Forest Ecology and Management 619 (2026) 124026

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

The influence of provenance on climate response and drought resilience of lodgepole pine in the southern Rocky Mountains, U.S.

Katarina J. Warnick [a,*,1], Wade T. Tinkham [b], Mike A. Battaglia [b], Katherine M. Nigro [b,c], Sarah J. Hart [a]

[a] Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, CO, USA
[b] USDA Forest Service Rocky Mountain Research Station, Fort Collins, CO, USA
[c] Oak Ridge Institute for Science and Education, Oak Ridge Associated Universities, Oak Ridge, TN, USA

ARTICLE INFO

Keywords:
Pinus contorta var. latifolia
Provenance
Assisted migration
Climate adaptation
Drought response
Dendrochronology

ABSTRACT

Climate change is increasing temperatures and the frequency and severity of drought events in the western United States (U.S.), raising concerns about the persistence of widespread, ecologically important species like lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.). We sampled a long-term provenance trial in north-central Colorado, U.S. to examine intraspecific differences in tree size, survival, growth-climate response, and drought tolerance. Using thirty years of tree-ring data and climate data relativized as the climatic distance between provenances and planting site, we evaluated the influence of provenance climate on growth-climate relationships and resistance, recovery, and resilience to a 2002 drought. We found that provenance did not impact tree size and survival, but a weak trend suggests that provenances from areas with greater growing season precipitation had larger average basal area increments. Overall, local site climate influenced annual growth more than provenance origin. Significant differences in drought resistance were found among provenances, notably, populations from warmer and wetter climates showed significantly greater resistance to drought than populations from colder, drier climates. Resilience differed between provenances with populations from cooler and wetter growing seasons showing greater resilience than populations from colder and drier growing seasons. Findings suggest that while lodgepole pine from its more southern range may exhibit flexibility under favorable conditions, climate-informed seed sourcing may become increasingly important as drought frequency and intensity increase. Long-term provenance trials provide critical insight for guiding forest adaptation efforts like forest assisted migration to enhance forest resilience under future climate change.

1. Introduction

Climate change is reshaping forest ecosystems across the globe, with rising temperatures as the primary driver of these shifts (Allen et al., 2010; IPCC et al., 2023). Trees, the foundational element in forests, support ecosystem productivity, biodiversity, and carbon storage, but are particularly vulnerable to climatic changes (Birdsey et al., 2019; Renwick and Rocca, 2015; Twardek et al., 2023). Historically, climate has shifted slowly, allowing trees to adapt or migrate to more suitable habitats over the course of thousands of years through seed dispersal across relatively unfragmented landscapes (Renwick and Rocca, 2015). Because trees are locally adapted to their growing environments, rapid shifts in climate can leave populations vulnerable to maladaptation or even extirpation (Aitken and Whitlock, 2013; Aitken et al., 2008; Rehfeldt et al., 1999; Williams and Dumroese, 2013). Indeed, there is evidence that the rates of tree population migration are being outpaced by the rapid rate of climate change (Aitken and Bemmels, 2015; Bower et al., 2024; Gray et al., 2016). As a result, many tree populations now face growing environments that are beyond their adaptive capacity (Wang et al., 2006).

One management strategy aimed at overcoming the lag in tree adaptation to climate is forest assisted migration (FAM), or the intentional movement of seeds to locations where they are better matched to projected future climates (Park and Talbot, 2018; Pedlar et al., 2012; Royo et al., 2023; Sáenz-Romero et al., 2020; Williams and Dumroese, 2013). For widely distributed tree species, assisted population

* Corresponding author.
E-mail address: kjwarnick@mac.com (K.J. Warnick).
[1] Present address: College of Forest Resources and Environmental Science, Michigan Technological University, Houghton, MI, U.S.A.

https://doi.org/10.1016/j.foreco.2026.124026
Received 13 April 2026; Received in revised form 30 May 2026; Accepted 1 June 2026
Available online 29 June 2026

migration, or moving populations within a species' natural range, is particularly relevant, as it maintains species ecological function while introducing new populations that are better suited to future expected climate conditions (Park and Talbot, 2018; Ste-Marie et al., 2011). This facet of FAM is generally considered less risky than other types of assisted migration (Bower et al., 2024; Pedlar et al., 2012). Practitioners and researchers posit that reforestation after disturbance is the most practical means of implementing FAM, and when implemented deliberately, seed transfer can match populations to projected climate and enhance resilience and genetic diversity (Liepe et al., 2016; Worrall and Rehfeldt, 2021).

The intentional movement of tree populations to areas where they are best adapted has been a common forestry practice for centuries (Langlet, 1971). Transfers are traditionally based on evidence of local adaptations from provenance experiments, which compare different populations of trees grown in a common environment. Past provenance experiments demonstrate that population performance differs based on a tree's adaptation to its local climate (Aitken et al., 2008; Risk et al., 2021) but also show maladaptation of some populations when transferred far outside their provenance climate origin (McLane et al., 2011). In this context, provenance climate refers to the historical climate conditions at a population's seed source location. Local climate refers to the climate conditions experienced at a planting or growing site. Differences between provenance climate and local climate, commonly called climate distance, can alter tree growth and survival following transfer. Findings surrounding local adaptation of trees to their climate led to the development of seed transfer guidelines, which establish how far in elevation, latitude or longitude a seed can be moved while still maintaining its adaptation to the local environment (Rehfeldt, 1983). However, rapid climate warming may challenge established seed transfer guidelines (Gray and Hamann, 2013; Pedlar et al., 2012). FAM practices are intended to re-align populations with their optimal climate conditions in the face of a shifting baseline so that forests maintain productivity (Pedlar et al., 2012). Although FAM has been implemented experimentally across the world, it has not been widely adopted (Twardek et al., 2023). Identifying suitable seed sources and clarifying population-level variation in climate responses is critical in moving FAM from concept to practice.

Rocky Mountain lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.; hereafter, "lodgepole pine") is one of the most widespread conifer tree species in North America, with a distribution that spans from its northern range in Yukon, Canada to its southern range in the Southern Rocky Mountains in Colorado, United States (U.S.) (Anderson, 2003; Lowery, 1984). Provenance research has shown that northern lodgepole pine populations exhibit substantial intraspecific variability in climate response due to local adaptations (Gray et al., 2016; Illingworth, 1978; Isaac-Renton et al., 2018; Rehfeldt, 1988). These local adaptations offer an opportunity to leverage this variability to sustain lodgepole pine persistence in western North America (Williams and Dumroese, 2013) and to potentially plant it beyond its current geographic range (Zhao and Wang, 2023). Despite extensive research on the growth-climate relationships of northern lodgepole pine populations (Chhin et al., 2008; McLane et al., 2011; Montwé et al., 2016), comparatively little is known about southern lodgepole pine populations in the western U.S., particularly relating to drought, which is a major threat facing these forests (Allen et al., 2010; Halofsky et al., 2018; Worrall and Rehfeldt, 2021). This knowledge gap constrains the development of climate-informed seed transfer guidelines in this region.

