

Tree growth response to growing season frost and drought is shaped by species traits and competition in temperate-boreal transition zone forests

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ABSTRACT

Understanding how species-specific traits and density-dependent competition modulate the effects of extreme climate events is essential for informing future forest management strategies. We analyzed the radial growth of western larch (*Larix occidentalis*) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) trees growing in unmanaged old-growth stands — and western larch grown at two experimentally controlled densities — at four sites across western Montana, USA. Differences in leaf habit (deciduous vs. evergreen) and divergent water use strategies (anisohydric vs. isohydric) of western larch and Douglas-fir provided a model for linking growth–climate relationships to functional traits. We evaluated resistance, resilience, and recovery of basal area growth to drought and growing season frosts between (a) species and (b) experimental stand densities. Western larch growth exhibited a negative relationship with previous autumn frost (October freezing degree days; FDD), while Douglas-fir showed no response. Radial growth response to spring frost (May–June FDD) was negative for both species, with western larch exhibiting greater sensitivity. Both species showed reduced growth in years following drought conditions (previous July–August Palmer Drought Severity Index; PDSI), while only Douglas-fir was sensitive to contemporaneous July–August PDSI. Growth of larch trees in low-density stands was more resistant and resilient to previous summer drought and spring frost than that of trees in high-density stands. Furthermore, observations of greater soil volumetric water content in low-density stands provide a mechanistic link for drought responses. However, growth response to autumn frost was density independent. Our results suggest that early thinning has the potential to limit the negative impacts of summer drought and spring frost in sensitive species, and that species-specific physiological traits can drive divergent growth responses to extreme climate events.

1. Introduction

Climate is a fundamental control on tree growth (Anderson-Teixeira et al., 2022; Chmura et al., 2011) and extreme climate events (*sensu* Vitasse et al., 2019) (e.g., drought and growing season frosts) have negative impacts on radial growth across a wide variety of tree species (Ma et al., 2019; Truettner et al., 2018; Vanoni et al., 2016; Vitasse et al., 2019). In seasonally constrained northern temperate and southern boreal forests, growth can be restricted due to water limitation or cold temperatures (Monson, 2013), with some species facing both — drought stress during the summer and low temperature stress in spring and autumn. Rising average temperatures and shifting precipitation patterns are expected to result in the increased prevalence of drought in forest

ecosystems (Allen et al., 2010; Brodribb et al., 2020; Gregory et al., 1997), and may cause trees to exit dormancy earlier thereby heightening the risk of damage from freezing temperatures in the spring (Inouye, 2000; Ma et al., 2019). Phenological mismatches in the autumn (i.e., early autumn frost events) have received less attention (Gallinat et al., 2015), yet there is evidence that extension of the growing season may lead to elevated risk of frost damage in the autumn as well (Norby et al., 2003).

Predicting the consequences of future extreme climate events on tree growth requires recognition of the role that functional trait diversity plays in shaping species- and community-level responses to such events (e.g., McDowell et al., 2008). Drought can directly impair a tree's ability to assimilate carbon (McDowell et al., 2008) or lead to hydraulic failure

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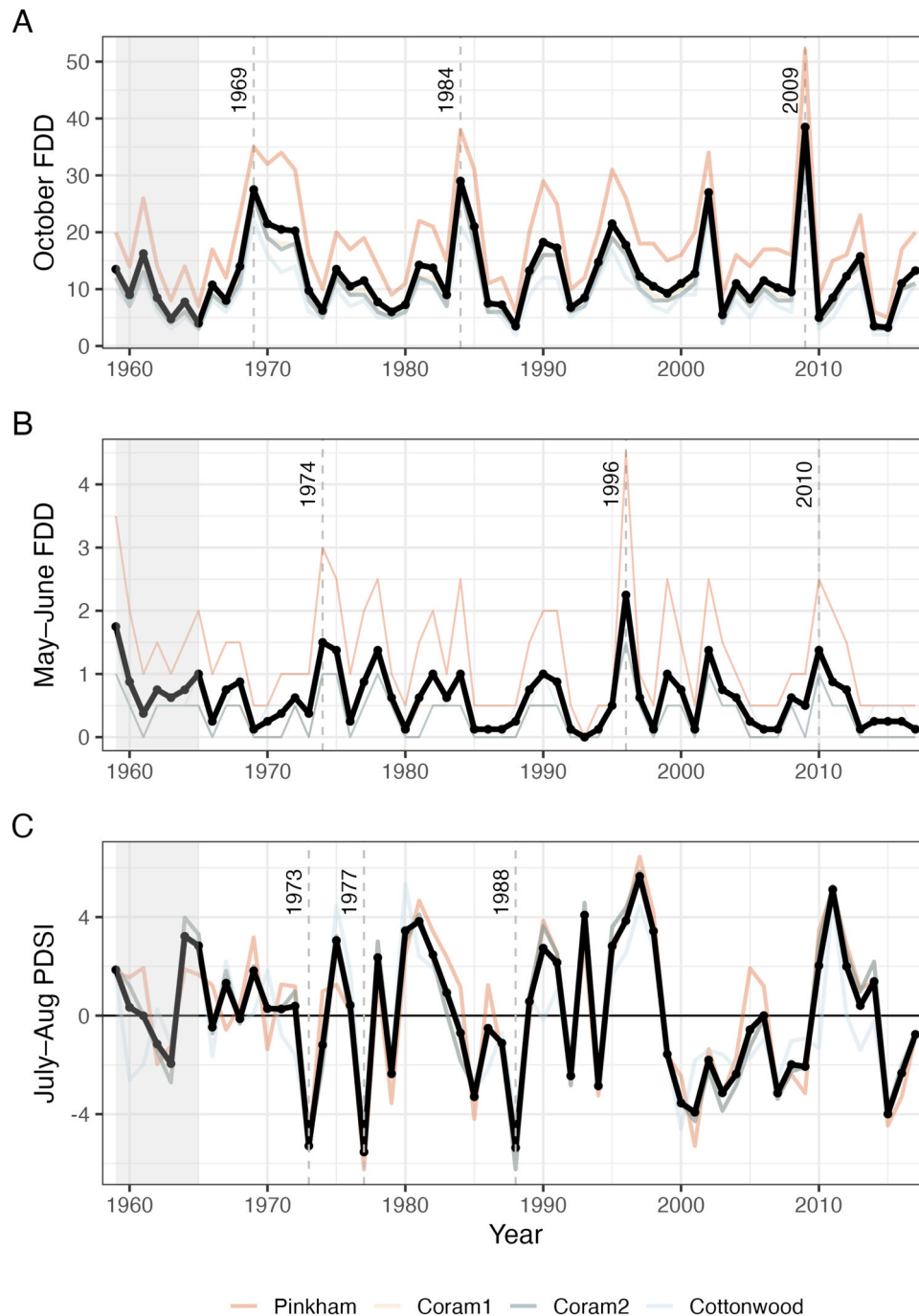


Fig. 1. Climate record across sites from 1959 to 2017 (site-level observations denoted by color with regional average in black) for seasonal variables: **A)** October Freezing Degree-Days (FDD), **B)** May–June Freezing Degree-Days (FDD), and **C)** July–August Palmer Drought Severity Index (PDSI). Shaded period (1959–1964; light gray) indicates years that were included in climate-growth analysis for trees in unmanaged stands but pre-date the available growth record in experimental stands. Dashed vertical lines mark event years for each variable identified for resistance, resilience, and recovery analysis.

and disrupt carbohydrate transport (Sala et al., 2010), yet not all species respond in the same way. The variety of strategies which plants employ to cope with moisture stress is often categorized along a continuum from isohydric to anisohydric (McDowell et al., 2008; Tardieu and Davies, 1993; Tardieu and Simonneau, 1998). Isohydric species are characterized by high levels of stomatal regulation and more conservative water relations (i.e., plants that close stomata to maintain constant internal water potentials and reduce evapotranspiration at the cost of carbon gain). In contrast, anisohydric species have relatively poor stomatal control and allow water potentials to become more negative with increasing evaporative demand, continuing to assimilate carbon at the

risk of hydraulic failure (McDowell et al., 2008).

