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Research paper

Contrasting survival strategies for seedlings of two northern conifer species to extreme droughts and floods

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Lowland northern white-cedar (*Thuja occidentalis L.*) forests are increasingly exposed to extreme droughts and floods that cause tree mortality. However, it is not clear the extent to which these events may differentially affect regeneration of cedar and its increasingly common associate, balsam fir (*Abies balsamea* (L.) *Mill.*). To test this, we measured how seedlings of cedar and fir were able to avoid, resist and recover from experimental drought and flood treatments of different lengths (8 to 66 days). Overall, we found that cedar exhibited a strategy of stress resistance and growth recovery (resilience) from moderate drought and flood stress. Fir, on the other hand, appears to be adapted to avoid drought and flood stress and exhibited overall lower growth resilience. In drought treatments, we found evidence of different stomatal behaviors. Cedar used available water quickly and therefore experienced more drought stress than fir, but cedar was able to survive at water potentials > 3 MPa below key hydraulic thresholds. On the other hand, fir employed a more conservative water-use strategy and therefore avoided extremely low water potential. In response to flood treatments, cedar survival was higher and only reached 50% if exposed to 23.1 days of flooding in contrast to only 7.4 days to reach 50% mortality for fir. In both droughts and floods, many stressed cedar were able to maintain partially brown canopies and often survived the stress, albeit with reduced growth, suggesting a strategy of resistance and resilience. In contrast, fir that experienced drought or flood stress had a threshold-type responses and they either had full live canopies with little effect on growth or they died suggesting reliance on a strategy of drought avoidance. Combined with increasingly variable precipitation regimes, seasonal flooding and complex microtopography that can provide safe sites in these forests, these results inform conservation and management of lowland cedar stands.

Graphical Abstract

Key words: *Abies balsamea*, mortality, *Thuja occidentalis*, tree growth, turgor loss point, water potential,

Introduction

Northern white-cedar (*Thuja occidentalis L.*, hereafter cedar) is experiencing low rates of regeneration and recruitment in lowland stands across parts of its range, and, in some cases, is being replaced by balsam fir (*Abies balsamea* (L.) *Mill.*; hereafter fir) (Miller et al. 1990; Heitzman et al. 1999; Larouche et al. 2011). Lowland cedar stands have variable moisture regimes that include seasonal flooding in generally poorly drained mineral and organic soil (Pregitzer 1991; Thompson and Sorenson 2000). However, climate change is increasing the likelihood and potential duration of both droughts and floods (Martel et al. 2020), both of which can negatively affect trees in these stands (Housset et al. 2015). Drought and flood impacts may be both ameliorated and exacerbated by the broad range of microtopographic positions in lowland stands, which create widely varying soil moisture conditions within meters of each other (Allogio et al. 2021). Therefore, there is an increasing need to understand how cedar and fir regeneration may respond to these changing moisture regimes to better predict future forest dynamics and management options.

Drought-induced tree mortality is challenging to predict (Trugman et al. 2021) because it can be a complex process with interactions between water, carbon and biotic agents (McDowell et al. 2022). When exposed to drought, trees may avoid (e.g. deep roots, conservative water use) or tolerate

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(e.g. desiccation tolerance, resisting turgor loss, limiting embolism spread in xylem) and recover from drought stress. Experiments using containerized plants provide key insights into these avoidance and resist-and-recover strategies and can identify important mortality thresholds (Barigah et al. 2013; Bolte et al. 2016; Hartmann et al. 2018; Hammond et al. 2019; Lalor et al. 2023). A tree's ability to limit progressive declines in water potential can allow it to avoid drought stress. However, continued water use or sustained drought can cause trees to exceed critical hydraulic stress thresholds (e.g. turgor loss point, TLP; water potential driving high percent loss of xylem conductivity, PLC). Exceeding these thresholds can either indirectly (through carbon starvation or weakened resistance to biotic agents) or directly cause reduced growth and mortality (McDowell et al. 2008; Adams et al. 2017; Thompson et al. 2023). Therefore, to better identify the strategies to avoid stress (e.g. hydraulic capacitance, minimum conductance following stomatal closure) and the hydraulic mechanisms that lead to mortality during stress (e.g. TLP, xylem water potential [Ψ_x] dynamics), we need an improved understanding of species-specific hydraulic traits (Scholz et al. 2011; Bartlett et al. 2012; Mcculloh et al. 2014; Duursma et al. 2019; Hammond et al. 2019; McDowell et al. 2022).

Climate change may increase flood-induced tree mortality in some places, yet is also challenging to predict (Kozlowski 2002; Martel et al. 2020; Evans et al. 2022). Similar to drought, the ability of certain tree species to either avoid (e.g. regenerate in favorable microtopographic positions (Roy et al. 1999; Allogio et al. 2021)) or resist (Justin and Armstrong 1987; Keller et al. 2023) root mortality during flooding is key to their survival in flood-prone forests. Although many plants can survive short (<1 day) floods, flood-induced mortality can manifest quickly for some species (Green 1947; Menezes-Silva et al. 2019; Keller et al. 2023) through disruptions to carbon metabolism and root mortality from anoxic conditions that can limit water uptake and lead to plant dehydration (Yamamoto and Kozlowski 1987; Megonigal and Day 1992; Baker et al. 2001; Menezes-Silva et al. 2019). Compared with drought avoidance and resistance traits, there is a paucity of known traits that correlate with flood avoidance and resistance of woody plants, underscoring the need for more whole-plant survival studies (Carpenter and Mitchell 1980; Glenz et al. 2006).

The ecology and physiological traits of cedar and fir (Frank 1990; Johnston 1990; Denneler et al. 2008) suggest that cedar would be more resistant and resilient (ability to recover) to both droughts and floods compared with fir (Matthes-Sears and Larson 1991; Larson et al. 1994). Although the two species are typically found on similar microsites in lowlands (Allogio et al. 2021), cedar can be found in extremely varying hydrologic conditions, including swamps and exposed limestone cliff faces (Matthes-Sears and Larson 1991; Kelly et al. 1992). Fir, on the other hand, tends to dominate in a broad range of generally favorable, but less extreme, conditions (Cornett et al. 1997). General abiotic stress tolerance rankings suggest that fir is less drought tolerant than cedar and that they have similar flood tolerance (Niinemets and Valladares 2006). Unfortunately, however, we have limited data on the degree to which they may be adapted to avoid stress or resist the stress and recover. The data available for key physiological thresholds such as the TLP (Collier and Boyer 1989; Pothier and Margolis 1990; Anderegg et al. 2016) and P_{50} (Ψ_x at 50% PLC) (Tyree and Dixon 1986; Hacke and Jansen 2009; Choat et al. 2012) are similar for these two species, suggesting their drought tolerance may not be as different as their ecology suggests. However, cedar may be more resilient to these abiotic stressors because of its ability to survive in extreme cliff-side habitats with partial canopies (Kelly et al. 1992; Larson et al. 1994) and because of its continuous growth throughout the growing season in contrast to fir that has a shorter period of growth (Kozlowski and Ward 1961; van Kampen et al. 2022).

The goal of this study was to improve our understanding of how cedar and fir avoid or resist drought and flood stress and the degree to which they can recover from these stressors. To accomplish this, we exposed containerized seedlings of cedar and fir to droughts and floods of different durations and tracked the onset of stress, quantified drought avoidance and resistance traits and measured growth and survival in the treatment year and a recovery year. We hypothesized that (i) cedar would resist stress from both droughts and floods longer than fir, (ii) cedar would have overall higher survival and lower amounts of brown foliage in the canopy from both droughts and floods than fir, (iii) growth of surviving cedar would be resilient to stress and recover to match controls and surviving fir would not and (iv) patterns of growth and survival by species would be related to hydraulic traits.