In its southern range, lodgepole pine is a dominant subalpine species with intraspecific variability in annual radial growth responses to climate (Fritts, 1974; Villalba et al., 1994). Its production of serotinous cones allows for the persistence of viable aerial seed banks after high-severity fire, promoting rapid post-fire regeneration and giving it the ability to dominate large swaths of forested landscapes (Lowery, 1984; Rhoades et al., 2022; Rhoades et al., 2025). Despite this, the species is increasingly vulnerable to climate change, particularly in western U.S. subalpine forests (Halofsky et al., 2018). Lodgepole pine populations in this region are at their southern range margin, making them more sensitive to climate maladaptation compared to more northern populations because they are already living at the edge of their climatic tolerances (Burns and Honkala, 1990; Leech et al., 2011; Renwick and Rocca, 2015). Bioclimatic niche models further project widespread habitat loss and the potential extirpation of southern lodgepole pine populations in this region due to climate change (Worrall and Rehfeldt, 2021).

The goal of this study is to investigate growth-climate relationships of southern lodgepole pine and compare drought resilience across climatically diverse populations. Specifically, our research is driven by two main questions. First, does seed source climate influence the radial growth responses of lodgepole pine trees to climate in its southern range? Second, do lodgepole pine trees from drier source climates exhibit greater radial growth drought resistance, recovery, and resilience than those from less dry source climates? For our first question, we hypothesize that seed-source climate influences the radial growth responses of lodgepole pine trees in its southern range, given that this has been found elsewhere in the species range (Chhin et al., 2008; Illingworth, 1978; Montwé et al., 2016). For our second question, we hypothesize that trees from drier source climates will exhibit greater radial growth drought resistance, recovery, and resilience at our study site, due to adaptations shaped in response to their source climates, as was found at more northern sites in British Columbia, Canada (Isaac-Renton et al., 2018; Montwé et al., 2016). By quantifying the drought resilience of different seed sources of lodgepole pine in its southern range, this study contributes knowledge towards targeted FAM efforts in the western U.S. region aimed at supporting long-term forest health and productivity for future generations.

2. Methods

2.1. Study Site

We sampled a 40-year-old provenance trial in Fraser Experimental Forest (FEF) in north-central Colorado, U.S. (Fig. 1). It is located in a subalpine, high-elevation (2706 m) ecosystem that experienced an average temperature of 3°C and average annual precipitation of 590 mm throughout our study period, 1992–2021, with most precipitation occurring during the late-winter and mid-spring months (Wang et al., 2016). To establish the experiment, cones were collected from lodgepole pine trees in 1979 along a latitudinal (37.6°N to 48.3°N) and elevational (1372 m to 3506 m) gradient, resulting in 34 populations from La Veta Pass, Colorado to Marias Pass, Montana (Moore, 1981; Fig. 1). The 34 populations represent gradients in mean annual temperature from −1.3°C to 5.9°C and mean annual precipitation from 225.8 mm to 1035.5 mm (Wang et al., 2016; Supplementary Table 1; Supplementary Figure 1). Seeds were greenhouse-germinated and grown for two growing seasons before being outplanted in a clearcut lodgepole pine stand in 1982. The planting involved 45 seedlings from each of the 34 provenances, arranged randomly in three adjacent blocks measuring 84 m x 84 m each. Within each block, 447 seedlings were planted at a square spacing of 3.0 m with one empty space, totaling 1341 trees across three blocks (Moore, 1981).

2.2. Field Sampling

Field data were collected in 2022 and 2023. Survival (live/dead) was recorded for each individual (n = 1341). Radial growth, diameter at breast height (DBH), and height measurements were collected on a sample of trees (n = 212) distributed across the three blocks and across provenances. To reduce any potential confounding effects of competition, we limited our sampling to trees that were not located on the edge of a block and had live, intact neighbors on all four sides. These requirements, coupled with tree mortality, limited our sampling

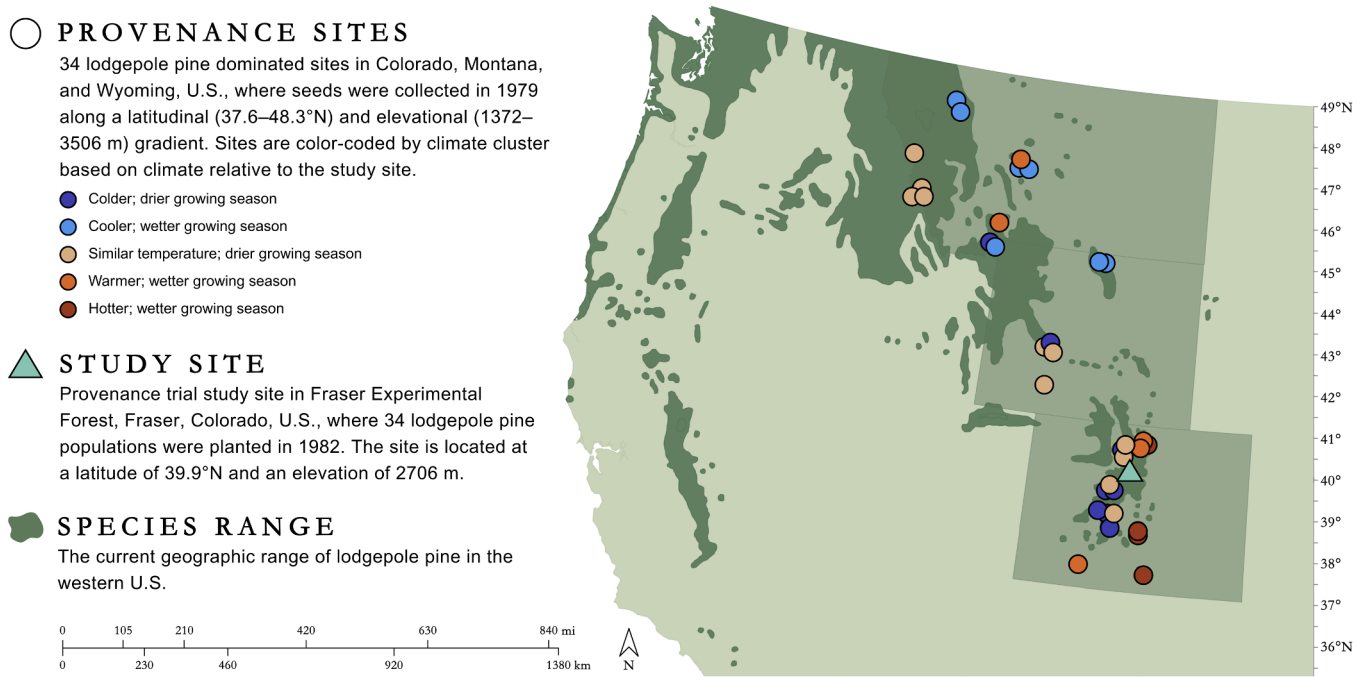

Fig. 1. Geographic distribution of lodgepole pine (*Pinus contorta* var. *latifolia*) provenance sites and study site location in the western United States (U.S.). Circles represent the 34 provenance sites from which seed was collected in 1979 across Colorado, Montana, and Wyoming, spanning a latitudinal (37.6–48.3°N) and elevational (1372–3506 m) gradient. Provenance sites are color-coded by climate cluster derived from k-means clustering based on temperature and precipitation conditions relative to the study site. The triangle indicates the Fraser Experimental Forest provenance trial study site in Fraser, Colorado, U.S., where populations were planted in 1982 (39.9°N, 2706 m). The shaded area represents the current geographic range of lodgepole pine in the western U.S. (Little, 1971).