Alternatively, late spring frost events cause tissue damage and mortality during the seasonal transitions between dormancy and growth in temperate and boreal forests (Vitasse et al., 2014) when tissues are particularly sensitive to freezing temperatures (Vitra et al., 2017; Weiser, 1970). Negative impacts of spring frosts on radial growth have been documented for temperate broadleaf deciduous species in western North America (Birch et al., 2023), as well as a variety of temperate deciduous and evergreen species across Europe (Vanoni et al., 2016; Vitasse et al., 2019). Damage to new tissues during this period is especially impactful for deciduous species because their entire

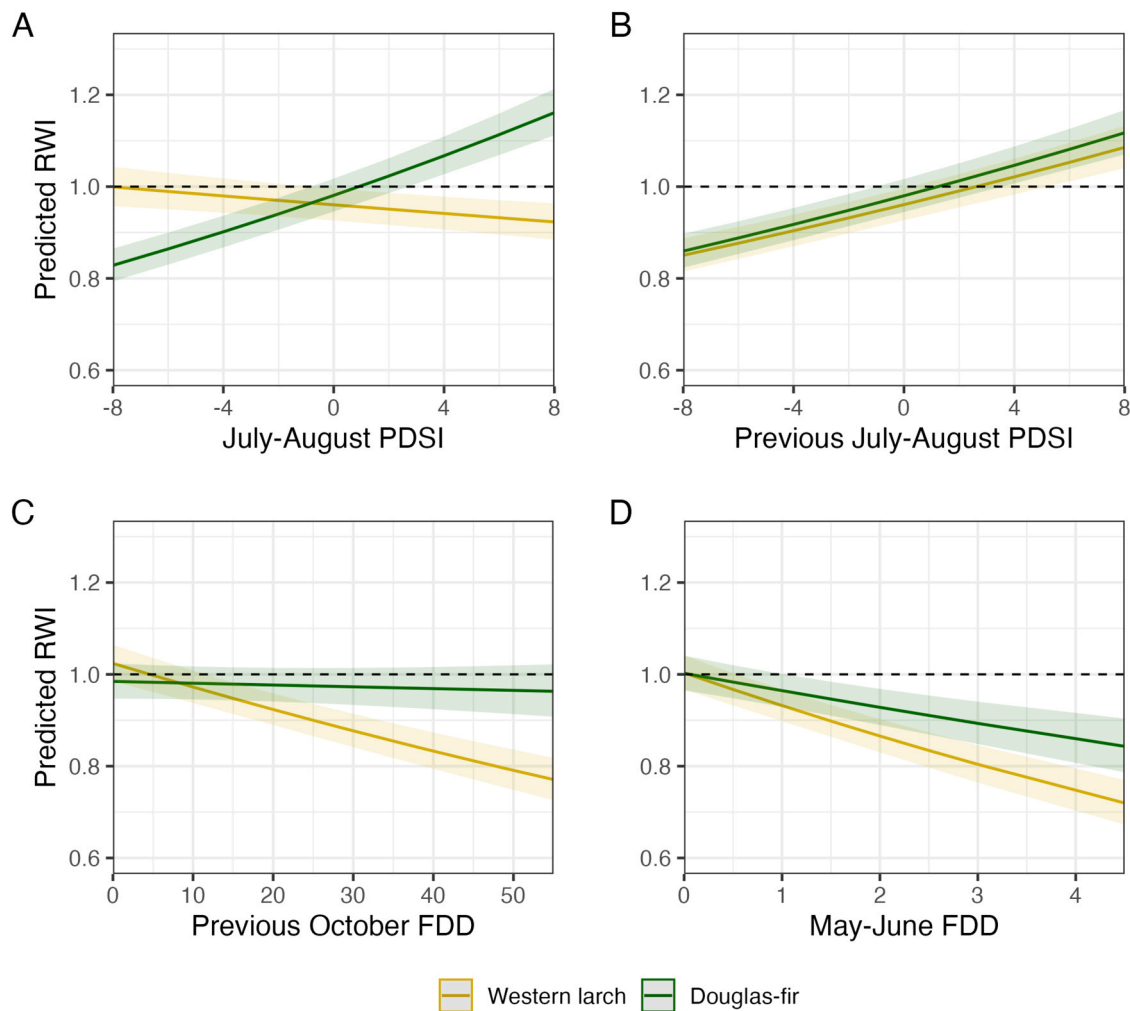


Fig. 2. Estimated marginal means ($\pm$ 95 % CI) derived from GLMM for ring-width index (RWI) by species for A) July-August PDSI, B) Previous July-August PDSI, C) Previous October Freezing Degree Days (FDD), and D) May-June Freezing Degree Days (FDD). Paired climate-growth observations for these variables in unmanaged stands span the period 1959–2017.

photosynthetic area may be affected (Vitasse et al., 2014). In contrast, only a small percentage of evergreen leaves pass through this period of vulnerability each growing season, and frost tolerance in evergreen species tracks climate more closely (i.e., relatively greater frost resistance in colder climates) (Kikuzawa et al., 2013; van Ommen Kloeke et al., 2012).

Autumn frosts can interfere with the cessation of growth but are generally thought to be less impactful given that most species begin the process of winter hardening well before the occurrence of freezing temperatures (Vitasse et al., 2014). Yet, an early autumn freezing event can cause leaf mortality in deciduous species prior to leaf senescence thereby preventing remobilization of non-structural carbohydrates (NSCs) and nutrients in those tissues (Norby et al., 2003). Such severe autumn frost events are likely to disrupt nutrient cycling and growth in the following year, suggesting deciduous species may be uniquely sensitive to early autumn frosts as compared to co-occurring evergreen species.

Competition also mediates climate-growth relationships (Buechling et al., 2017; Carnwath and Nelson, 2016; Clark et al., 2011; Ford et al., 2016), and for species that are sensitive to a given climate stressor, available evidence suggests that density-dependent competition will magnify negative effects. High stand densities amplify drought-related growth declines (Gleason et al., 2017; Primicia et al., 2015) via increased rates of evapotranspiration (Roche et al., 2018; Y. Wang et al., 2019) leading to reduced local-scale soil moisture availability (del

Campo et al., 2019; Jiménez et al., 2008; Tatum et al., 2025). Evidence that competition reduction treatments (i.e., thinning) can alleviate these effects and increase tree resistance/resilience to and recovery from drought in seasonally dry forests (Bottero et al., 2017; Sohn et al., 2016; Young et al., 2023) indicates that the impacts of such events may be mitigated with active forest management. It is virtually unknown if competition reduction via thinning modulates tree growth responses to late spring or early autumn frost events, though recent evidence from European beech (*Fagus sylvatica*) suggests that thinning may buffer growth impacts from spring frosts (Rubio-Cuadrado et al., 2024).

Most studies investigating the effects of stand density and thinning on tree growth response to extreme climate events have focused on drought impacts on the genera *Pinus* and *Quercus* in dry-temperate or Mediterranean climates, and in stands that were thinned 20+ years after stand initiation (Corcuera et al., 2006; Fernandes et al., 2016; McDowell et al., 2003; Simonin et al., 2006; Sohn et al., 2016; Thomas and Waring, 2015). Much less is known about how thinning affects tree growth responses to drought and/or growing season frost in boreal and cool, montane temperate forests — especially those that were thinned within the first decade of stand development.