Materials and methods

Experimental design

To determine how droughts and floods of different lengths impact the survival, growth and the physiological response of cedar and fir seedlings, we conducted a controlled experiment in a 6 × 11 m high-tunnel greenhouse on the University of Maine campus in Orono, Maine starting in May 2021. The greenhouse was covered with a polyethylene sheet to control water availability, but with 1.2-m tall sidewalls left open to facilitate air circulation (van Kampen et al. 2022). Hygrochron model DS1923 iButtons (Maxim Integrated, San Jose, CA, USA) were installed inside and outside the greenhouse and protected with custom radiation shields to log hourly temperature and vapor pressure deficit (VPD) (van Kampen et al. 2022). In June, July and August of 2021, the average daily maximum temperature inside the greenhouse was 32.2 °C, 28.8 °C and 32.9 °C, respectively and averaged 1.5 °C warmer than the ambient conditions. In those same months, the average daily maximum VPD inside the greenhouse was 3.2 kPa, 2.2 kPa and 2.9 kPa, respectively and averaged 0.39 kPa greater than ambient conditions.

In May 2021 (27 May, start-of-season, SOS 2021), 205 3- to 4-year-old cedar (78.8 ± 0.8 cm tall, mean ± standard error; Cold Stream Farm, Free Soil, MI, USA) and fir (36.1 ± 1.1 cm tall; Redrock Farm, Chelsea, VT, USA) seedlings were planted individually into 7.5-L containers in a nursery potting mix consisting of fine aged pine bark and sphagnum peat (Jolly Gardener, Poland Spring, ME, USA) supplemented with a 5.9 g L^{-1} of Osmocote 18-6-12 slow-release granular fertilizer and 1/3 coarse perlite to facilitate drainage and limit water holding capacity (van Kampen et al. 2022). Plants were allowed to acclimate for 1 month and were watered with a drip irrigation system (3 L of water per plant three times per week).

To determine the lethal drought and flood threshold for each species, all drought and flood treatments were initiated on 5 July 2021 (start-of-treatment, SOT 2021; Fig. 1A). Cedar and fir seedlings (total of 72 per species: four seedlings

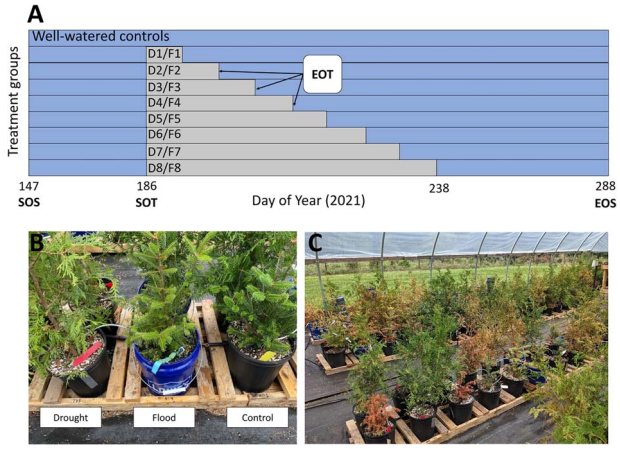

Figure 1. Schematic representation of the experimental design used to test how varying lengths of flood or drought impacted the physiology, growth and survival of cedar and fir. (A) Each species had a total of 17 treatment levels (control, eight levels of drought [D1 to D8] and eight levels of flood [F1 to F8]) that were replicated four times in the greenhouse (experimental blocks). All seedlings were regularly irrigated (blue bars) from the start of the season (SOS) to the end of the season (EOS) unless experiencing drought or flood treatments (gray bars). (B) Controls were irrigated the entire season, drought seedlings had their irrigation stopped and flood seedlings had root systems submerged in water at the start of the treatment (SOT) until the end of their treatment (EOT). Treatments lasted between 8 and 66 days. (C) Within each experimental block, the location of paired cedar and fir trees assigned to a given treatment was randomized. In the following year, 2022, all trees were regularly irrigated.

per species and treatment length per treatment type) were arranged into four experimental blocks with 36 seedlings each. Each experimental block consisted of two columns with 18 rows. Each row consisted of a pair of cedar and fir seedlings randomly assigned to one of eight drought treatment lengths (ranging from 8 to 66 days), one of eight flood treatment lengths (ranging from 8 to 53 days), or one of two replicates of irrigated controls (Fig. 1B and C). Drought treatments were initiated by stopping irrigation and flood treatments were initiated by placing the seedling containers in 7.5-L containers full of water (Fig. 1B). Water was replaced in the flooded containers weekly. Of the initial 205 seedlings planted in May, the seedlings not used in the main experiment ($n = 61$) were irrigated and used for destructive sampling of plant traits (more details below).

At SOS 2021, height, stem diameter and seedling vigor were measured on all seedlings and at SOT 2021, volumetric water content (VWC; 25 measurements, one measurement per seedling) was measured on a subset of randomly selected seedlings across the two species and four blocks (details for each measurement are below). Height was measured from the media surface along the longest shoot and diameter was measured as the average of two perpendicular stem diameter measurements at 2 cm above the media surface. During the treatment period, eight 'sampling events' occurred just before each drought and flood treatment length was ended (end of treatment, EOT; Fig. 1A). During each EOT sampling event, all seedlings for which treatments were ending (plus a randomly selected pair of cedar and fir control seedlings in each block) were measured for VWC, shoot midday water potential (Ψ_{MD}), height, stem diameter and vigor. Fir in the drought treatment were slow to dry down (see Results), therefore we extended the longest drought treatment (initially 53 days) for fir by an additional 13 days. At the end of the growing season (15 October, end-of-season, EOS 2021), 36 days after the final treatment had ended, all measurements except for Ψ_{MD} were repeated on all the seedlings. On 3 November 2021, all seedlings were moved outside of the greenhouse for overwintering and the space between containers was packed with straw to insulate roots from freezing damage (van Kampen et al. 2022). In spring 2022 (19 May, SOS 2022), the straw was removed and the seedlings were irrigated through fall 2022 (29 October, EOS 2022).

Quantifying survival and growth

Vigor assessments were conducted at SOS 2021, each EOT 2021, EOS 2021, SOS 2022 and EOS 2022 (Fig. 1A). Vigor was estimated visually as the percentage of brown foliage in 5% increments relative to all the foliage on the seedling. A seedling with 100% brown foliage was recorded as dead. To determine how growth was impacted by the drought and flood treatments, in addition to the first measurement at SOS 2021, we measured height and stem diameter after each EOT 2021 as well as at EOS 2021 and EOS 2022.

Environmental and physiological measurements

VWC was measured with a moisture meter (HydroSense II, Campbell Scientific, Logan, UT, USA) on a subset of seedlings at SOT 2021, each EOT 2021 and EOS 2021. For each seedling, we conducted two measurements by inserting the 12-cm tines vertically into the media. During EOT 2021 sampling events, VWC was paired with Ψ_{MD} measurements to quantify the minimum water potential experienced by each measured seedling in response to our treatments and to help determine the onset of hydraulic stress and identify lethal hydraulic thresholds (Hammond et al. 2019). Ψ_{MD} was measured on the seedlings for which treatments were ending (four drought- and four flood-treated individuals of each species), plus one random control seedling per species per block (24 total seedlings per sampling event). For each seedling, samples for Ψ_{MD} were collected between 11:00 and 13:00 h by cutting two current-year shoots (10 to 20 cm long) that were then enclosed in a foil-lined plastic bag and stored in a cooler during transport to the lab for measurement. Within 2-h of collection, the Ψ_{MD} of the shoots was measured with a Scholander pressure chamber (Model 1000; PMS Instruments, Albany, OR, USA).