distribution and resulted in sampling 2–6 trees per provenance for a total of 160 trees. Annual radial growth was sampled by extracting one increment core from each sample tree using a 5.15 mm diameter increment borer at approximately 0.30 m above ground level to capture early growth patterns. Our single-core per individual approach was informed by Bottero et al. (2017) and was selected because the site occurs on a relatively flat stand, where we expected compression wood to be minimal.

2.3. Lab Processing

Tree cores were processed using standard dendrochronological techniques (Speer, 2010). Cores missing the pith by >3 rings or obscured by knots were resampled in 2023. Cores that lacked distinguishable annual rings due to poor sampling or preparation were excluded from further analysis. To ensure that annual rings were assigned to the correct year, we first visually crossdated tree-ring series using the list method outlined by Yamaguchi (1991) (Supplementary Figure 2), followed by graphical crossdating which was performed while measuring tree-ring series using Cybis Dendro Dating Program software (CDendro; Larsson, 2003; Maxwell and Larsson, 2021). These methods have been shown to be just as accurate as traditional skeleton-plotting (Maxwell et al., 2011) and are particularly efficient when tree-rings are generally wide and missing rings are rare, such as what we observed here. The *dplR* package (Bunn, 2008, 2010; Bunn et al., 2023) was used in R (R Core Team, 2023) to statistically confirm crossdating. Cores with an interseries correlation <0.4 were excluded to ensure accurate dating. The final dataset included 160 tree cores (Table 1). We selected the years 1992–2021 as our study period based on the availability of clear and consistently crossdated ring-width data and to focus on a period during which climatic influences on growth were more consistently reflected, as early establishment effects may obscure growth-climate relationships. Annual basal area increment (BAI) was calculated for each tree during this period to assess annual radial growth.

2.4. Climate Data

To characterize the climatic conditions that provenance trees were adapted to prior to seed collection, we used 30-year normal monthly climate data from ClimateNA (Wang et al., 2016) using latitude, longitude, and elevation. ClimateNA calculates site specific climate variables first by bilinear interpolating the four neighbor grid cells based on each point's distance to the cell centers and then adjusts this value for elevation by calculating a local lapse rate by fitting a linear regression of climate difference and elevation difference for the cell and the eight surrounding cells. From this we extracted 30-year normal (1951–1980) monthly climate data for FEF and each provenance site to calculate climate transfer distances and extracted actual monthly climate data (from 1992 to 2021) for FEF to calculate correlations between annual radial growth and annual climate at the plantation site. Four climate variables were selected based on previous studies on lodgepole pine: minimum monthly temperature (Tmin), mean monthly temperature (Tave), maximum monthly temperature (Tmax), and monthly precipitation (PPT) (Chhin et al., 2008; Savva et al., 2007). Given that radial growth of lodgepole pine is often correlated with climate conditions over several months (Chhin et al., 2008; Villalba et al., 1994), we conducted a sliding window analysis for each FEF climate variable to identify the periods most strongly associated with annual BAI. Using the *dendroTools* package (Jevšenak, 2020) in R, we tested windows ranging from 1 to 12 months from the previous April to the current October of each growth ring year. This approach allowed both prior- and current-year climate conditions to be evaluated, as climate during the previous growing season can influence tree growth during the current season through lagged physiological effects (Teets et al., 2022; Villalba et al., 1994).

Using the climate windows for each metric with the strongest correlation to annual BAI, 30-year normal (1951–1980) monthly climate data from each provenance site was summarized (either averaged for temperature or summed for precipitation across the best window) and relativized to the FEF 30-year climate window average (also

Table 1
Location, elevation, and the number of trees sampled and dated (n) in 2022 and 2023 for the 34 provenances (n = 160) (Moore, 1981). Provenances are grouped by climate cluster (climate distance from the planting site climate; see Section 2.5 for details) and sorted by latitude.

Climate cluster	Provenance	Location	Lat (°)	Long (°)	Elev (m)	n
Colder; drier growing season	CO−6	Maysville, CO	38.5	−106.3	3338	3
	CO−8	Tincup, CO	38.8	−106.4	3079	6
	CO−9	Tincup, CO	38.8	−106.4	3506	4
	CO−10	Copper Mountain, CO	39.4	−106.3	3178	5
	CO−11	Copper Mountain, CO	39.4	−106.3	3201	7
	CO−14	Rand, CO	40.4	−106.1	2835	4
	WY−5	Lander, WY	42.7	−108.9	2920	3
	MT−12	Schusters Place, MT	44.9	−111.4	2287	4
Cooler; wetter growing season	WY−1	Burgess Junction, WY	44.8	−107.4	2287	2
	WY−2	Burgess Junction, WY	44.8	−107.5	2591	5
	MT−11	Grayling, MT	44.8	−111.2	2012	5
	MT−2	Forest Green, MT	46.8	−110.7	2164	6
	MT−1	Wolsey, MT	46.8	−110.8	1875	6
	MT−5	Snowslip, MT	48.3	−113.4	1524	6
	MT−4	Snowslip, MT	48.3	−113.4	1555	5
Similar temperature; drier growing season	CO−7	Buena Vista, CO	38.8	−106.3	3003	4
	CO−12	Minturn, CO	39.5	−106.4	2652	5
	CO−13	Granby, CO	40.3	−106.1	2652	5
	CO−15	Rand, CO	40.4	−106.1	2683	6
	WY−4	Point of Rocks, WY	41.7	−108.9	2591	6
	WY−6	Atlantic City, WY	42.6	−108.8	2668	3
	WY−3	Lander, WY	42.7	−108.9	2439	4
	MT−9	Sula, MT	45.7	−113.9	1951	6
	MT−7	Colter Creek, MT	45.7	−114.0	2134	7
	MT−8	Colter Creek, MT	45.7	−114.0	2210	5
	MT−6	Hot Springs, MT	46.7	−114.5	1372	5
Warmer; wetter growing season	CO−2	Livermore, CO	40.6	−105.5	2588	6
	CO−16	Livermore, CO	40.6	−105.5	2805	3
	MT−10	Big Sky, MT	45.4	−111.2	1783	3
	MT−3	Neihart, MT	47.0	−110.8	1561	6
Hotter; wetter growing season	CO−3	Muleshoe, CO	37.6	−105.2	2805	4
	CO−4	Cañon City, CO	38.4	−105.4	2744	4
	CO−5	Parkdale, CO	38.5	−105.4	3049	3
	CO−1	Stove Prairie Landing, CO	40.6	−105.4	2378	4

summarized to the best windows) to assess climate transfer effects following Savva et al. (2007) using Eq. 1.