We initially intended to investigate how stand density (manipulated via early thinning) modulates the response of radial growth to drought in the deciduous, anisohydric conifer western larch (*Larix occidentalis*). However, preliminary investigation indicated that the sensitivity of western larch radial growth to drought was more nuanced than

Table 1

Model summary for growth-climate generalized linear mixed effects model (GLMM, gamma with log-link) including species (western larch set as reference level), tree size, and all seasonal climate variables as fixed effects. Random effects account for the hierarchical structure of the data with trees nested within sites, and a first-order autoregressive (AR-1) correlation structure applied at the tree level between subsequent years.

	Estimate	Std. Error	z value	p-value
Fixed Effects				
Intercept	0.0256	0.0341	0.7490	0.4538
Species (Douglas-fir)	-0.0083	0.0370	-0.2238	0.8229
Summer PDSI	-0.0050	0.0015	-3.3990	0.0007
Summer PDSI _{t-1}	0.0153	0.0014	10.7036	< 0.0001
October FDD _{t-1}	-0.0052	0.0006	-9.1973	< 0.0001
May-June FDD	-0.0739	0.0073	-10.0710	< 0.0001
Estimated DBH _t	0.0010	0.0006	1.7071	0.0878
Species (Douglas-fir) × Summer PDSI	0.0261	0.0021	12.6210	< 0.0001
Species (Douglas-fir) × Summer PDSI _{t-1}	0.0011	0.0020	0.5666	0.5710
Species (Douglas-fir) × October FDD _{t-1}	0.0048	0.0008	6.1080	< 0.0001
Species (Douglas-fir) × May-June FDD	0.0355	0.0103	3.4481	0.0006
Species (Douglas-fir) × Estimated DBH _t	-0.0012	0.0008	-1.4279	0.1533
Random Effects				
	Std. Dev.	Correlation		
Tree / Site (Intercept)	< 0.0001	—		
Site (Intercept)	0.0328	—		
Tree (AR-1)	0.1986	0.64		

expected, and growth time series revealed strong signals potentially associated with known frost events (e.g., 2009 early October frost; Bernhardt, 2009). Thus, we expanded our inquiry to address questions about trait-based responses of tree radial growth to both drought and growing season frost, as well as assessment of how density-dependent competition affects sensitivity to these extreme climate events. Our study therefore sought to answer the following questions:

- 1) Do co-occurring conifer species with divergent traits (deciduous/anisohydric versus evergreen/isohydric), exhibit differential growth responses to drought and growing season frost?
- 2) Do these species differ in their resistance, resilience, and/or recovery to extreme drought and growing season frost events?
- 3) Does competition along an experimental stand density gradient affect the resistance, resilience, and/or recovery of a deciduous, anisohydric conifer in response to extreme summer drought or growing season frost events?
- 4) Does soil volumetric water content differ between high-density and low-density stands?

To investigate these questions, we used co-occurring western larch and Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) growing in unmanaged old-growth stands — and western larch growing in experimentally thinned stands — as a model system to disentangle species-specific ecophysiology (Q1–2) from the effects of density-dependent competition in monospecific larch stands (Q3–4). We hypothesized that western larch's deciduous habit and anisohydric hydraulic strategy would result in greater relative importance of breaking and entering dormancy and continued carbon assimilation under low moisture conditions, suggesting that western larch will be more sensitive to growing season freezing events while being less sensitive to summer drought, as compared to Douglas-fir. We further expected that for climate variables to which larch growth is sensitive, trees in low-density stands would be more resistant, resilient, and show greater recovery than those in high-density stands because of reduced density-dependent competition and greater per-tree access to essential growth-limiting resources, such as soil nutrients and water.

2. Methods

2.1. Study species and locale

Douglas-fir and western larch provide an ideal contrast given their many commonalities coupled with several key differences. Both species are important components of forest ecosystems across the inland Pacific Northwest and Northern Rocky Mountains and share a common insect defoliator in western spruce budworm (*Choristoneura occidentalis*) (Fellin and Dewey, 1982). Furthermore, the genera *Pseudotsuga* and *Larix* share a clade within the family *Pinaceae* (Gernandt and Liston, 1999). However, the two species display highly divergent physiological traits. Western larch, like all species in the genus *Larix*, is a deciduous conifer (Schmidt, 1995), whereas Douglas-fir displays an evergreen leaf habit. Western larch exhibits poor stomatal regulation, low intrinsic water use efficiency (iWUE) (Marshall and Zhang, 1994), and maintains high stomatal conductance at xylem pressure potentials as negative as -1.5 MPa (Higgins et al., 1987). In contrast, Douglas-fir exhibits high iWUE (Marshall and Zhang, 1994) reflecting greater stomatal regulation in response to increased evaporative demand. The genus *Larix* has a circumboreal range and covers vast land areas where it occurs alone or in mixed-species stands with evergreen conifers (e.g., Douglas-fir) (Gower and Richards, 1990; Mamet et al., 2019; Schmidt, 1995; Usoltsev et al., 2002). Our study system thus provides insights relevant to forest management decisions across the northern temperate and boreal forest biomes.

The distribution of western larch is characterized as cool and wet, with a majority of precipitation falling as snow — though annual mean temperature ($2.7 - 11.1$ °C) and precipitation ($47.7 - 127$ cm) vary considerably (Schmidt et al., 1976). Fire regimes in western larch forests include low-severity, mixed-severity, and stand replacing regimes (Arno et al., 1995). Thick bark and a high crown base (Stevens et al., 2020; Schmidt et al., 1976) and a preference for bare mineral soil and high-light environments (Hopkins et al., 2014; Schmidt et al., 1976) allow western larch to succeed across this spectrum of disturbance regimes. On cooler, wetter sites, larch co-occurs with southern boreal/subalpine species (*sensu* Agee, 1999) such as lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*), though its range extends to relatively warm, dry sites dominated by ponderosa pine (*Pinus ponderosa*) (Schmidt et al., 1976). Western larch is sympatric with Douglas-fir across much of its range (Hermann and Lavender, 1990; Schmidt and Shearer, 1990); however,