We observed rapid declines in VWC for cedar but not fir. Therefore, to quantify evapotranspiration, on Day 16 of the treatments (22 July 2021; day-of-year 203), we measured whole plant evapotranspiration rates of irrigated controls and drought-treated cedar and fir. Seedlings from one control and two drought treatments for each species were randomly selected from each block. Measurements were conducted on a clear, sunny day. To estimate water loss, the whole container including the seedling was weighed in the morning (08:00 to 09:00 h) and evening (20:00 to 21:00 h) to the nearest 0.001 kg (Catapult 1000, Ohaus, Parsippany, NJ, USA). We compared total evapotranspiration rates and evapotranspiration rates standardized by seedling height to partly account for differences in plant size.

To estimate how tightly each species could close its stomata during drought, we harvested shoots from four drought-treated seedlings and six control seedlings per species for minimum epidermal conductance (g_{min}) measurements ($n = 20$ shoots total). Current-year shoots (10 to 20 cm long) were

harvested at 9:00 h on 19 August 2021 (Day 52 of the drought treatment for the drought-treated plants). Shoots were placed in a black plastic bag containing a moist paper towel and transported to the lab to be recut underwater and rehydrated overnight. The following morning, we excised ~3 cm long samples from the ends of these shoots, sealed the cut ends with petroleum jelly and suspended them in a box with fans cycling air (23 to 24 °C, 73% to 76% relative humidity). Note that cedar needles are appressed to the entire 3 cm shoot, suggesting that for cedar, g_{min} is an estimate of leaf conductance. For fir, as much as about 10% of the sample area could be bark area, suggesting that g_{min} includes a small amount of bark conductance but is mostly leaf conductance. For 1.5 h, we measured leaf mass (PRACTUM224-1S, Sartorius AG, Göttingen, Germany), air temperature and relative humidity (HOBO MX1101 Data Logger, Bourne, MA, USA) every 15 to 20 min. Leaf area was determined at the end of the measurements with a digital scanner and was used in the final calculation of g_{min} (Sack and Scoffoni 2010).

To determine the leaf TLP and capacitance at full turgor (C_{FT}) for each species, we conducted leaf pressure-volume (PV) curves on the extra seedlings not included in the main experiment during two sampling campaigns: in mid-June and again in mid-August, 2021 (Sack et al. 2010). PV parameters were determined by air-drying leaves of both species on the lab bench. For this method, during each sampling campaign, five to six shoots (25 to 40 cm long) per species were harvested in the early evening and their stems were recut underwater and placed in floral water tubes to rehydrate overnight. The next morning, one 10 to 20 cm shoot was cut from each larger shoot and was placed in a humidified Whirl-Pak bag. The shoot water potential (Ψ_{shoot}) was measured with the pressure chamber and paired with measurements of shoot mass. Shoots were then removed from their bags, placed on the bench near circulating fans to dry them further (10 to 120 min). They were then placed back into the Whirl-Pak bags and left to equilibrate for 10 to 30 min before remeasurement of Ψ_{shoot} and mass. TLP and C_{FT} were estimated following the protocol from Sack et al. (2010).

To quantify the declines in xylem hydraulic conductivity and water storage associated with drought stress, we tested if xylem relative water content (RWC) declined predictably with Ψ_{shoot} in a separate bench dry-down experiment. RWC is a rapid measurement of water status related to mortality (Sapes and Sala 2021; Mantova et al. 2023). Many conifers have relatively simple xylem composed almost completely of tracheids that can transport water. Therefore, xylem RWC is a reasonable approximation of the percentage of embolized xylem tracheids (Rosner et al. 2019). RWC measurements were conducted on a randomly selected subset of extra seedlings from 19 August to 20 August 2021. We harvested three to four shoots (>20 cm long) from seven seedlings per species and cut ends were immediately placed in floral water tubes. Shoots were recut underwater and left to rehydrate overnight. The next morning, the ends of four randomly selected shoots for each species were recut and sealed with petroleum jelly, equilibrated in plastic bags before measuring Ψ_{shoot}. To estimate xylem RWC, we then cut a 2-cm long section from the middle of the stem, removed the bark with a razor blade and immediately measured the mass of the xylem sample. The rest of the shoots were laid out on the bench and left to dry in ~12-h intervals. After each 12-h interval, xylem samples from two shoots of each species were weighed, as above and Ψ_{shoot} was measured. After each measurement, xylem samples were vacuum infiltrated with distilled water for 24 h and reweighed to obtain saturated mass. RWC was calculated relative to the saturated mass of each xylem sample.

Statistical analysis

To assess how the drought and flood treatments impacted the percent brown foliage, we modeled how treatment length relates to percent brown foliage by species using smoothing spline models (maximum knots set to 5) to capture the wide range of variability in response patterns. Significant differences between models were determined from nonoverlapping 95% confidence intervals. In addition to these percent-brown-foliage models that characterize the average amount of brown foliage on a seedling, we also assessed how treatment length could predict the probability of mortality of individual seedlings (seedlings with 100% brown foliage) using logistic regression. To compare species and treatments, we used the percent brown foliage and mortality models to predict the number of days of exposure to treatments that lead to 25% or 50% brown foliage and mortality when they reached those levels. To determine how growth was impacted by treatment length, we calculated the relative height and diameter of each seedling at EOS 2021 and EOS 2022 relative to SOS 2021. Relative height and diameter were compared with 95% confidence intervals for growth of control seedlings. One fir tree from the shortest drought treatment length was excluded from all analyses because it died shortly after treatments began, but before soil moisture declined.

To determine if evapotranspiration and g_{min} differed by species and treatment, we used an analysis of variance (ANOVA; $\alpha = 0.05$ for all significance tests) with an interaction between species and treatment. If the interaction was significant, a Tukey's Honest Significant Difference (HSD) test was used to compare means. If the interaction was not significant, the interaction was removed and only main effects were assessed. To determine if drought stress could predict tree ultimate tree vigor (and mortality) at the end of the study for both cedar and fir, we tested if the minimum water potential experienced during 2021 treatments (EOT 2021 Ψ_{MD}) predicted percent brown foliage at EOS 2022 using Michaelis–Menten models and 95% confidence intervals from 1000 bootstraps. To test if xylem RWC declined with Ψ_{shoot} for cedar and fir in the bench-top dry down experiment, we built linear models predicting RWC as a function of Ψ_{shoot} including testing for an interaction with species. All statistics and figures were conducted using R version 4.3.0 (R Core Team 2023). Other packages used in data organization, visualization and analysis were: "dplyr" (Wickham et al. 2022), "doBy" (Halekoh and Højsgaard 2022), "npreg" (Helwig 2022) and "nlstools" (Baty et al. 2015).

Results

Vigor and growth responses to drought and flood

Overall, we found that in the drought treatments, VWC declined significantly for both species relative to their controls and more so for cedar than for fir (Fig. 2A). During the first sampling event on treatment Day 8, we found VWC had declined from an overall pretreatment level across both species of 18.9 ± 1.2% (mean ± standard error; $n = 26$ randomly

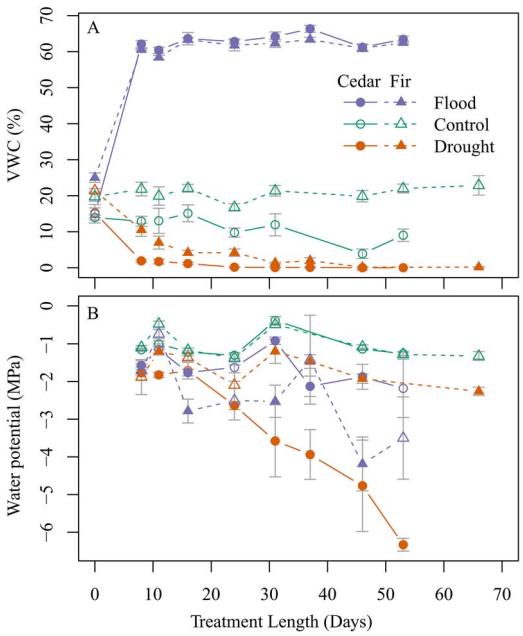

Figure 2. (A) Mean volumetric water content (VWC) of container media or (B) midday leaf water potential (MPa) at the end of each treatment length for cedar and fir. Each data point represents the mean with standard error bars (representing one standard error) three to four individuals taken just before a treatment was ended. When drought and flood treatments were ended, seedlings were irrigated the same as controls. Filled symbols indicate statistically significant differences (nonoverlapping 95% confidence intervals) from each species control group at each treatment length. Due to missing control data at treatment length 37, control data for treatment length 31 were used for statistical significance tests here. Note that the drought treatment for the fir seedlings was extended an additional 13 days (see Materials and methods).