$$Climate\ Distance_i = Provenance\ Norm_i - FEF\ Norm_i \quad (1)$$

Where $Climate\ Distance_i$ is the difference of the 30-year *Provenance Norm* minus the 30-year *FEF Norm* for a single climate variable (i). Positive Climate Distance values indicate that the provenance site climate normal is warmer/wetter than the observed climate at FEF, representing a transfer to a drier/colder site. Negative values indicate that the provenance site climate normal is cooler/drier than the observed climate at FEF, representing a transfer to a wetter/warmer site.

2.5. Climate Clusters

Provenances were grouped into climate-based categories using k-means clustering on the window-summarized climate distance metrics after removing collinear variables ($|r| \geq 0.7$). Clustering was performed using *tidymodels* (Kuhn and Wickham, 2020) in R, and the number of clusters (k) was selected using the "elbow" method to identify the clustering that minimized within group sum of squares and maximized between group sum of squares. Clusters were assigned descriptive labels (e.g., "Cooler; wetter growing season") based on the relative position of cluster centroids along temperature (Tave) and precipitation (PPT) gradients.

2.6. Climate Cluster Influence on Survival, DBH, and Height

The climate clusters were used as categorical predictors to explain differences in field observations of survival, DBH, and height. Survival proportion was determined for each provenance within each climate cluster and compared using a one-way analysis of variance (ANOVA), followed by a Tukey's HSD post-hoc test using *emmeans* in R (Lenth, 2025). DBH and height were analyzed in a similar manner using ANOVA followed by a Tukey's HSD post-hoc test.

2.7. Climate Analysis

We fit two sets of models to evaluate annual climate effects on growth at FEF during the study period. Site-level growth-climate relationships were assessed using univariate linear mixed-effects models to predict annual BAI as a function of each FEF climate variable. Annual FEF climate predictors were summarized to optimal seasonal windows identified in the sliding window analysis (Section 2.4). Provenance and year were included as random effects. Models were fit in R using the *lme4* package (Bates et al., 2015) in R. Both linear and quadratic model forms were tested; quadratic terms were included to capture potential nonlinear responses such as thermal or moisture optima (Savva et al., 2007).

To evaluate climate distance effects, we averaged the annual BAI for each tree as the response variable (one observation per tree) and constructed separate models where each provenance climate distance metric was used as the only predictor variable (Savva et al., 2007) and provenance identity was included as a random effect. Models were fit using *lme4* (Bates et al., 2015) in R. Both linear and quadratic model forms were also tested in this set of models, as climate transfer functions often follow a quadratic form (Rehfeldt et al., 1999; Rehfeldt et al., 2002; Savva et al., 2007).

For both model sets, the best-fitting model form (linear or quadratic) for each climate variable was determined by selecting the model with the lowest value of the Akaike Information Criterion (AIC). For variables with significant model fits, model performance was evaluated using marginal and conditional R^2 (Nakagawa and Schielzeth, 2013; Nakagawa et al., 2017) from the *performance* package (Lüdecke et al., 2021) in R. We tested spatial autocorrelation by assessing model residuals in relation to tree planting position using Moran's I from the *ape* package (Paradis and Schliep, 2019) in R. We confirmed that final models were not affected by spatial autocorrelation (Supplementary Figure 3).

2.8. Drought Resilience Analysis

We used the Standardized Precipitation Evapotranspiration Index (SPEI) to evaluate drought response by calculating SPEI at 1- to 24-month timescales for 1992–2021 using the *SPEI* package (Beguería

and Vicente-Serrano, 2023) in R. We applied the same window selection process used in our climate analysis to select the SPEI window with the greatest correlation to average annual BAI by testing different seasonal windows and durations. BAI was used rather than detrended ring-width chronologies to preserve interpretable variation in growth response relevant to drought analyses (Biondi, 1999; Bottero et al., 2017). To assess whether detrending was warranted, we evaluated long-term temporal patterns in BAI through visual inspection and linear mixed-effects models. We used window selection to identify drought periods using a threshold of ≤ -0.5 SPEI. This threshold was selected to capture the mild to moderate droughts characteristic of the subalpine system at FEF and allow us to select a drought with sufficient temporal distance to other droughts to avoid compound drought effects. We then investigated drought impacts on growth using BAI (Biondi and Qeadan, 2008; Bottero et al., 2017).

For each tree, we quantified resistance (*Rt*), recovery (*Rc*), and resilience (*Rs*) following Lloret et al. (2011) using average BAI four years before and after the drought (Eqs. 2–4).

$$Rt_i = Dr_i \,/\, PreDr_i \tag{2}$$

$$Rc_i = PostDr_i \,/\, Dr_i \tag{3}$$

$$Rs_i = PostDr_i \,/\, PreDr_i \tag{4}$$

Where for each tree (i), *Dr* is the average BAI during the drought, *PreDr* is the average BAI for the four years prior to the drought year, and *PostDr* is the average BAI for the four years after the drought year. *Rt* reflects the ability of a tree to maintain growth during a drought, *Rc* represents post-drought growth compensation, and *Rs* reflects the capacity to return to pre-drought growth levels after a drought (Lloret et al., 2011). We selected the four-year time interval to reduce interannual variation and noise from other drought events. We analyzed differences in *Rt*, *Rc*, and *Rs* among climate clusters using ANOVA with provenance as a random effect and conducted Tukey's HSD post-hoc tests for pairwise comparisons (Lenth, 2025).

3. Results

3.1. Tree-Ring Analysis

The final tree-ring dataset included 160 cores spanning 1984–2022, though it was restricted to our study period, 1992–2021, to maximize overlap among trees and maintain consistent sampling depth. Visual and statistical crossdating showed noticeable synchrony in patterns of annual growth across individuals, particularly in marker years, such as during droughts in 2002, 2012, and 2016. Mean ring-width averaged 2.09 mm across provenances and ranged from 1.302 to 3.268 mm, indicating modest variation in annual radial growth among seed sources (Supplementary Table 2). Standard deviation of ring-widths ranged from 0.551 to 1.709 mm, and Gini coefficients ranged from 0.13 to 0.428, suggesting modest interannual growth variability within provenances (Supplementary Table 2). First-order autocorrelation (AR1) values ranged from 0.50 to 0.919 (mean = 0.80), indicating moderate temporal persistence in annual growth (Supplementary Table 2; Supplementary Figure 4).

