	^a 6.20 (1.48)	^a 3.32 (0.17)
Red oak (<i>Quercus rubra</i>)	^c 58.85 (1.63)	^{cd} 2.98 (0.52)	^{bc} 1.91 (0.18)

Superscript compact letter displays from a Tukey *post-hoc* test are shown to compare values within a column. For each value of LMA and g_{\min} , $n = 6$. For root:shoot, $n = 27-100$ depending on species.

the timing of heat and drought stress. For example, the timing of the heat treatments occurred after most of these species had completed much of their height growth (i.e., relative height growth during treatment period near zero; Schulz et al., 2024; van Kampen et al., 2022). Further, studies that expose first-year seedlings to heat and altered precipitation throughout the growing season note increased growth, particularly for temperate broadleaves, under warmed conditions and regardless of precipitation regime (Fisichelli et al., 2014). Net photosynthesis has been used to explain increases in growth under experimental warming, as warming increases photosynthesis of temperate broadleaves and, to a lesser extent, northern conifers when soils are moist (Reich et al., 2018). However, the temperatures experienced in our chambers were likely regularly above temperature optima for photosynthesis (Cheesman and Winter, 2013; Gagne et al., 2020; Sendall et al., 2015). Furthermore, the warming may have increased vapor pressure deficit that, in extreme cases, can lead to hydraulic damage (Schönbeck et al., 2022) and mortality. However, for the seedlings that survived, stomatal closure to avoid hydraulic failure may still have reduced photosynthesis (Jalakas et al., 2021; Will et al., 2013). Therefore, growth reductions in response to warming may not be detectable until the following year due to reduced carbohydrate storage from reduced photosynthesis and increased respiration rates.

Drought has also been shown to profoundly impact tree growth in other studies, both in the drought year and following years (Barry et al., 2024; Kannenberg et al., 2019). However, like our results for heat, we did not find that drought impacted growth in the treatment year. The issue of drought timing may be particularly relevant here for similar reasons as for heat: stomatal closure reducing photosynthesis and carbohydrate storage (Woodruff et al.,

2024; Zargar et al., 2017). However, drought can also reduce water potential in ways that directly reduce turgor-driven cell expansion (Hsiao, 1973). Because most species completed growth prior to the onset of drought stress, this may suggest that, for seedlings, timing growth in early spring when moisture is often abundant limits the likelihood that low water potentials reduce growth. Species with extended growth phenologies may exhibit reduced growth rates during early-season droughts and recover by increasing growth rates after droughts cease (van Kampen et al., 2022). Indeed, spring droughts have profound effects on current-year growth yet, to our knowledge, there are no studies that investigate the effects of how late-season droughts may drive reductions in growth the following year for small seedlings (for evidence of drought lagged effects in adult trees, see Bigler et al., 2007; Foster, 2014; Huang et al., 2018). Therefore, because both the timing of heat and the timing of drought impact seedling growth, future seedling survival in natural conditions will depend on the timing of future heat, drought, and combined heat and drought events, which are likely to disproportionately impact growth more than just heat or drought alone (Allen et al., 2010; Williams et al., 2012).

Species-level traits partly explain patterns in survival

Compared to the temperate broadleaves, we found that the northern conifers tended to have higher LMA, similar g_{\min} and lower root-to-shoot biomass ratio. Despite the lack of linear correlations among traits in this study, these differences represent fundamental tradeoffs in leaf and plant structure and function that have been shown in other studies to relate to plant performance across a range of conditions (Maynard et al., 2022; Sastry et al., 2018; Wright et al., 2010). Unlike some studies, we did not find simple relationships among these traits and seedling survival. For example, g_{\min} has emerged as a key trait of interest for plant desiccation tolerance yet did not explain survival in our study (Ziegler et al., 2024). This discrepancy may be related to the relatively small leaf area of these seedlings and their limited capacity to buffer moisture changes with hydraulic capacitance (Scholz et al., 2011). This is supported by our survival and growth results, which suggest a threshold-type response whereby if the seedling survives the stressful conditions, growth is not impacted this year. Our results support the findings of others that root:shoot is a key trait related to supply and demand of moisture that may be especially important at this early life stage, and higher and more variable in seedlings than in adult trees (Ledo et al., 2018; Poorter et al., 2012).