selected seedlings) down to 1.9 ± 0.3% for drought-treated cedar and to 10.5 ± 1.8% for drought-treated fir (Fig. 2A). However, midday leaf water potential for drought-treated cedar was already significantly lower than controls in the first two sampling intervals but did not decline below −2 MPa until after 16 days of drought before dropping consistently beyond that point (Fig. 2B). In contrast, although water potential of drought-treated fir was significantly below controls in almost all sampling events, fir avoided a long-term decline and maintained midday leaf water potentials near −2 MPa even in the longest treatment length (Fig. 2B). In contrast to the drought, by the nature of the experimental design, a significant increase in VWC for flood treatments occurred quickly and maintained an average of 63.0 ± 0.7% for cedar and 61.6 ± 0.6% for fir for the duration of the treatment period (Fig. 2A). Flood-treated cedar and fir typically had significantly lower water potentials than their controls and this difference was larger for fir (Fig. 2B).

Generally, drought treatments resulted in larger increases in percent brown foliage for cedar than fir (Fig. 3A and B). Overall mortality rates from drought across all treatment lengths (individual seedlings were classified as dead if they reached 100% brown foliage) were similar for both species (cedar: 4 of 32; fir: 3 of 31), but mortality was only clustered at longer drought lengths for cedar (Fig. S1A and B, available as Supplementary data at *Tree Physiology* Online). Both cedar and fir experienced significant increases in brown foliage at EOT reaching 25% brown foliage by Day 35 (cedar; Fig. 3A) or Day 65 (fir; Fig. 3B). However, only cedar experienced a significant increase in mortality by the end of the first year (Fig. S1A, available as Supplementary data at *Tree Physiology* Online). In the following year, cedar foliage browned significantly more for longer treatment lengths and exceeded 50% brown foliage if it had experienced a drought treatment of more than 49 (SOS 2022; not shown) to 50 days (EOS 2022; Fig. 3A). However, mortality did not change in the second year (Fig. S1A, available as Supplementary data at *Tree Physiology* Online) and cedar seedlings that had experienced drought treatment lengths < 50 days had mostly recovered (Fig. 3A). In contrast to cedar, by the EOS 2022, mean brown foliage of fir did not increase beyond EOT and fir seedlings mostly recovered from the drought treatment and had little to no brown foliage (Fig. 3B) and only a small increase in mortality by EOS 2022 (Fig. S1B, available as Supplementary data at *Tree Physiology* Online).

Generally, flood treatments resulted in more rapid and sustained increases in percent brown foliage (Fig. 3C and D) and ultimately more mortality (100% brown foliage) than the drought treatments for both species (Fig. S1C and D, available as Supplementary data at *Tree Physiology* Online). Across all flood treatment lengths, cedar experienced 59% mortality (19 of 32) and fir experienced 93.8% mortality (30 of 32). Cedar and fir experienced significant browning of foliage and reached 25% brown foliage after 21 days for cedar (EOT, Fig. 3C) and 27 days for fir (EOT, Fig. 3D). Cedar also reached significantly higher levels of percent brown foliage at EOT than fir as the flood progressed beyond ∼30 days (Fig. 3C and D). Despite cedar having generally more brown foliage at EOT than fir, we found that many cedar continued to have increases in brown foliage by EOS 2021 (Fig. 3C), but they still survived that first year and morality did not increase until the end of the second year (Fig. S1C, available as Supplementary data at *Tree Physiology* Online). In contrast, brown foliage of fir continued to increase significantly following the treatments (Fig. 3D) and experienced extensive mortality by the end of the first year (EOS 2021) which got even more extreme in the second year (Fig. S1D, available as Supplementary data at *Tree Physiology* Online). By EOS 2022, our models predicted 50% mortality of cedar that had been exposed to 23.1 days of flooding, whereas fir reached 50% mortality if it had been exposed to only 7.4 days of flooding (Fig. S1C and D, available as Supplementary data at *Tree Physiology* Online). We found no strong differences between SOS 2022 and EOS 2022 estimates of percent brown foliage (not shown), but we did find that mortality continued to increase between EOS 2021, SOS 2022 and EOS 2022 (Fig. S1C and D, available as Supplementary data at *Tree Physiology* Online).

Cedar started the study (SOS 2021) significantly larger than fir in both height and diameter (*P*-values < 0.001; Fig. S2A and B, available as Supplementary data at *Tree Physiology* Online); however, to account for different starting sizes, we used SOS 2021 as a baseline for all relative height and diameter metrics. In response to drought treatments, the relative height of cedar seedlings at EOS 2021 was trending lower than controls if exposed to treatment lengths of 24 days and was consistently below relative height of control seedlings for all treatment lengths beyond 37 days (Fig. 4A). However, by the end of the following year (EOS 2022), cedar that had survived in all but the longest drought treatment matched the total relative height of the controls, even if its relative height