To evaluate whether long-term temporal trends in BAI warranted detrending prior to further analyses, we assessed annual BAI visually and using a linear mixed-effects model with year as a fixed effect and tree ID as a random effect to account for repeated measurements (Supplementary Table 3, Supplementary Figure 5). Although year had a significant effect on BAI ($F = 217.44$, $p < 0.001$) growth patterns were nonlinear and exhibited substantial interannual variability rather than a strong age-related trend typically observed in raw ring-width chronologies (Supplementary Table 3; Supplementary Figure 5). Therefore, BAI was retained for subsequent climate and drought analyses.

3.2. Analysis of Climate Clusters

K-means clustering of the climatic distance metrics retained after collinearity testing was optimized to five climate groups ($k = 5$; Fig. 1). These clusters represent gradients in provenance climate distances from FEF, ranging from cooler/warmer to drier/wetter origins. Geographic distribution of clusters shows that similar climate types can span wide latitudinal ranges across multiple states (Fig. 1), and that the sampled provenances span the dominant climatic conditions of lodgepole pine across its range in the southern Rocky Mountains (Fig. 2).

3.3. Climate Clusters vs. Survival, DBH, and Height

We found no significant differences in tree survival, DBH, or height among climate clusters. Survival was moderate across all clusters, with the mean ± standard error ranging from 64.6 ± 4.1% (colder; drier growing season) to 71.7 ± 6.1% (hotter; wetter growing season) (Table 2). Mean DBH ranged from 14.3 ± 0.5 cm (colder; drier growing season) to 15.4 ± 1.5 cm (warmer; wetter growing season) with no significant differences among clusters ($p > 0.05$; Supplementary Table 2). Mean height ranged from 7.4 ± 0.2 m (colder; drier growing season) to 8.1 ± 0.8 m (warmer; wetter growing season), with no significant differences detected ($p > 0.05$; Table 2; Supplementary Table 2).

3.4. Relationship Between Growth and Plantation Climate

At the planting site (FEF), BAI from 1992 to 2021 was significantly related to seasonal temperature and precipitation variables derived from optimal climate windows (Table 3; Supplementary Figure 6). The window analysis indicated that June through September (growing season) mean minimum monthly temperature (Tmin), June through August (growing season) total monthly precipitation (PPT), September of the previous year to January (fall/winter) mean monthly temperature (Tave), and September of the previous year to January (fall/winter) mean maximum monthly temperature (Tmax) had the strongest relationship with annual BAI. Evaluation of collinearity retained June-September Tmin, June-August PPT, and previous September-January Tave and removed previous September-January Tmax.

Evaluation of how the planting site climate impacted annual BAI highlighted both linear and quadratic effects (Table 4). Growing season precipitation (June-August PPT) was positively associated with BAI in a linear form, with annual growth increasing by ~13 mm^2 per 1 mm increase in growing season precipitation (Fig. 3a; Table 4). Growing season mean minimum temperature (June-September Tmin) exhibited a significant quadratic relationship with BAI, with growth declining at both low and high summer Tmin extremes (Fig. 3b; Table 4). Mean fall/winter temperature (previous September-January Tave) also showed a quadratic relationship, where years with fall/winter temperatures above 1°C or below −1°C were associated with decreased growth rates (Fig. 3c). Overall, the climate variables explained relatively little variation compared to the random effects in the models.

3.5. Relationship Between Performance and Provenance Climate

3.5.1. Univariate Models of Climate Distance and BAI

In provenance-level analyses, only two of the climate distance metrics produced weak relationships with BAI (Table 5). The quadratic model for mean temperature (previous September-January Tave) had a lower AIC (AIC = 2127.242) than the linear form (AIC = 2131.638); however, the quadratic term was not significant, suggesting little evidence for a non-linear response or a clear optimum near climate distance = 0. Therefore, the linear form was retained as the best model fit (Table 5). The linear model for mean growing season precipitation (June-August PPT) had a lower AIC (AIC = 2132.984) than the quadratic form (AIC = 2134.895) and was retained as the best model fit (Table 5).

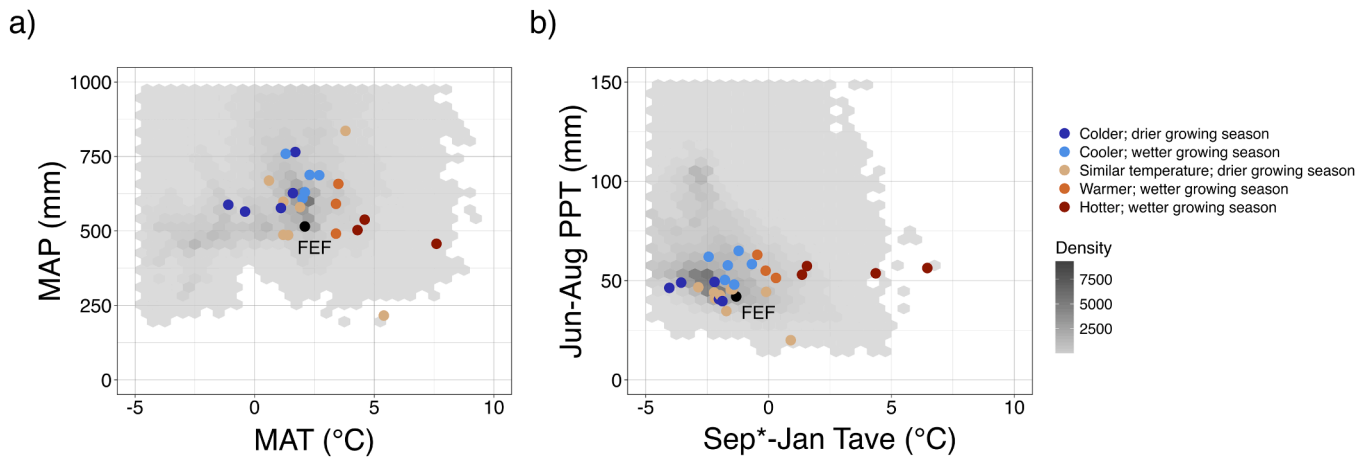

Fig. 2. Lodgepole pine climate space characterized by (a) mean annual precipitation (MAP, mm) and mean annual temperature (MAT, °C) and (b) June through August (growing season) total monthly precipitation and previous September to January (fall/winter) mean monthly temperature used in the climate cluster analysis. In both panels, the background hexagonal shading represents the density of climates across the range of *Pinus contorta* Dougl. var. *latifolia* Engelm., where darker shades indicate greater frequency. This was constructed by extracting ClimateNA data (Wang et al., 2016) from within the variety's current range, as defined by Mathys et al. (2014) and Little (1971). Individual points are colored by the climate cluster of each provenance site, with the black point indicating the Fraser Experimental Forest study site.