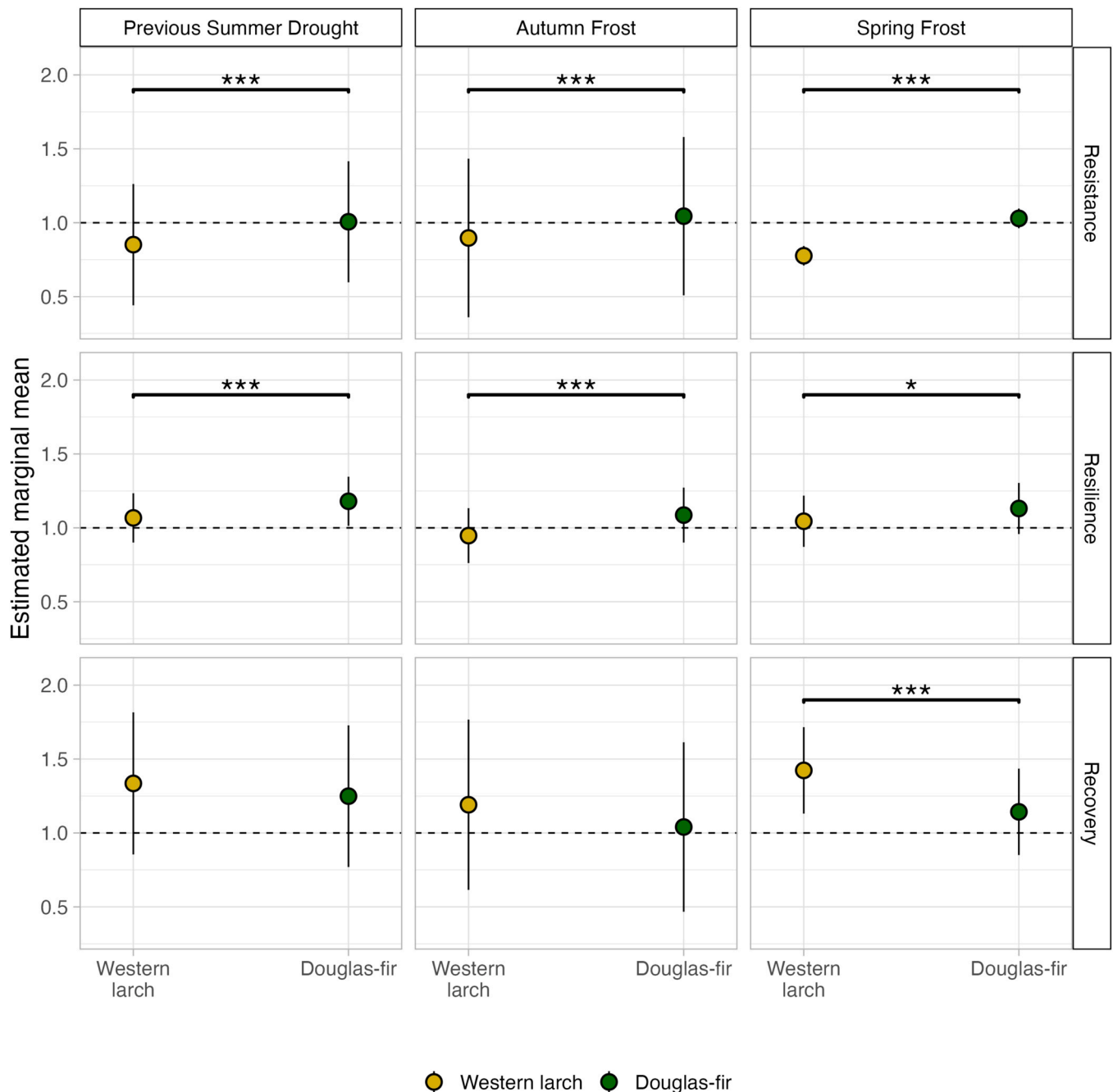


Fig. 3. Estimated marginal means (EMMs) ($\pm$ 95 % CI) of linear mixed effect models for resistance (top), resilience (middle), and recovery (bottom) across species (western larch, Douglas-fir) in unmanaged stands in response to extreme climate events — previous summer drought (previous July-August Palmer Drought Severity Index), previous autumn frost (October Freezing Degree Days) and spring frost (May-June Freezing Degree Days). EMMs reflect responses to the three most extreme years for a given variable. Asterisks denote p-values for pairwise contrasts (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Douglas-fir has a much broader overall distribution that extends from southern British Columbia to northern Mexico (Hermann and Lavender, 1990). Rocky Mountain Douglas-fir (var. *glauca*) overlaps with the core climatic range of western larch, though it is more limited on the coolest, wettest sites and can tolerate relatively warmer, drier conditions (Hermann and Lavender, 1990; Schmidt and Shearer, 1990).

Range-wide gradients in climate, associated tree species, and disturbance regimes highlight *Larix* as occupying a transitional zone between the cold, snow-dominated systems of the southern boreal forest (Kuennecke, 2008) and the more mild climatic conditions associated with temperate mixed-conifer forests. Across their broad distribution, *Larix* species are expected to undergo distributional shifts as a result of

global change (Rehfeldt and Jaquish, 2010; S. Wang et al., 2025), and stand density management may offer a means of mitigating undesirable impacts and maintaining ecosystem services (Crotteau et al., 2019; Peng et al., 2018; H. Wang et al., 2013; Xu et al., 2020; Zhang et al., 2024). As such, our analysis of western larch and Douglas-fir provides a valuable model system for enhancing our understanding of how management interventions may influence forest dynamics and climate sensitivity across temperate-boreal transition zone forests.

2.2. Experimental design

We leveraged a network of long-term experimental plots established

Table 2

Summary of pairwise contrasts of response indices between species in unmanaged stands for Autumn Frost, Previous Summer Drought, and Spring Frost events.

Climate Event	Response	Contrast	Estimate	SE	p-value
Autumn Frost	Resilience	Larch – Douglas-fir	-0.1390	0.0424	0.0013
	Resistance	Larch – Douglas-fir	-0.1477	0.0381	0.0002
	Recovery	Larch – Douglas-fir	0.1506	0.1042	0.1504
Previous Summer Drought	Resilience	Larch – Douglas-fir	-0.1125	0.0421	0.0083
	Resistance	Larch – Douglas-fir	-0.1547	0.0348	< 0.0001
	Recovery	Larch – Douglas-fir	0.0864	0.0514	0.0952
Spring Frost	Resilience	Larch – Douglas-fir	-0.0862	0.0418	0.0407
	Resistance	Larch – Douglas-fir	-0.2528	0.0328	< 0.0001
	Recovery	Larch – Douglas-fir	0.2805	0.059	< 0.0001

as the Western Larch Density Management Study (WLDMS) in 1961 (Schmidt, 1964). This plot network comprises four replicated, randomized blocks distributed across the spectrum of western larch productivity in western Montana. Detailed descriptions of the full original study design, implementation, and maps are available in Schaedel et al. (2017a–c). All sites were harvested using even-aged methods between 1951 and 1953, and prolific natural larch regeneration occurred at each site in the year following harvest (Schmidt, 1964). Experimental units were established between the summer of 1961 and the winter of 1962 and stand age at initial treatment averaged 8 years. Treatment areas are square 20.12 m × 20.12 m plots surrounded by a buffer of at least 10–20 m that received the same treatment to avoid edge effects. Thinning treatments were randomly assigned within each block. Experimental units are dominated by western larch (*Larix occidentalis*), with scattered individuals of Engelmann spruce (*Picea engelmannii*), Douglas-fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*), and paper birch (*Betula papyrifera*) that have recruited into the understory during the intervening seven decades since stand initiation.

Sampling focused on plots that were thinned once to reach target densities of 494 trees ha⁻¹ (low density) and 1680 trees ha⁻¹ (high density) which represent the high and low end of density treatments present at all four replicates. In low-density plots we sampled all tagged trees in the experimental unit at a given site (n = 18–20). We achieved a comparable sample size in high-density plots by randomly sampling a subset of trees (n = 20) from a list of all live tagged trees in a given plot. Trees in unmanaged stands were sampled by first identifying and temporarily tagged 30 trees which were > 25 cm DBH (to ensure adequate growth record), and then randomly selecting 20 of these trees for sampling.

2.3. Tree-ring series

Annual growth data were collected from trees via increment cores taken at breast-height (1.37 m). We collected at least two opposite-radii cores from each tree and processed them using the standard methods of mounting, drying, sanding, and scanning (Speer 2010). Western larch trees (experimental and unmanaged) were sampled at the Cottonwood, Pinkham, and Coram 1 sites in October of 2017 and at Coram 2 in the autumn of 2023. Douglas-fir cores were collected from unmanaged stands at all sites in 2024. Processed cores were measured in the CooRecorder program and statistical cross-dating was carried out in the accompanying CDendro program (Larsson and Larsson 2023). Cores which did not meet statistical thresholds (cross-correlation >= 0.40 or t-test >= 6.0) were examined further to identify and account for missing and/or false rings (Dial et al., 2024). Statistics for tree ring series, including number of trees/cores per series and expressed population signal (EPS), are summarized in Table S1. Raw ring-width measurements were averaged within each tree prior to further analysis or transformation.

To analyze climate-growth relationships, individual tree ring-width measurements were detrended using a cubic smoothing spline with a

fixed 50 % frequency cutoff at 30 years for all series (Klesse, 2021) and then dividing the splines from the original ring-widths, resulting in a unitless ring-width index (RWI; see section S1.1, Fig. S1 in Supporting Information). We chose spline-detrended RWI as our response for analyzing climate-growth relationships of trees growing in unmanaged, old-growth stands as this approach seeks to remove variability resulting from long-term age/size or disturbance related trends, and retains inter-annual to inter-decadal variation resulting primarily from climate (Cook and Peters, 1981; Frank et al., 2022).