We expected TLP to vary more by species within our study. However, while TLP has been shown to vary by species in multiple environments (Álvarez-Cansino et al., 2022; Visakorpi et al., 2024), this is often related to plant distribution in environments where drought is common and does not always correlate to drought vulnerability (Farrell et al., 2017). The relatively mesic forests of eastern North America may not place a strong selective pressure on TLP, partially explaining the lack of variation among the species in this study. Furthermore, traits like TLP are not well studied in the first year of tree growth, and TLP may not actually vary strongly in first-year seedlings despite differences at later life stages

(Beikircher et al., 2025). In addition, while some species may be able to acclimate TLP to future drought by adjusting the concentration of solutes in their cells and retaining water during dry periods (Bartlett et al., 2014), to our knowledge this phenomenon has not been studied in first-year tree seedlings.

Conclusions and implications

In addition to the extensive biotic and abiotic factors that contribute to very low seedling survival in the first year, our study demonstrates how heat, drought, and combined heat and drought events can have strong effects on first-year seedling survival. At the temperate boreal ecotone in northeastern North America, climate change and extreme conditions have the potential to cause a reduction in the survival of northerly distributed trees common to the region, which may facilitate a shift in species composition.

Specifically, the state of Maine, located at the southeastern extent of the temperate-boreal ecotone in North America, is projected to warm 1–5 °C by 2100, and drought is projected to become increasingly common (Fernandez et al., 2020). These elevated baseline temperatures and more variable precipitation patterns will likely increase the frequency of heat and drought stress. Due to the difficulty with associating specific temperatures to treatments in this study, future research that quantifies first-year survival reductions in trees native to this region is advantageous to our understanding of the severity of future compositional changes. Specific compositional changes, like projected loss of spruce-fir forests, could lead to the loss of this regionally unique habitat and the services it provides (Andrews et al., 2022; Davis, 1966; Pohjanmies et al., 2017). Because combined heat and drought events are more detrimental to first-year survival than either stressor alone, landscape-level decisions can be made to reduce the probability of overlap of these conditions. For example, the impact of droughts may be less likely to cause widespread mortality to seedlings in forest understories, where the microclimate can prevent excess heat during heatwaves (Finocchiaro et al., 2024; Redmond et al., 2018). Additionally, regeneration of seedlings or plantings in thinned or open conditions may have higher survival if moisture deficits can be avoided (Brodribb et al., 2020; Pozner et al., 2022; Qie et al., 2019).

Traits that maximize moisture supply and limit demand may be critical for first-year seedling survival in stressful conditions. However, studies documenting the anatomical and physiological development of first-year seedlings is lacking, and future opportunities include qualifying traits beyond those included in this study throughout the first growing season to understand their potential variation across species' ranges. Further, studying the interactions among genotype, seed provenance, and species-level traits may provide additional insights to how climate sensitive species will respond to future abiotic stress. Collectively, our results emphasize the critical importance of first-year survival of seedlings and provide new evidence that the impacts of combined heat and drought events may have profound impacts on tree regeneration at the temperate-boreal ecotone that may ultimately manifest as long-term shifts in species composition.

Data availability statement

The datasets presented in this study will be publicly available in the Dryad data repository (DOI: [10.5061/dryad.k3j9kd5ph](https://doi.org/10.5061/dryad.k3j9kd5ph)).

Author contributions

EM: Formal analysis, Writing – review & editing, Methodology, Writing – original draft, Data curation, Conceptualization. MC: Writing – review & editing, Conceptualization. BP: Methodology, Conceptualization, Writing – review & editing. JW: Writing – original draft, Funding acquisition, Conceptualization, Formal analysis, Supervision, Methodology, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2025.1734405/full#supplementary-material>

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