Table 2
Survival, DBH, and height were summarized as the mean (± standard error) of the provenances belonging to each climate cluster and compared through a series of one-way ANOVAs that identified no significant differences among clusters ($p > 0.05$), as indicated by all clusters sharing the same letter.

Climate cluster	Survival (% live)	DBH (cm)	Height (m)
Colder; drier growing season	66.0 (2.9) a	14.3 (0.5) a	7.4 (0.2) a
Cooler; wetter growing season	65.8 (5.2) a	14.4 (0.5) a	7.9 (0.3) a
Similar temperature; drier growing season	64.6 (4.1) a	14.8 (0.4) a	7.8 (0.2) a
Warmer; wetter growing season	65.9 (3.0) a	15.4 (1.5) a	8.1 (0.8) a
Hotter; wetter growing season	71.7 (6.1) a	15.3 (1.3) a	7.6 (0.4) a

Table 3
Climate variables for Fraser Experimental Forest extracted from ClimateNA (Wang et al., 2016) and their optimal windows. The window is the month interval best correlated with annual basal area increment from the sliding window analysis, with R^2 describing the strength of the relationship. Asterisks (*) denote months from the year prior to the year of growth.

Variable	Description	Window	R^2
Tmin	Mean minimum monthly temperature (°C)	June-September	0.728
Tave	Mean monthly temperature (°C)	September*-January	0.589
Tmax	Mean maximum monthly temperature (°C)	September*-January	0.385
PPT	Total monthly precipitation (mm)	June-August	0.357

Previous September-January Tave showed a weak positive trend with average BAI, where trees from warmer winter climates relative to the planting site tended to exhibit greater growth, although this relationship was marginally non-significant (Fig. 4a). June-August PPT showed a significant positive linear relationship with average BAI (Fig. 4b), suggesting increased growth in trees from areas with wetter growing seasons relative to the planting site.

3.5.2. Climate Clusters vs. Drought Tolerance

Window analysis identified a four-month June to September SPEI−1 window as the strongest predictor of annual BAI ($R^2 = 0.435$; Fig. 5). Using a threshold of ≤ -0.5 SPEI, we identified multiple drought years during the study period; however, 2002 (mean June-September SPEI−1 = −0.680) represented one of the strongest drought signals, provided sufficient growth periods before (1998–2001) and after (2003–2006) the drought for analysis, and corresponds to a well-documented western U.S. drought event identified among the most severe in history (Andreadis et al., 2005). Additionally, in the years following the 2002 drought, June-September SPEI−1 values returned to relatively neutral or positive conditions (Fig. 5), thus reducing the likelihood that drought response metrics were strongly influenced by compound effects from successive drought events. Therefore, we selected the 2002 drought for subsequent analyses (Supplementary Table 5).

Average resistance to the 2002 drought was below one across climate clusters but differed significantly among clusters (Fig. 6), where populations from warmer climates with wetter growing seasons showed significantly greater drought resistance than populations from colder climates with drier growing seasons. All other clusters showed intermediate resistance values that did not differ significantly. Recovery values for all clusters exceeded one, reflecting greater post-drought growth rates relative to the drought period (Fig. 6; Supplementary

Table 4
Summary of final univariate climate models for the annual climate at Fraser Experimental Forest explaining annual basal area increment (BAI, mm^2) from 1992 to 2021, with year and provenance as random effects. *p*-values of significant variables ($p < 0.05$) are bolded.

Response	Predictor	Window	Model	Est	Std error	*p*	Marg R^2	Cond R^2
BAI	Tmin	Jun-Sep	Quadratic	698.55	227.24	**0.003**	0.169	0.856
	Tmin^2			−97.63	50.04	**0.005**		
	Tave	Sep*-Jan	Quadratic	−9.71	45.94	0.836	0.229	0.855
	Tave^2			−110.10	33.30	**0.001**		
	PPT	Jun-Aug	Linear	12.71	3.77	**0.001**	0.176	0.853

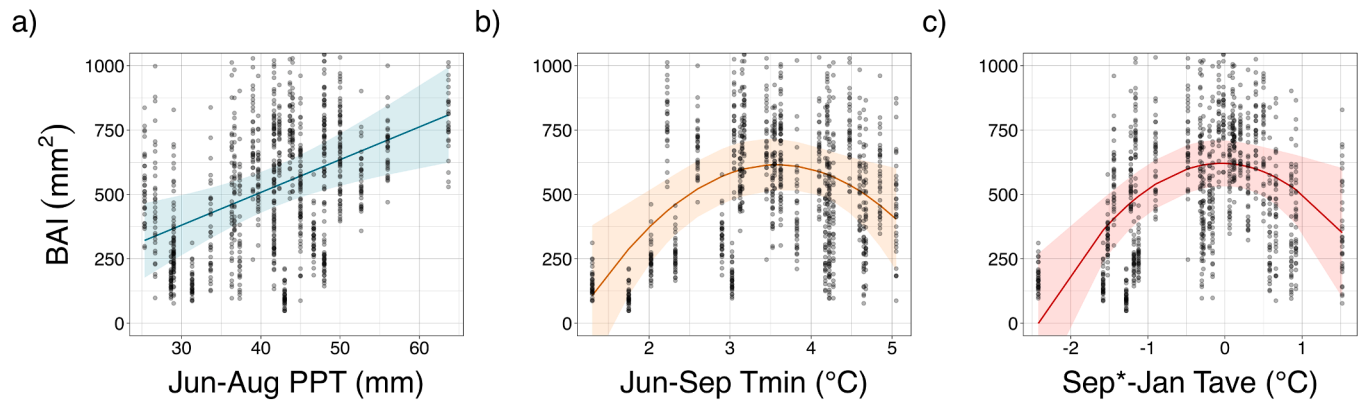

Fig. 3. Effects plots from the univariate linear mixed-effects models of seasonal climate variables at the Fraser Experimental Forest study site during the study period, 1992–2021. The three plots illustrate how annual basal area increment (BAI, mm²) of each individual tree responded to a) June-August total precipitation, b) June-September mean minimum temperature, and c) previous September-January mean temperature. Shaded areas around each line represent the 95% confidence interval of the model predictions. Black points show actual data.

Table 5
Summary of final univariate climate distance (CD) models for the annual relativized 30-year climate of the 34 provenances explaining mean basal area increment (BAI; mm²) for the study period, 1992–2021, where provenance is a random effect. *p*-values of significant variables ($p < 0.05$) are bolded.