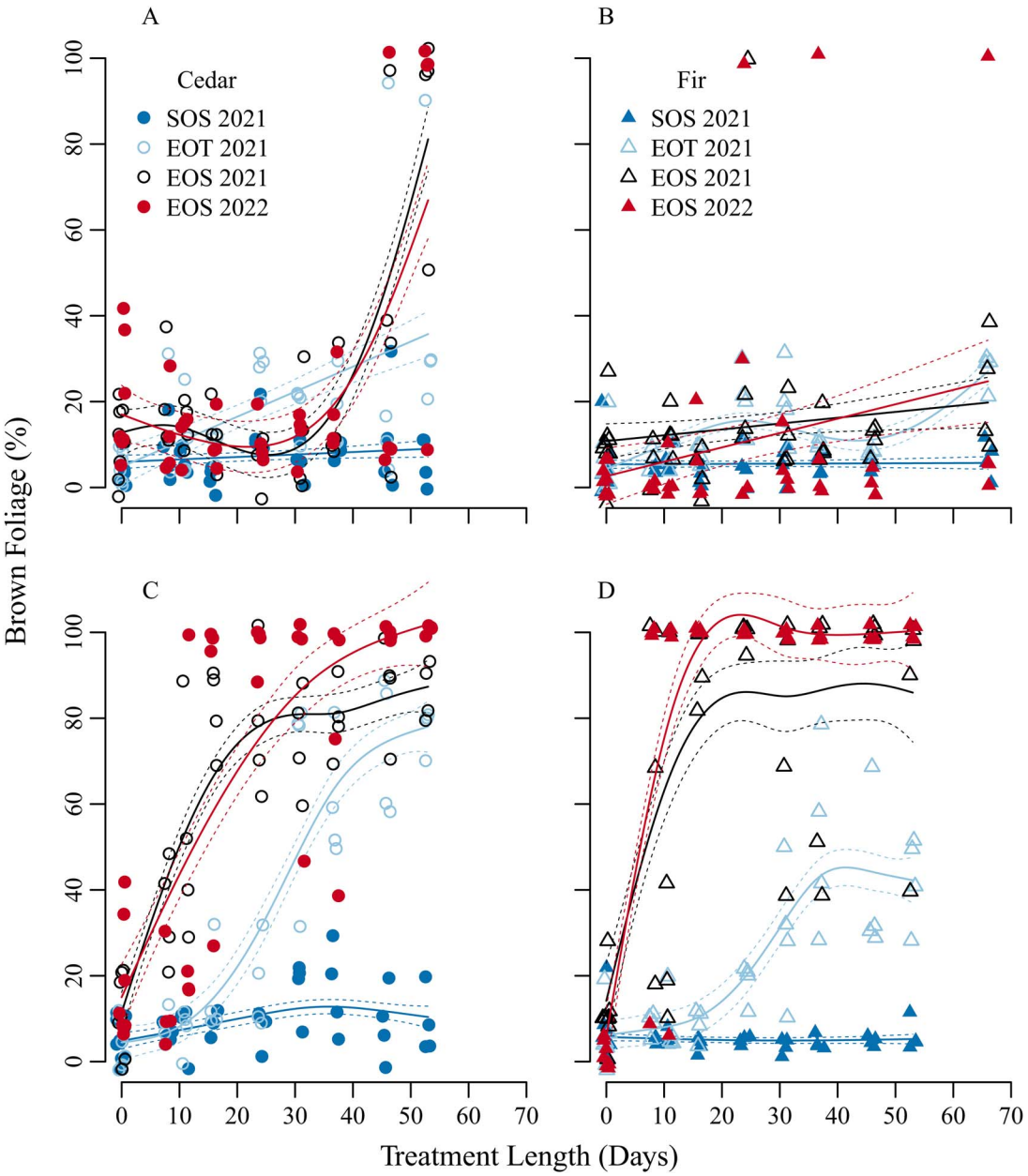

Figure 3. Percent brown foliage as measured at various times throughout the study in response to different treatment lengths of droughts (A and B) and floods (C and D) for both cedar (A and C) and fir (B and D) applied in 2021. Brown foliage measurements were conducted in 2021 at the start-of-season (SOS), immediately following the end-of-treatment (EOT) and at the end-of-season (EOS). SOS and EOS measurements were repeated in 2022 but were very similar so only EOS 2022 data are shown here. Each point represents the percent brown foliage estimate for one seedling (100% = mortality). Models represent smoothing splines to show the overall patterns in the data with 95% confidence intervals as dotted lines. Statistical significance between models was estimated by nonoverlapping 95% confidence intervals. Points offset slightly to avoid overlapping symbols.

had been lower than that of controls at EOS 2021 (Fig. 4A). Height growth of fir was mostly complete prior to initiating treatments (SOT) and, accordingly, relative height showed no response to the drought treatments in 2021 (Fig. 4B) and, as with cedar, did not differ from controls by EOS 2022 (Fig. 4B). In response to flood treatments, we found that cedar relative height by EOS 2021 was below controls if they had been exposed to treatment lengths of only 11 days and that surviving cedar beyond that threshold were unable to match relative height of the controls in the following year (EOS 2022; Fig. 4C). Relative height of fir by EOS 2021 showed only minor effects of the flooding at the longest treatment length (Fig. 4D) and by EOS 2022, the two surviving fir (treatment lengths of 8 and 11 days) matched controls (Fig. 4D).

In response to drought treatments, relative diameter of cedar appeared to be more resilient than height and was only impacted in the longest treatment group by EOS 2021 and, as with relative height, all surviving cedar matched relative diameter of controls in the following year (Fig. S3A, available as Supplementary data at *Tree Physiology* Online). Drought treatments did not reduce fir relative diameter growth in the treatment year compared with controls, and, as with cedar, all surviving fir matched the relative diameter of control seedlings the following year (Fig. S3B, available as Supplementary data

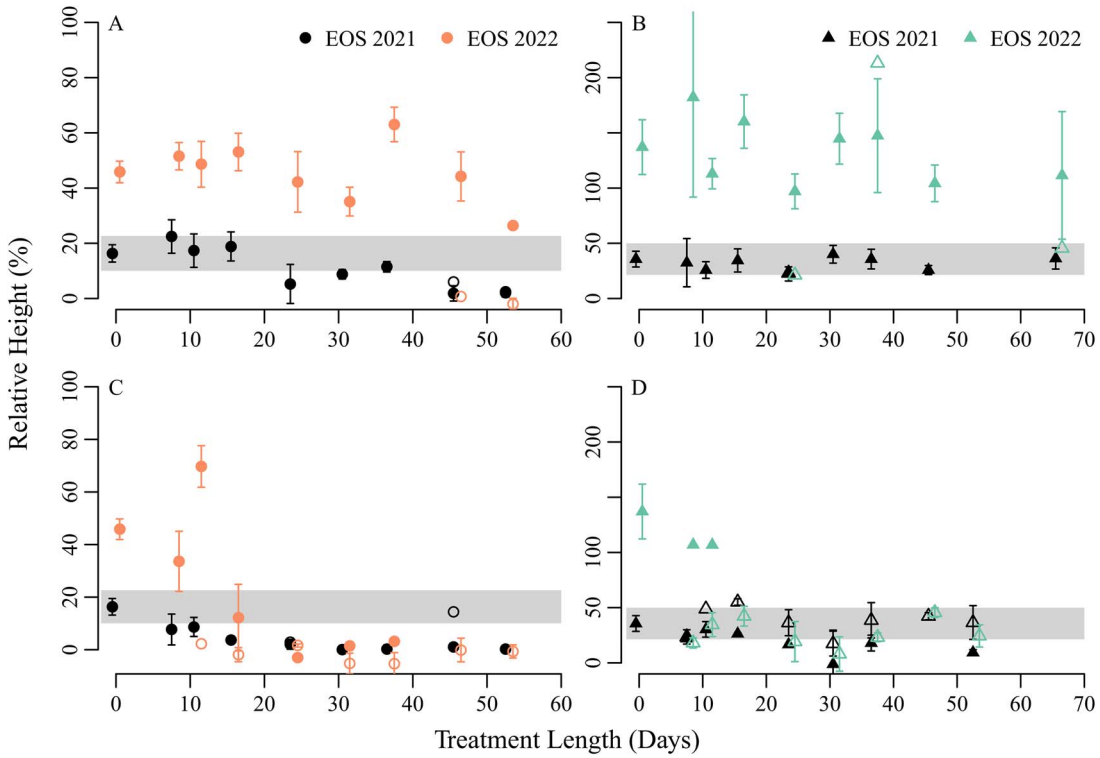

Figure 4. Changes in relative height in response to droughts (A and B) and floods (C and D) of varying lengths for cedar (A and C) and fir (B and D). In each panel, relative height at the end of the 2021 and 2022 seasons is calculated relative to the start of the growing season in 2021. Closed symbols represent seedlings that were alive (<100% brown foliage) during the measurement and open symbols represent seedlings that were dead (100% brown foliage). Points represent means and error bars represent ± one standard error. For treatment length = 0 in all panels, there were eight seedlings to calculate the mean value. At all other treatment lengths, as many as four seedlings were included in the mean (varies based on number living and dead). Standard error bars are represented only when there is more than one seedling. Color bands represent 95% confidence intervals (mean ± two standard errors) of the control seedlings for each species and year as reference for when the other points fall outside of that range. Note *x*- and *y*-axis lengths differ between panels. Points offset slightly on the *x*-axis for clarity.

at *Tree Physiology* Online). In response to flooding, relative diameter of cedar was only minorly impacted beyond treatment lengths of 31 days by EOS 2021 although only the two shortest treatment levels (8 and 11 days) were able to recover to match controls by EOS 2022 (Fig. S3C, available as Supplementary data at *Tree Physiology* Online). Flood treatments drove a large amount of mortality in fir and by EOS 2021, the surviving seedlings exhibited reduced relative diameter compared with controls if they had been exposed to just 8 days of flooding (Fig. S3D, available as Supplementary data at *Tree Physiology* Online). The two fir that survived the flooding through EOS 2022 matched the relative diameter of control seedlings by EOS 2022 (Fig. S3D, available as Supplementary data at *Tree Physiology* Online).