To assess growth responses to extreme climate events, we calculated basal area increments (BAI) for subsequent use in resistance, resilience, and recovery metrics (*sensu* Lloret et al., 2011) using the following equation from (Biondi and Qeadan, 2008),

$$BAI_t = \pi(w_t^2 + 2w_t R_{t-1}) \quad (1)$$

where w_t is the raw ring-width of the annual increment in year t and R_{t-1} is the stem radius at the beginning of that increment. Detrending and BAI calculations were carried out using the dplR package (Bunn, 2008) in the R statistical software (R Core Team, 2024). BAI was calculated using the outside-in method (Bunn, 2008), which implements the above equation (Eq. 1) in a stepwise process, starting with the outermost ring and adjusting R_{t-1} based on previous ring-widths. Inside bark radii for initialization were calculated by subtracting single bark thickness estimated from allometric equations (Lutes et al., 2012) from field measurements of outside bark radii.

Resistance, resilience and recovery indices were calculated following the methods of Lloret et al. (2011) using the following equations:

$$\begin{aligned} \text{Resistance}(R_t) &= \frac{BAI_t}{BAI_{t-2}} \\ \text{Resilience}(R_s) &= \frac{BAI_{t+2}}{BAI_{t-2}} \\ \text{Recovery}(R_c) &= \frac{BAI_{t+2}}{BAI_t} \end{aligned} \quad (2)$$

where BAI_t is the annual basal area increment during the corresponding year t , BAI_{t-2} is the average BAI for the 2 years before year t and BAI_{t+2} is the average BAI for the 2 years after year t . A 2-year window was chosen to balance competing goals of capturing a robust baseline while avoiding overlap between event years. In the case of lagged relationships (e.g., previous autumn frost or previous summer drought) year t corresponds to the year where growth impacts manifested, not the year in which the extreme climate event occurred (e.g., $t = 2010$ for the autumn frost event in 2009).

2.4. Climate data

A suite of modeled monthly climate time series data were retrieved for each site from the TerraClimate (Abatzoglou et al., 2018) and

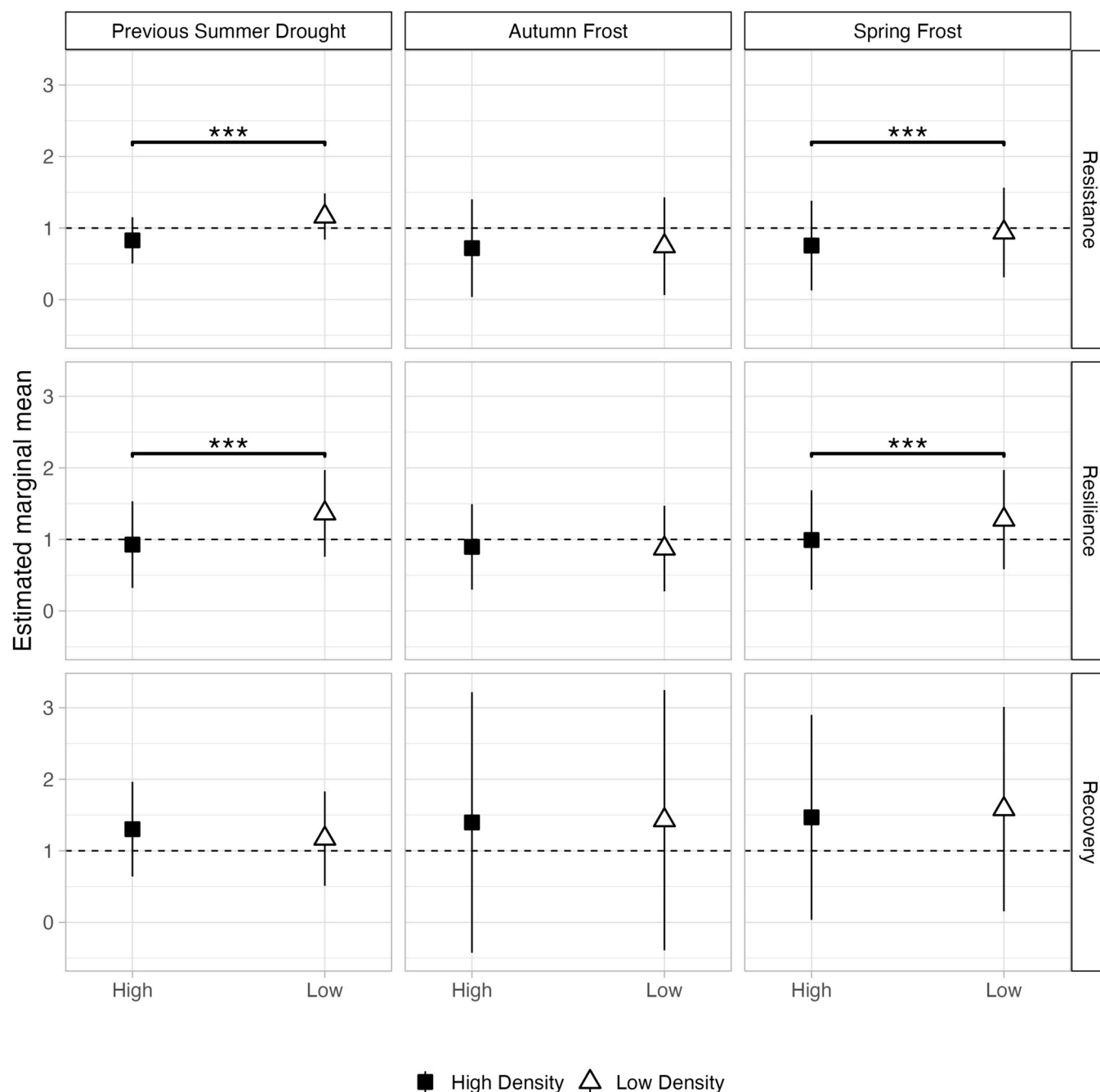


Fig. 4. Estimated marginal means (EMMs) ($\pm$ 95 % CI) of linear mixed effect models for resistance (top), resilience (middle), and recovery (bottom) between high (1680 trees·ha⁻¹) and low (494 trees·ha⁻¹) experimental densities within the Western Larch Density Management Study in response to extreme climate events — previous summer drought (previous July–August Palmer Drought Severity Index), previous autumn frost (October Freezing Degree Days) and spring frost (May–June Freezing Degree Days). EMMs reflect responses to the three most extreme years for a given variable. Asterisks denote p-values for pairwise contrasts (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

ClimateNA (T. Wang et al., 2016) datasets (Table S2). Specifically, we used variables which could act as proxies for drought (Palmer Drought Severity Index; TerraClimate) and growing season (April – October) frost severity (Freezing Degree Days; ClimateNA). Palmer Drought Severity Index (PDSI) accounts for precipitation, temperature, and soil water when calculating relative drought conditions (Alley, 1984) and has been shown to outperform other drought metrics in the context of radial tree growth modeling (Kempes et al., 2008). Freezing degree days (FDD; sum of daily mean temperatures $< 0^{\circ}\text{C}$) was chosen as a measure of frost because it represents not only the occurrence of freezing temperatures, but an integrated measure of frost severity and duration.

We utilized moving-window regression analysis implemented with *climwin* in the R statistical software (R Core Team, 2024; van de Pol et al., 2016) to identify temporal windows for each variable which best explained mean annual growth for each species (see section S1.1, Fig. S2 in Supporting Information). The resulting temporal windows were growing year July–August PDSI, previous year July–August PDSI, May–June FDD for spring frost, and previous October FDD for autumn frost (Fig. 1; Table S2). Temporal windows that extend across multiple months represent the mean of monthly values for given variable at a given site, and these site-level, window-specific means were used as the predictor variables in our growth models.