Response	Predictor	Window	Model	Est	SE	*p*	Marg R^2	Cond R^2
BAI	CD_{Tave}	Sep*-Jan	Linear	18.873	9.718	0.054	0.023	
	CD_{PPT}	Jun-Aug	Linear	6.319	2.460	**0.026**	0.051	0.065

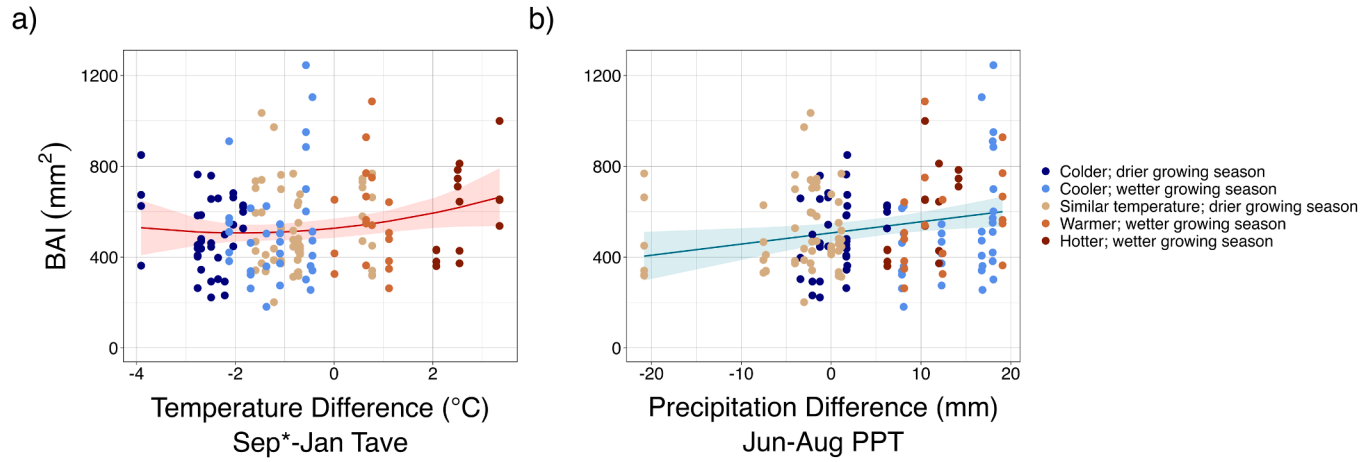

Fig. 4. Effects plots from the univariate linear mixed-effects models of climate distance from the Fraser Experimental Forest study site. The two plots illustrate how average 30-year provenance basal area increment (BAI; mm²) responds to climate distance differences in a) previous September-January mean temperature, and b) June-August average total precipitation. Climate distance predictors are expressed as differences from the Fraser Experimental Forest climate. Shaded areas around each line represent the 95% confidence interval of the model predictions and points are colored by the cluster each tree belongs to.

Table 6). Resilience also differed among climate clusters, with cooler populations from wetter growing seasons showing greater resilience than colder populations from drier growing seasons (Fig. 6). However, across all clusters, mean resilience values exceeded one, indicating that populations generally rebounded to pre-drought growth performance in the four years following the drought (2003–2006) (Fig. 6; Supplementary Table 6).

4. Discussion

Overall, we found that provenance climate explained little variation in growth compared to site climate, as observed across survival and field growth metrics. However, differences in drought response among climate origins suggest that local adaptation may be expressed more clearly under climatic stress than under non-limiting site conditions.

4.1. Provenance Influence on Survival and Growth

Analyses of survival and field growth at FEF indicated no significant differences among climate clusters for survival, DBH, or height. This contrasts previous studies of northern (Canadian) lodgepole pine populations where McLane et al. (2011) found that provenance climate exerted greater control over growth, and Montwé et al. (2016) and Ukrainetz et al. (2018) found substantial growth differences between populations from contrasting climates. One explanation for our findings is that the relatively mild conditions at our study site did not impose sufficient climatic stress to cause differential cumulative growth between provenances during most years (Park and Rodgers, 2023). While lodgepole pine is generally considered physiologically "conservative" across its range (Andrews et al., 2012), it has also been shown to exhibit "opportunistic" growth responses during periods of high moisture

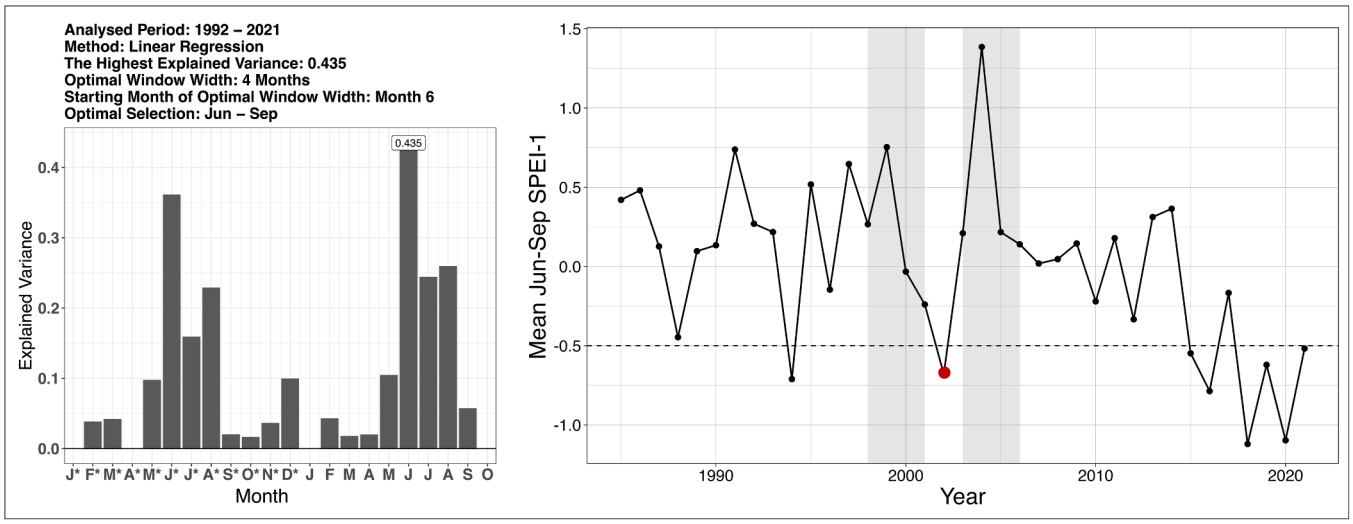

Fig. 5. Interannual variation in mean June-September SPEI−1 at the Fraser Experimental Forest study site from 1992 to 2021 and drought selection criteria used in this study. The left panel shows results of the climate window selection analysis used to identify the optimal SPEI period for predicting annual basal area increment (BAI), with the June-September SPEI−1 window identified as the strongest predictor ($R^2 = 0.435$). The right panel shows annual mean June-September SPEI−1 values across the study period. The dashed horizontal line indicates the drought threshold (SPEI ≤ -0.5). The red point denotes the selected 2002 drought event. Shaded regions indicate pre-drought, drought, and post-drought periods used to calculate drought resistance, recovery, and resilience metrics.