Water use and stress resistance characteristics

We used two proxies for daily evapotranspiration in this study. Percent change in combined container and plant mass in 1 day (Fig. 5A) and, to partly account for size differences between the tree species (Fig. S2, available as Supplementary data at *Tree Physiology* Online), change in mass standardized by seedling height (Fig. 5B). We found that control cedar had the largest percent decline in mass, but fir in both treatments and drought-treated cedar all had similar percent declines in mass (Fig. 5A). In contrast, when standardizing mass lost by seedling height, we found that there was no difference between controls of cedar and fir, but drought-treated fir and cedar lost significantly less than their controls (Fig. 5B).

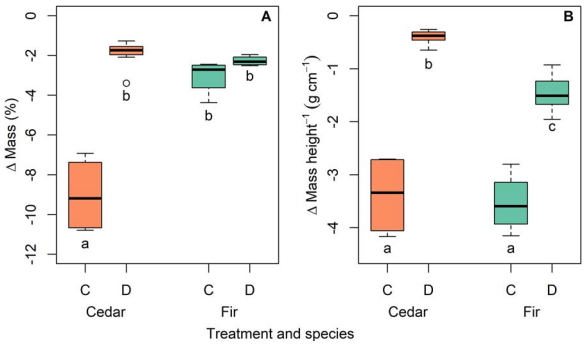

Figure 5. Evapotranspiration estimates from 22 July 2021 according to species and treatment (control, C, $n = 4$ per species; drought, D, $n = 8$ per species) on Day 16 of the drought. Evapotranspiration was estimated as the percent change in mass between an early morning and evening measurement of container and plant mass (A) or as the total mass loss (g) per height of the seedling (cm) to account for some variation in tree size (B). Boxes represent the median and middle 50% of values with whiskers extending to data points as much as 1.5 times the interquartile range. Groups that do not share a letter within a panel are statistically significantly different (Tukey's Honest Significant Difference *P*-value < 0.05).

We found that cedar had a significantly higher g_{min} than fir ($P \leq 0.001$), but there was no significant difference between drought-treated and control seedlings of the same species (Fig. 6). PV curves from leaves revealed that cedar

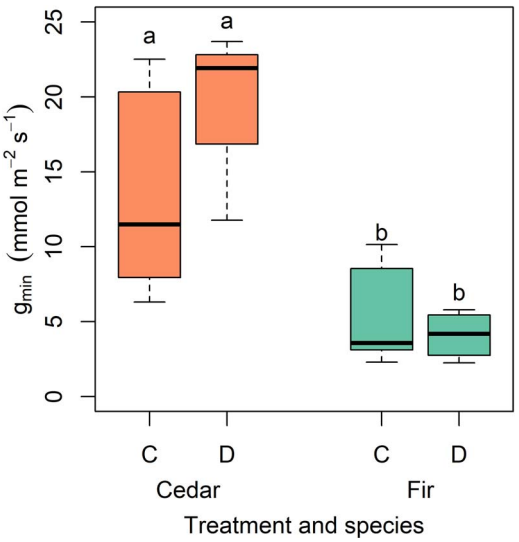

Figure 6. Minimum epidermal conductance (g_{min}) for fir and cedar trees on 19 August 2021. Ten leaves were sampled per species from irrigated control trees (C; $n = 6$) and drought trees (D; $n = 4$) on Day 52 of drought. Boxes represent the median and middle 50% of values with whiskers extending to cover data points as much as 1.5 times the interquartile range. Groups that do not share a letter are statistically significantly different (Tukey's Honest Significant Difference P-value < 0.05).

had significantly higher C_{FT} than fir regardless of month (cedar: 0.124 ± 0.004 MPa^{-1}; fir: 0.056 ± 0.024 MPa^{-1}; P-value < 0.001; mean $\pm$ standard error). Furthermore, in June, cedar had significantly lower TLP (-2.19 ± 0.22 MPa) than fir (-1.52 ± 0.07 MPa; P-value $= 0.009$), but by August, irrigated seedlings of both species had similar TLP (cedar: -1.44 ± 0.05 MPa; fir: -1.52 ± 0.13 MPa). Our lab bench dry-down of shoots suggested that both species lose water from the xylem at similar rates during drought (overall slope: $8.9 \pm 0.6\%$ MPa^{-1}), but at any given Ψ_{shoot}, on average, fir had 13.6% lower RWC than cedar (Fig. S4, available as Supplementary data at *Tree Physiology* Online).

Indicators of mortality

When testing the Ψ_{MD} that leads to increases in brown foliage and ultimately mortality of cedar and fir, we found that cedar could reach Ψ_{MD} below -6 MPa during the drought treatment without significant increases in percent brown foliage by EOS 2022 (Fig. 7A). In contrast, fir experienced increases in percent brown foliage around -3 MPa (Fig. 7B). However, due to the longer dry-down rates for fir (see discussion), this model is heavily influenced by the only fir seedling to reach water potentials below -3 MPa and should be interpreted with caution (Fig. 7B). As expected, Ψ_{MD} was not a reliable indicator of stress for flooded seedlings yet, regardless of species, we did see complete mortality (100% brown foliage) of seedlings whose water potentials declined below -2 MPa (Fig. S5A and B, available as Supplementary data at *Tree Physiology* Online).

Discussion

Response to drought

Contrary to our expectation, we found that cedar did not avoid drought stress longer than fir. Instead, cedar drew down VWC quickly (Fig. 2A) and 8 to 16 days after reaching low VWC, water potential declined below the TLP (Fig. 2B). In contrast, fir experienced almost no drought stress, despite us extending the final drought treatment an additional 13 days (Fig. 2). The lower water potentials experienced by cedar aligned with the increase in brown foliage (Fig. 7A) and mortality (Fig. S1A, available as Supplementary data at *Tree Physiology* Online) beyond 46 days of drought (Fig. 3A). Unfortunately, we have limited data for fir at low water potentials, so our data are inconclusive related to our second hypotheses although they do suggest that for similar levels of water potential, cedar had less brown foliage and lower mortality than fir (Fig. 7). Although few fir experienced drought stress, we have some evidence to support our third hypotheses that growth of surviving cedar was more resilient than fir because most cedar that experienced drought stress recovered to match height (Fig. 4A) and diameter (Fig. S3A, available as Supplementary data at *Tree Physiology* Online) of controls during the treatment year or the recovery year. Finally, we found support for our fourth hypothesis suggesting that cedar's higher water-use (Fig. 5) may be related to higher g_{min} (Fig. 6) after stomatal closure and an increased reliance on leaf capacitance. We expand on all these points below.

We found that the drought progressed rapidly for cedar and that many cedar seedlings reached water potentials far below published P_{50} values (-3.57 MPa for seedlings (Tyree and Dixon 1986)) as early as 31-day treatment lengths (Fig. 2B). The rapid decline in VWC for cedar relative to fir (Fig. 2A) may have been driven by the larger size of the cedar during this study that drove higher water use (1.7× and 0.3× larger initial height and diameter (SOS 2021), respectively; Fig. S2, available as Supplementary data at *Tree Physiology* Online). However, evapotranspiration of control seedlings when standardized by seedling height did not show any differences between species (Fig. 5). Although future research should confirm this on a leaf-area basis, our data suggest that at least when well-watered, there are similar rates of water loss by size between species. This contrasts with cedar seedlings that were experiencing drought; they showed significantly lower evapotranspiration than fir seedlings experiencing drought (likely because the fir still had more water at Day 16 of the drought when this was measured). It is also possible that different stomatal behaviors caused cedar to maintain transpiration at lower water potentials. Although we do not have data on diurnal stomatal behavior, when stomata were closed, cedar's higher g_{min} still suggest that cedar may have been relying on higher C_{FT} to buffer daily declines in water potential (Lamont and Lamont 2000; Scholz et al. 2011) and therefore transpiring more water than fir during the drought treatments driving continued declines in VWC and water potential.