Table 3

Summary of pairwise contrasts of response indices between western larch experimental stand densities for Autumn Frost, Previous Summer Drought, and Spring Frost events.

Climate Event	Response	Contrast	Estimate	SE	p-value
Autumn Frost	Resilience	High Density - Low Density	0.0235	0.0373	0.5298
	Resistance	High Density - Low Density	-0.0271	0.0237	0.2545
	Recovery	High Density - Low Density	-0.0315	0.1404	0.8227
Previous Summer Drought	Resilience	High Density - Low Density	-0.4365	0.0537	< 0.0001
	Resistance	High Density - Low Density	-0.3339	0.0356	< 0.001
	Recovery	High Density - Low Density	0.1320	0.1361	0.3336
Spring Frost	Resilience	High Density - Low Density	-0.2849	0.0664	< 0.0001
	Resistance	High Density - Low Density	-0.1830	0.0393	< 0.0001
	Recovery	High Density - Low Density	-0.1154	0.1398	0.4102

Event years for resilience, resistance, and recovery analysis were chosen as statistically extreme years (≥ 2 standard deviations from the mean) during our period of observation (Fig. S3). This resulted in three distinct event years for July-August PDSI (i.e., summer drought) and October FDD (i.e., early autumn frost) (Fig. 1; Table S2; Fig. S3). Values for May-June FDD exhibited a narrower distribution than the other two variables, with only one year exceeding our threshold (Fig. S3). In this case, we selected the next most extreme years for May-June FDD (1974, 2010). Climate data observations for this analysis were restricted to the period from 1966 to 2017 as this constituted the growth record available at all sites.

2.5. Soil moisture

Soil moisture data across experimental units within the WLDMS was collected using soil neutron probes, with four measurement tubes established in each plot (Hayes et al., 2022; Schmidt, 1964). Volumetric water content (VWC) was calculated from probe measurements during the period 1967–1991 at 2-week intervals during the growing season (Hayes et al., 2022). We accessed the available data for all 494 trees·ha⁻¹ and 1680 trees·ha⁻¹ plots across the experiment. Data were collected at multiple depths; however, we focus here on measurements at 30 in (76.2 cm), as the majority of western larch roots are found at or above 50 in (127 cm) (Schmidt and Shearer, 1990) and this depth had high measurement resolution across study sites (Hayes et al., 2022). We averaged measurements within individual neutron probe tubes for July and August, with mean values for this window representing our observational unit for comparison across densities. Full dataset and associated methods are available in Hayes et al. (2022).

2.6. Statistical analysis

We used a generalized linear mixed-effects model (GLMM; Gamma distributed with log-link) to quantify the influence of drought (PDSI) and frost (FDD) variables on the annual growth (RWI) of unmanaged western larch and Douglas-fir. Models included species, summer drought (July–August PDSI), lagged summer drought (previous year July–August PDSI), autumn frost (previous October FDD), spring frost (May–June FDD), tree size (DBH) and all species-by-climate interactions as fixed effects. Random intercepts for site and tree within site accounted for the hierarchical structure of the data, and an autoregressive correlation structure (AR1) was included to model temporal autocorrelation within individual tree ring series.

To assess resistance (Rt), resilience (Rs), and recovery (Rc) following extreme climate events, we fit separate linear mixed-effects models (LMM) for each index using values calculated for identified event years (Fig. 1; Fig. S3; Table S3). These models compared (a) unmanaged larch and Douglas-fir (species as fixed-effect) and (b) larch across low- and high-density experimental stands (categorical stand density as fixed

effect). All models included tree size (DBH) as a covariate and nested random effects for tree within site and year. Pairwise comparison of estimated marginal means (EMMs) for each response index was used to assess differences between species or stand densities. EMMs were calculated using the *emmeans* (Lenth, 2024) and *ggeffects* (Lüdtke, 2018) packages within the R statistical environment (R Core Team, 2024).

We analyzed VWC measurements across experimental units to evaluate stand density effects on soil moisture. A LMM was used with stand density as a categorical fixed effect and nested random intercepts for replicate, plot, and measurement tube. An AR1 correlation structure was included to account for temporal autocorrelation at the measurement tube level. A full description of all model equations is provided in section S1.2 in the Supporting Information (eqns. S1–4).

3. Results

3.1. Effect of species-specific traits on climate-growth relationships in unmanaged stands

We observed a positive relationship between Douglas-fir RWI and July-August PDSI, indicating greater growth under high moisture conditions and reduced growth under drought conditions (Fig. 2A; Table 1). In contrast, larch growth was negatively related to current year July-August PDSI; however, this relationship was weak in magnitude (Fig. 2A; Table 1). Both Douglas-fir and larch had positive relationships with previous year July-August PDSI (Fig. 2B; Table 1) with no differences between groups, indicating a lagged effect of drought on RWI for both species.

Western larch and Douglas-fir radial growth displayed differential sensitivity to growing season frost consistent with predictions based on their respective deciduous and evergreen leaf habits. Deciduous larch RWI exhibited a strong, negative relationship with previous October FDD whereas evergreen Douglas-fir RWI was insensitive to this climate variable (Fig. 2C; Table 1). RWI of both species responded negatively to May-June FDD (Fig. 2D; Table 1); however, larch RWI appeared more sensitive than that of Douglas-fir (Fig. 2D; Table 1). There was no evidence of an effect of individual tree size on RWI for either species (Table 1).

3.2. Interspecific variation in resistance, resilience, and recovery of growth to extreme climate events

Interspecific comparison within unmanaged stands revealed greater Rt and Rs in Douglas-fir BAI relative to western larch in response to previous year summer PDSI (Fig. 3; Table 2). Douglas-fir exhibited greater mean Rt and Rs to spring frost compared to unmanaged western larch, however western larch Rc was greater (Fig. 3; Table 2). Douglas-fir showed greater Rt and Rs values in response to autumn frost events