These results support other work that suggests cedar may be anisohydric and therefore is more likely to experience, and is adapted to survive, low water potential during drought (Brodribb et al. 2014). For example, many cedar seedlings in our study surpassed published values of P_{50} (-3.57 MPa (Tyree and Dixon 1986)) by as much as 2 MPa with little or no increase in mortality (Fig. 7A). As seen in other studies (Collier and Boyer 1989; Edwards and Dixon 1995), cedar expressed a high degree of plasticity in TLP that can acclimate to reach relatively low values for the northeastern US (below -3 MPa). Although we only have TLP estimates from control trees throughout our study, drought-treated cedar may have acclimated their TLP to limit turgor loss (Bartlett et al. 2014).

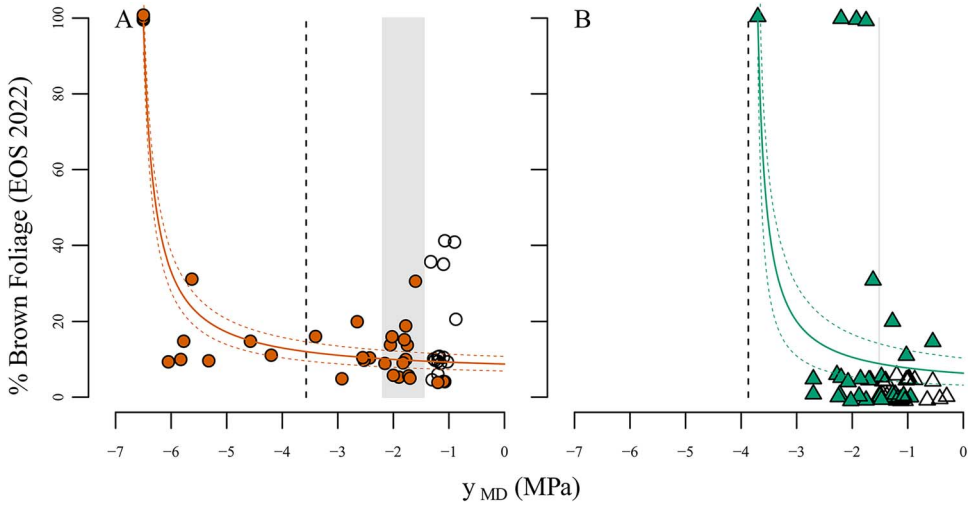

Figure 7. End of treatment (EOT) Ψ_{MD} of drought-treated and irrigated cedar (A) and fir (B) compared with percent brown foliage assessed at end of the 2022 growing season (EOS 2022); 100% brown foliage indicates mortality. Gray bands span the two mean estimates of turgor loss point (TLP) for each species (June and August sampling periods) and the dashed black vertical lines indicate the published P_{50} (water potential the leads to 50% loss of xylem hydraulic conductivity) for each species from Tyree and Dixon (1983) and Hacke and Jansen (2009). Curved models are represented as solid lines with dotted lines for 95% confidence intervals. Open symbols are the irrigated control seedlings and closed symbols are drought-treated seedlings. Note: points offset slightly on the *y*-axis to avoid perfectly overlapping symbols.

Our data on the RWC of xylem showed a marked decline for both cedar and fir just above their published P_{50} values (Fig. S4, available as Supplementary data at *Tree Physiology* Online), suggesting that RWC is capturing the rapid spread of embolisms and loss of stored water (Tyree and Yang 1990; Mcculloh et al. 2014; Rosner et al. 2019). Furthermore, for cedar we found that at leaf Ψ_{MD} below −6 MPa, there was a large increase in mortality (Fig. 7) as was found in other studies of conifers at PLC values exceeding p80 (Hammond et al. 2019). Although the limited data for cedar suggest that p80 may be closer to −4.25 MPa (Tyree and Dixon 1986), our results still support other work with cedar suggesting that hydraulic failure from low water potential caused the mortality (Zhao et al. 2013). However, hydraulic segmentation (as documented in some species; Johnson et al. 2016, Wason et al. 2018), radially sectored hydraulic pathways that allow individual roots to supply water to individual shoots (observed in cedar; Larson et al. 1994), or within-canopy variation in vulnerability to cavitation (Johnson and Brodribb 2023; Tonet et al. 2024) may explain why some cedar had partial canopy mortality at moderate drought treatment lengths and were able to recover the following year (Fig. 3A). Regardless, we found that cedar growth was quite resistant to the effects of the drought treatments, as it had only minor effects on height (Fig. 4A) and stem diameter (Fig. S3A, available as Supplementary data at *Tree Physiology* Online) growth in the longest treatments at the end of the drought year (EOS 2021) and almost complete recovery (i.e. no lagged effects) by the end of the following year (EOS 2022). Although there may be lagged effects on carbon allocation below ground (Hagedorn et al. 2016), lags may be more common in canopy trees (Kannenberg et al. 2019; Beloiu et al. 2022). Combined, these results suggest that the drought treatments in this study did not result in a carbon limitation to above-ground growth. Furthermore, unlike species such as fir and pine (*Pinus* spp.) that set buds for next year's growth relatively early and may have lagged effects on growth the following year, cedar seedlings have continuous growth and can recover quickly from drought stress even within a year, particularly if there are no other limitations on growth (e.g. competition, nutrients) (Andivia et al. 2020; van Kampen et al. 2022).

In contrast to cedar, the onset of drought stress progressed more slowly for fir, causing us to extend the last drought treatment length for that species by 13 days to further reduce VWC and achieve lower water potentials (Fig. 2). Even with this extended drought treatment lasting a total of 66 days without water and achieving extremely low VWC, only one fir seedling reached water potentials close to published P_{50} values (−3.87 MPa for seedlings (Hacke and Jansen 2009)). Our xylem RWC data suggest that like many conifers (Mcculloh et al. 2014), these species may also have a similar capacity to release water from tissues during drought (capacitance). Therefore, the slow decline in VWC and water potential for fir is likely driven by their smaller size in the present study (potentially lower leaf area, discussed above), their lower g_{min} and lower leaf C_{FT}. These factors may have compounded to result in a slow decline in water potential typical of isohydric species, especially following stomatal closure in response to drought (Duursma et al. 2019) and allowing this species to avoid catastrophic hydraulic failure. Indeed, other studies have found that in ambient temperatures, fir was able to maintain photosynthesis and growth down to at least 5% VWC (Reich et al. 2018, 2022) though there is very little information about more extreme conditions below 5% VWC. Regardless, future work should focus on quantifying stomatal behaviors that optimize carbon gain and/or water conservation during drought stress (Cocozza et al. 2016).

In contrast to cedar's strategy of resisting and recovering from drought, our results suggest a strategy of drought avoidance for fir. Indeed, fir seems less able to resist and recover from low water potentials since it has a relatively high TLP and, although not assessed in this study, others report a lower plasticity in TLP (Bartlett et al. 2014). Like some other conifers (Oberhuber 2017), the growth phenology of fir may support a strategy of avoidance, as it completes height growth before the likelihood of drought increases

in late summer (Rossi et al. 2009), whereas cedar height growth is continuous (van Kampen et al. 2022). However, fir rarely experienced extreme water potentials in this study and growth was not impacted in the current or following year (Fig. 4B and Fig. S3B, available as Supplementary data at *Tree Physiology* Online). In contrast to canopy trees (Kannenberg et al. 2019), our results are in line with the limited but less consistent evidence for lagged effects on seedling tree growth (Beloiu et al. 2022), including species that finish growth earlier in the growing season like fir (Andivia et al. 2020). Therefore, despite our limited data for fir at low water potentials, our results and other recent studies suggest that fir is adapted to avoid drought conditions rather than resist them (D'Orangeville et al. 2018; Vaughn et al. 2021). However, if droughts in the field happen earlier in the growing season, they may disproportionately impact species that stop growth early in the season like fir (Kozlowski and Ward 1961) compared with species with continuous growth like cedar (van Kampen et al. 2022).

Response to flood

We also assessed our four hypotheses relative to floods. We found that the rapid and sustained high VWC (Fig. 2A) resulted in fluctuating water potentials that diverged from controls within 16 days for both species, but that were generally lower for fir than cedar (Fig. 2B). These results suggest that cedar may be better able to avoid or tolerate flood stress thus supporting our first hypothesis. This aligns with results relative to our second hypotheses with clear evidence that cedar experienced overall higher survival (Fig. S1C and D, available as Supplementary data at *Tree Physiology* Online) and lower amounts of brown foliage (Fig. 3C and D) than fir when exposed to floods of similar lengths. Indeed, almost all fir trees exposed to floods died (94% mortality) and, unlike cedar (Fig. 3C), no fir survived through the recovery year with partial brown foliage (Fig. 3D). We did not find support for our third hypotheses apparently because many cedar survived floods with partial canopies and therefore had reduced growth in the treatment and following year, whereas the few fir trees that survived floods maintained full canopies and matched growth of control trees. We found little to no support for our fourth hypothesis to suggest that hydraulic traits (primarily water potential; Fig. S5, available as Supplementary data at *Tree Physiology* Online) may relate to flood responses of cedar and fir. Combined, these results suggest a stronger threshold response for fir than cedar in response to floods, but cedar may maintain overall higher survival despite reductions in canopy greenness and growth. We expand on all of these points below.

In contrast to the drought, we found that flood treatments had much more rapid and sustained effects on the survival (Fig. S1, available as Supplementary data at *Tree Physiology* Online) and growth (Fig. 4 and Fig. S3, available as Supplementary data at *Tree Physiology* Online) of both species. However, as with drought, our data suggest that cedar may be more flood tolerant than fir. For cedar, there were many seedlings with partial surviving canopies after the first year (Fig. 3C) and, although most of them died by the following spring, some did survive through the recovery year (total of 59% cedar mortality from all flood treatments; Fig. S1C, available as Supplementary data at *Tree Physiology* Online). However, the surviving seedlings with partial canopies had extremely reduced height and diameter growth (Fig. 4C and Fig. S3C, available as Supplementary data at *Tree Physiology* Online), suggesting extensive stress. As with drought, radially sectored hydraulic pathways (Larson et al. 1994) may have allowed some roots to survive and support these partial canopies. The cedar seedlings that survived flood treatments of ≤ 11 days had minor effects on height and diameter growth in the flood year (EOS 2021), mostly recovered their canopies by the start of the next spring (SOS 2022) and had mostly recovered to match total height and diameter growth of control seedlings the second year (EOS 2022). Overall, flood-treated cedar in our study experienced lower survival than other flood-duration studies, one of which lasted 66 days (Yamamoto and Kozlowski 1987) and the other that lasted as many as 105 days without mention of mortality (Keller et al. 2023). At least part of this apparent contradiction may be driven by the strong lagged response in mortality that we observed, which is not captured by shorter term studies (Fig. S1C, available as Supplementary data at *Tree Physiology* Online). This highlights the need for longer term monitoring efforts when assessing tree survival in response to flooding (Green 1947).

Our limited physiological data on the flood treatments suggest that the decline in water potential near 16 days (Fig. 2B) may signify the onset of physiological stress that aligns with percent brown foliage exceeding 50% the following year (Fig. 3C) and increasing mortality (Fig. S1C, available as Supplementary data at *Tree Physiology* Online). Indeed, these results support other work suggesting that flooding can cause root mortality thus limiting water uptake and leading to desiccation of the canopy and increased sensitivity to subsequent drought from reduced root systems (Kozlowski 1997; Chen et al. 2023; Mattos et al. 2023). Indeed, although there was no relationship between water potential and mortality above −2 MPa, all flood-treated seedlings with water potentials below −2 MPa died (Fig. S5, available as Supplementary data at *Tree Physiology* Online). Future studies could also sample flood-treated trees in their recovery period to see if declining water potential post-flood is a driver of mortality (Menezes-Silva et al. 2019). However, there are a range of complex responses to flooding that can drive mortality (Kozlowski 2002) and it is not clear from our data what the exact factors may be. Future studies could also test if the mechanism of flood mortality is a disruption of root metabolism and subsequent root mortality, which eventually leads to reduced water transport capacity and may ultimately be observable as shoot desiccation (Coutts 1981) as we observed here. As with our results relative to drought and our understanding of the ecology of cedar in forested wetlands (Chimner and Hart 1996), it appears that cedar is able to resist moderate flooding and can even survive in some extreme cases but with reduced canopies and growth.

In contrast to cedar, fir was even more sensitive to flooding with only two surviving seedlings across all the flood treatment levels (94% mortality; Fig. S1D, available as Supplementary data at *Tree Physiology* Online). Initially, fir appeared resistant to flooding and only exhibited partial canopy mortality at the end of the treatments (EOT) that were longer than 30 days (Fig. 3D). Like cedar, flood-treated fir experienced a decline in water potential by Day 16, but this decline was to lower water potentials than cedar and was sustained for most of the rest of the study. However, by spring of the following year, almost all the flooded fir had died (Fig. S1D, available as Supplementary data at *Tree Physiology*

Online). Furthermore, in contrast to cedar, we found that fir seemed to have a threshold-type response wherein they either lived with relatively full canopies or died (Fig. S1D, available as Supplementary data at *Tree Physiology* Online and Fig. 3). This aligns with other studies that suggest fir is not flood tolerant (Denneler et al. 2008) and although it may be found in seasonally wet places, favorable microsite conditions that avoid inundated soils may be even more important for this species than for cedar (Allogio et al. 2021). Although fir height growth was only moderately impacted in the treatment year, we did see that all flooded fir had large reductions in diameter growth in the treatment year compared with controls (Fig. S3D, available as Supplementary data at *Tree Physiology* Online). Further supporting this notion of fir's threshold response to flooding, the two surviving fir were able to match height and diameter growth of control seedlings the following year. However, we cannot assess this for longer flood lengths because of the large amount of mortality. Our results align with our general understanding of the physiology (e.g. lack of radially sectored hydraulic pathways) and ecology (generalist) of fir, further supporting the premise that it may be adapted to avoid extensively flooded conditions.

Conclusions

In this study, we found that in response to droughts and floods, cedar seedlings are adapted to resist and recover from some of the stressors, whereas fir seedlings may rely more on a strategy of avoidance. Generally, the results suggested that hydraulic failure was a key factor leading to mortality from drought, whereas root mortality and an eventual lack of water to the canopy may be driving mortality from flooding. For cedar and fir that coexist in lowland forest stands, our results reinforce the importance of coarse woody material as a regeneration substrate that retains moisture and of favorable microtopographic positions such as mounds (hummocks) that may help avoid flood stress (Scott and Murphy 1987; Chimner and Hart 1996; Allogio et al. 2021). Although mortality of forest trees is a complex process involving many interacting factors, as climate changes our study suggests that in the absence of other stressors (e.g. deer browse, pests, disease), cedar may be better adapted than fir to the widely varying moisture conditions that accompany future precipitation extremes.

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Authors' contributions

K.A.S., L.S.K. and J.W.W. conceptualized and designed the study; K.A.S. and A.B. collected the data; K.A.S., A.B. and J.W.W. analyzed the data; K.A.S. and J.W.W. wrote the first version of the manuscript and all authors contributed to the final manuscript.

Supplementary data

Supplementary data are available at *Tree Physiology* Online.

Conflict of interest

The authors declare no competing interests.

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Data availability

All data used to prepare the manuscript are publicly available through the US Forest Service's research data archive: https://doi.org/10.2737/RDS-2024-0061.

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