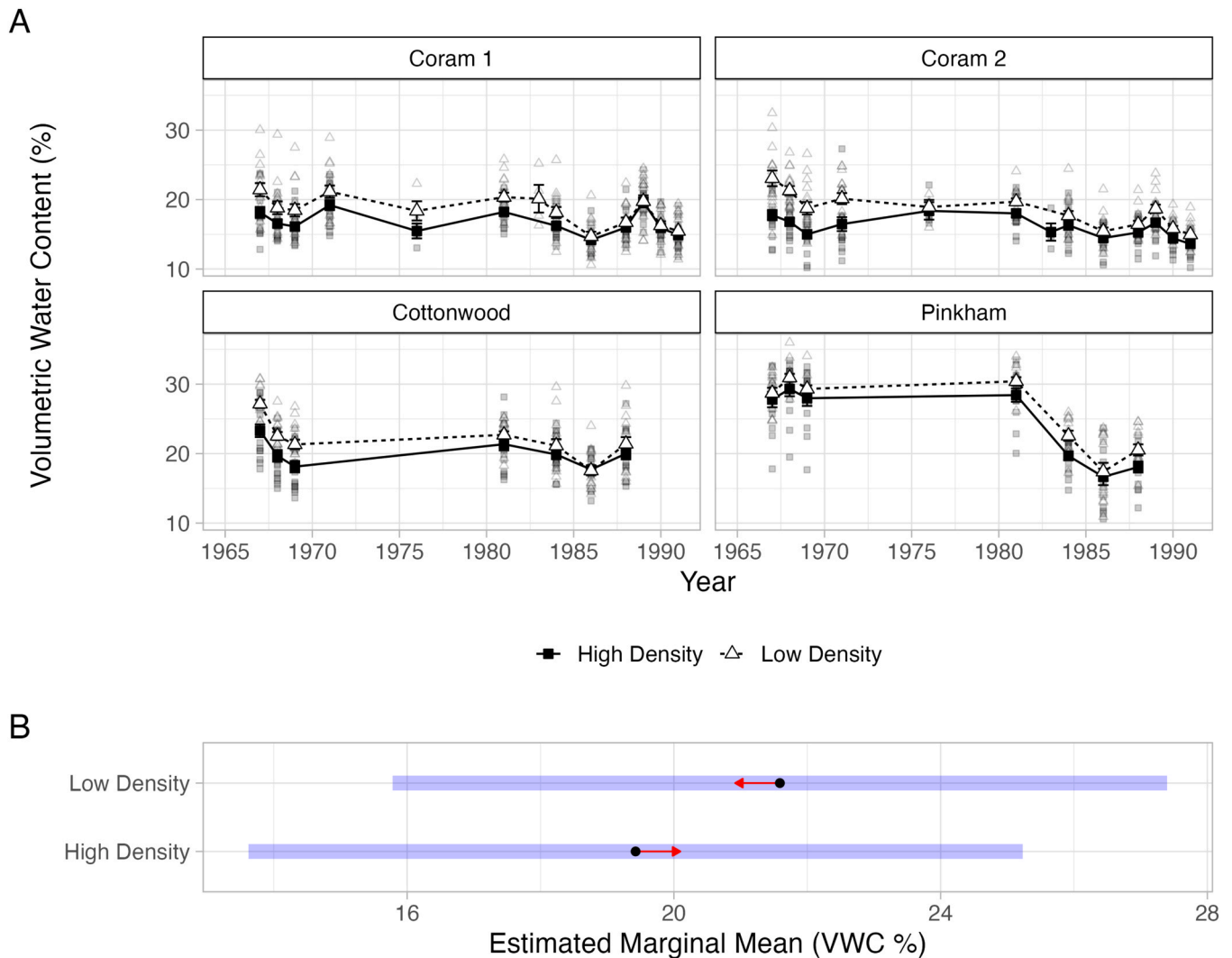


Fig. 5. Effects of stand density treatment on July-August soil volumetric water content (VWC, % at 76.2 cm depth) with (A) annual trends in VWC from 1967 to 1990 across the four Western Larch Density Management (WLDMS) replicate sites. Bold lines and points represent density treatment group means ($\pm$ SE) for high-density (solid square, solid line) and low-density (open triangle, dashed line) plots within a given replicate. Semi-transparent points for each group represent measurement values at individual neutron probes. (B) Estimated marginal means (black points), including $\pm$ 95% confidence intervals (blue bars) of VWC by treatment derived from a linear mixed-effects model. Red arrows illustrate statistical comparison between estimated means, with non-overlap indicating a pairwise contrast with $p < 0.05$.

(Fig. 3; Table 2), however no evidence of a difference in R_c values was observed for these events. Individual model coefficients are reported in the Supporting Information (Table S1).

3.3. Effect of stand density on resistance, resilience, and recovery to extreme climate events

Across WLDMS experimental stands, we observed that both R_t and R_s of western larch BAI to extreme previous summer drought events was greater for trees in low-density stands as compared to high-density stands (Fig. 4; Table 3). Moreover, mean estimates of R_t and R_s for low-density stands were > 1 , suggesting that growth rates in these trees were maintained in the wake of extreme drought and even outperformed predrought baselines. The ability of trees growing in both densities to recover in the years following an extreme drought is evidenced by the more homogenous R_c estimates, which were generally ≥ 1 and did not differ between groups (Fig. 4; Table 3).

A similar pattern for R_t and R_s was also observed in response to extreme spring frost events — greater values in low-density stands as compared to high-density stands (Fig. 4; Table 3). In this case, R_c was

also insensitive to stand density. There were no clear differences in R_t , R_s , or R_c values across experimental density treatments in response to autumn frost events (Fig. 4; Table 3). Individual model coefficients are reported in the Supporting Information (Table S4).

3.4. Stand density effects on soil volumetric water content

We observed greater volumetric water content (VWC) in low-density stands as compared to high-density stands across WLDMS replicates (Fig. 5). The coefficient estimate for stand density suggests that — on average — low-density stands exhibited $\sim 2\%$ greater VWC during the summer growing season as compared to high-density stands (Fig. 5; Table S5).

4. Discussion

4.1. Species-specific climate-growth relationships

Differences in the sensitivity of radial growth to climate across our two focal species generally followed expectations based on species traits.

Douglas-fir growth responded negatively to current year summer drought while larch was relatively insensitive (Fig. 2), reflecting their isohydric and anisohydric strategies, respectively. The response we observed in Douglas-fir aligns with previous findings which reported decreased growth in response to increased evaporative demand (Littell et al., 2008; Restaino et al., 2016). The evidence we observed for a small but significant negative relationship between western larch RWI and summer PDSI (i.e., growth reduction under wetter conditions) was unexpected, but the small slope value ($\beta = -0.004$; Table 1) in relationship to the scale of RWI values (Fig. 2) suggests a very limited effect.

The evidence we observed for a lagged negative effect of summer drought on growth for both species (i.e., drought was associated with reduced growth in the subsequent year) (Fig. 2) suggests that there are multiple pathways through which drought influences subsequent radial growth. Legacy effects are a common phenomenon in the response of tree rings to drought, with proposed mechanisms varying widely across species and ecoregions (Kannenberg et al., 2020). The observation of both an immediate and lagged drought response in Douglas-fir suggests that reductions in photosynthesis during drought resulted in an immediate reduction in C allocation to radial growth, as well as the subsequent depletion of stored C to meet maintenance respiration costs (McDowell, 2011) or a shift in C allocation pathways (Galiano et al., 2017).

The preeminence of a lagged drought effect in western larch suggests that larch maintains radial stem growth under late summer drought conditions but incurs a penalty in the following year. Drought legacy effects on radial growth may be the result of changes in growth cessation/onset, shifting allocation of resources, or some combination of the two. Even if conditions improve in the subsequent year, trees may continue to preferentially allocate carbon towards NSC pools (Galiano et al., 2017) or roots (Kozłowski and Pallardy, 2002) at the expense of radial growth. The anisohydric strategy of larch is also linked to hydraulic damage and related disruptions in C assimilation, delaying post-drought recovery (Kannenberg, Novick, and Phillips, 2019). Repair or replacement of damaged xylem is primarily accomplished through the mobilization of stored C (Tomasella et al., 2017; Trifilò et al., 2019), presenting another potential C pathway that may be prioritized over radial growth in anisohydric species following drought conditions.

The sensitivity of both species to late spring frosts — and the relatively steeper slope associated with larch — (Fig. 2; Table 1) fits within our expectations regarding both the negative impact of late spring frosts and the idea that such events have an outsized impact on deciduous species (Vitasse et al., 2014). While most trees have the ability to re-foliate in the wake of these events without long-term consequences (D'Andrea et al., 2019; Vitasse et al., 2014), repeated events in a short period of time may compound and/or amplify negative impacts on carbon balance, leading to reduced growth resistance in sensitive species (Rubio-Cuadrado et al., 2021).

In the case of early autumn frosts, the strong negative growth response of western larch and the lack of a response in Douglas-fir fits with our mechanistic understanding that such an event can interfere with remobilization of nutrients in deciduous species (Norby et al., 2003). Nitrogen reabsorption from old leaves in deciduous species directly influences rates of canopy photosynthesis (Hikosaka, 2005), further emphasizing the importance of this process and the consequences that early autumn frost can have on subsequent C assimilation.

Ultimately, our results suggest that species-specific traits drive divergent responses of these co-occurring conifer trees to seasonal climate stressors. Differences in how the growth of each species responds to drought implies that — at least in the context of short-term drought events — the “riskier” anisohydric strategy employed by larch results in relatively higher radial growth/wood production in the drought year. However, the growth declines we observed in western larch in the year following drought may imply that these reductions are simply delayed. Repeated climate-induced growth reductions are likely to diminish or delay stand yields in the context of timber harvest, and non-stem C sinks

have much shorter turnover times (Kannenberg, Novick, Alexander, et al., 2019) indicating that these negative lagged effects have the potential to alter long-term C dynamics.

4.2. Species-specific patterns of resistance, resilience, and recovery of growth following extreme climate events

Differences in response index values between species generally followed our expectations predicated on the relationships we observed in our climate-growth model. Douglas-fir was more resistant and resilient to autumn frost events and the legacy effects of previous summer drought, indicating that evergreen leaf habit and more conservative (i.e., isohydric) water use strategies confer protection against radial growth reductions in response to these events. Mean recovery values were ≥ 1 for both species across all event types (Fig. 3) suggesting that negative growth impacts from these events were generally limited to the annual ring where growth impacts manifested (see Methods). Larch showed greater recovery values in the wake of spring frost suggesting that despite lower resistance and resilience, growth in the two years following the event year as compared to the event year was greater relative to that of Douglas-fir. This likely reflects the differing relationships between larch and Douglas-fir in response to late spring frost (Fig. 2) — larch is more severely affected, resulting in a relatively smaller denominator for Rc calculations and correspondingly greater overall values.

4.3. Stand density effects on resistance, resilience, and recovery of radial growth following extreme climate events

The greater resistance and resilience of western larch radial growth in low-density stands as compared to high-density stands in the case of previous summer drought (Fig. 4; Table 3) supports our hypothesis that reduced competition would mitigate the negative growth impacts of drought events. Increased resistance to previous year drought in low-density stands is likely the outcome of reduced rates of local-scale evapotranspiration (Roche et al., 2018; Y. Wang et al., 2019) resulting in relatively greater soil moisture when stem densities are lower (del Campo et al., 2019; Jiménez et al., 2008; Tatum et al., 2025). This harmonizes with our measurements of soil moisture in which low-density stands exhibited greater average summer VWC across multiple decades (Fig. 5). This indicates that the intensity of drought stress experienced by trees in low-density stands was less than their high-density counterparts, conferring increased resistance and resilience to the expected impacts of broader climatological drought conditions.

Increased resistance and resilience to spring frost in western larch grown in a low-density environment likely reflects the greater long-term nutrient and carbohydrate capital of those trees. Trees growing in low-density stands experience less competition for light, water, and soil nutrients, and are likely to have relatively greater NSC reserves (Cao et al., 2024). Thus, these trees tend to be more vigorous and can produce a second set of buds and leaves with a relatively smaller impact on allocation to other functions. Our general results coincide with the findings of Rubio-Cuadrado et al. (2024) that thinning can mitigate negative growth impacts stemming from spring frost events; however, the exact mechanisms and their relative importance are difficult to discern. Furthermore, we acknowledge the limitations associated with the small number of extreme events available for analysis ($n = 3$) and any potential idiosyncrasies of those specific years. Future research should attempt to integrate phenology, microclimate, and whole tree C data to disentangle the mechanisms behind this effect.

The lack of differentiation in estimated response between western larch trees in our two experimental densities to autumn frost suggests that the mechanisms by which autumn frost reduces subsequent radial growth are density independent. Given the critical role that the reabsorption of foliar nutrients plays in the subsequent photosynthetic

capacity (Hikosaka, 2005) and growth (May and Killingbeck, 1992) of deciduous species — and the potential for an early autumn frost to interfere with this process (Norby et al., 2003) — these events likely result in proportionally greater losses which are independent of tree size, stand density, or previous nutrient stocks. In the case of spring frost, trees still have their nutrient and NSC capital primarily stored in tissues which remain tolerant to freezing temperatures — tissue damage and death in the response to these events is limited to tissues that have begun the process of exiting dormancy (Vitra et al., 2017). The existence of these stores is evidenced by the presence of reserve buds which are activated in the wake of spring frost damage (Baumgarten et al., 2023).

Severe autumn frosts represent an inverse scenario, where only the nutrients/NSCs that have been remobilized are “safe” and remaining foliar stocks are lost. Taken together, this implies that while increases in individual tree vigor and carbon/nutrient availability in low-density stands (Cao et al., 2024; Thibodeau et al., 2000) can compensate for smaller scale losses associated with spring frosts, higher proportional reductions in nutrient stocks in the wake of autumn frost events result in more uniform negative effects, and they appear insensitive to stand density and competition. Further investigation of these dynamics will be necessary to develop a more complete understanding of the potential risks of autumn frost events in deciduous species.

4.4. Conclusions and management implications

The divergent responses to seasonal climate stressors we observed in western larch and Douglas-fir underscore the principle that no adaptive trait — or set of traits — is universally advantageous under a given climate regime. The anisohydric nature of larch allows for uninterrupted radial growth rates in a year when drought conditions occur, potentially conferring an advantage on short timescales. However, the negative effects of drought on larch radial growth manifest in the following year. The deciduous leaf habit of larch was also found to confer greater sensitivity to both spring and autumn freezing events than the evergreen Douglas-fir. This, coupled with the expected increase of such events (e. g., Allen et al., 2010; Ma et al., 2019; Stott, 2016), suggests that the radial growth of deciduous species may be more sensitive to future climatic conditions compared to co-occurring evergreen species. While our two study species do not capture the full range of trait variation present across temperate-boreal forests, the divergent responses to extreme seasonal climate events which we observed emphasize the general benefits of mixed-species stands — and associated functional trait variation — for promoting resistance and resilience of radial growth to a wide variety of potential stressors and disturbance events (Jucker et al., 2014; Zhang et al., 2012).

Our experimental results demonstrate that stand density management can diminish negative effects of extreme climate events on growth under a broader set of traits and environments than previously demonstrated. Early thinning treatments improved resistance and resilience to both spring frost events and the lagged effects of drought in the anisohydric, deciduous western larch, likely by increasing soil moisture, nutrient, and light availability on a per tree basis. Our finding that forest thinning can reduce the negative impact of late spring frosts on radial growth in western larch represents a notable and under-recognized benefit of forest density reduction treatments. Together, these insights can help guide future research and adaptive management of *Larix* throughout its circumboreal range (Mamet et al., 2019; S. Wang et al., 2025; Zhang et al., 2024), as well as that of other deciduous species which are sensitive to spring frost events.

More broadly, competition reduction with density management can produce a wide range of long-term benefits in a variety of forest types. Much of the research regarding these practices has focused on the mitigation of drought impacts in a limited number of species and climate zones (see Sohn et al., 2016), the enhancement of resistance and resilience to fire-caused tree mortality and injury (Agee and Skinner, 2005; Brodie et al., 2024), and reduction of insect-caused mortality (Egan

et al., 2010; Hood et al., 2016). Here, we show that improved resistance and resilience to extreme climate events — specifically summer drought and spring frost — should be included in the conversation regarding the long-term benefits of early thinning, and that these findings can be extended to forests in the temperate-boreal transition zone. As the frequency and severity of both drought and growing season frost events increase alongside other disturbances, management practices that promote the development of mixed-species stands and reduce competitive stress among trees will be critical for sustaining forest productivity, maintaining ecosystem services, and supporting long-term carbon storage.

CRediT authorship contribution statement

Josh Beisel: Writing – original draft, Visualization, Methodology, Investigation, Conceptualization. **Colin T. Maher:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Justin S. Crotteau:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Andrew J. Larson:** Writing – review & editing, Resources, Methodology, Conceptualization.

Declaration of Competing Interest

The authors of this manuscript have no conflicts of interest to disclose.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123493.

Data availability

Data and R code supporting this analysis is available at <https://doi.org/10.6084/m9.figshare.30998029>

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