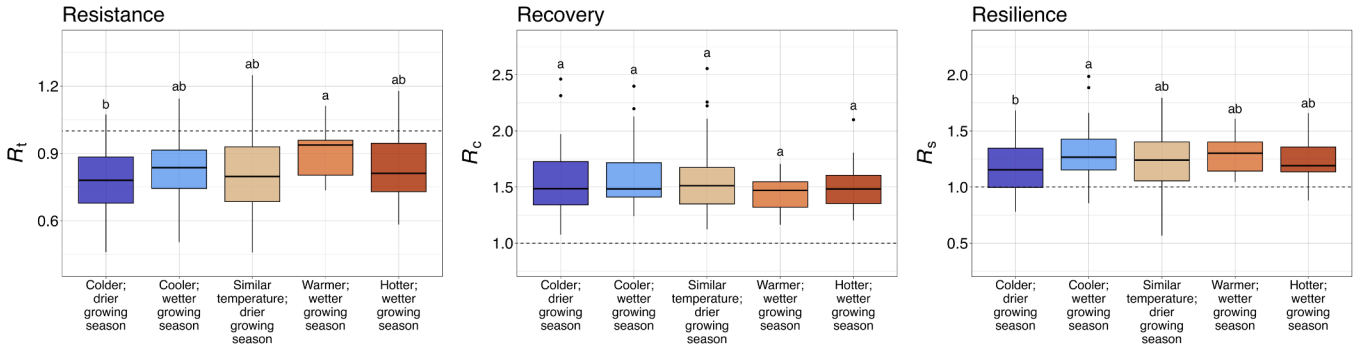

Fig. 6. Resistance, recovery, and resilience of 34 sampled lodgepole pine populations grouped and color-coded by climate cluster. Each boxplot represents a climate cluster based on previous September-January mean temperature and June-August total precipitation relative to the planting site at Fraser Experimental Forest. Letters above each boxplot indicate significance ($p < 0.05$). Clusters that share the same letter do not differ significantly, while clusters that do not share any letters are statistically different.

availability in its northern range (Chhin et al., 2008; McLane et al., 2011). More broadly, studies in woody plant systems have shown that populations originating from climatically variable environments can express greater phenotypic plasticity in growth and resource use, particularly in water-limited environments (Lázaro-Nogal et al., 2015). Together, these patterns may suggest that southern, trailing-edge lodgepole pine populations, which often occur in climatically-variable environments (DeRose, 2023), may rely more heavily on opportunistic growth and site acclimation, potentially reducing the expression of provenance-level differences in cumulative growth.

4.2. Growth-Climate Relationships at the Planting Site

Across all provenances, lodgepole pine annual growth at FEF from 1992 to 2021 was most strongly related to mean monthly temperature from the previous fall and winter, with growth declining in years with excessively warm or cold temperatures, indicating the presence of a temperature optimum. The lagged response observed here indicates that growth is impacted by previous-year temperatures, which is consistent with previous work showing that lodgepole is influenced by growing season climate both from the current year and the year prior (Bigler et al., 2007; Case and Peterson, 2007; Chhin et al., 2008). Winter conditions from the previous year likely influenced growth through several different mechanisms. A colder fall and winter in the year before a growing season with extreme cold can damage dormant buds or lead to xylem cavitation, both of which can limit growth in the following year (Casmey et al., 2022; Park and Rodgers, 2023; Sebastian-Azcona et al., 2019). In contrast, warmer fall and winter conditions may reduce snowpack, thus reducing snow insulation, exposing trees to cold injury or contributing to spring soil moisture limitation (Anderegg et al., 2013; Gleason et al., 2021; Westerling et al., 2006). Warmer conditions can also impact phenological timing, making trees more vulnerable to cold injury during transitional weather periods (Aitken et al., 2008; Park and Rodgers, 2023).

Growing season minimum monthly temperature also played an important role, with greater growth during years with more moderate temperatures. Similar responses have been reported in other lodgepole pine studies, where maximum growth occurs within a narrow thermal band and declines at climatic extremes (Chhin et al., 2008; Villalba et al., 1994). These optima-based growth responses indicate the importance of investigating responses to climate extremes, rather than just means, in the face of climate change (Dannenberg et al., 2019).

In contrast, precipitation had a positive linear relationship with growth, wherein greater water availability at the growing site led to

greater growth, following the well-established pattern of water availability as a dominant control on lodgepole pine growth (McLane et al., 2011; Montwé et al., 2016) and plant productivity more broadly (Nemani et al., 2003). However, the absence of an observed moisture optimum at FEF likely reflects that precipitation during the study period did not reach levels sufficient to limit growth, rather than indicating the absence of a moisture constraint. Notably, growing season precipitation, not winter precipitation or snow, was the most important predictor of growth. In southern lodgepole pine populations where growing seasons are longer and moisture availability is variable, in-season precipitation may play a more important role in sustaining growing activity than snow-derived moisture alone (Dye et al., 2022). In addition, our plantation site sits in the middle of lodgepole pine's climatic range in terms of growing season precipitation (Fig. 2), such that anomalously wet or dry growing seasons were still unlikely to fall outside the climatic tolerance of the species as a whole.

4.3. Provenance Influence on Climate Response

Provenance climate had little influence on average BAI growth. Provenances from warmer winter climates tended to show slightly greater average growth than those from similar or cooler winter climates relative to FEF, although this relationship was only marginally significant. Provenances from wetter growing season climates showed greater average growth than those from drier climates, though within-population variation remained relatively high. Our findings suggest that the influence of provenance on growth is more subtle than what has been found for northern lodgepole pine populations (Gray et al., 2016; Isaac-Renton et al., 2018; Rehfeldt et al., 1999; Wang et al., 2006).

4.4. Resistance, Recovery, and Resilience to Drought

Analysis of the 2002 drought at FEF revealed some significant differences in drought response among climate clusters. All provenances showed a decrease in growth during the drought event (i.e. resistance $<$ 1). Drought resistance differed significantly among provenances. Trees from relatively warmer and wetter climates compared to FEF exhibited the greatest resistance and maintained relatively more growth during the drought year, while trees from colder and drier source climates showed significantly lower resistance. This pattern does not support our second hypothesis that trees from drier source climates would exhibit greater drought resistance than those from less dry source climates, and instead could reflect differences in stress adaptation strategies between populations from resource-rich (warm and wet) vs. resource-poor (cold and dry) environments (Reinhardt et al., 2011). All remaining climate clusters showed a gradient of intermediate resistance values that did not differ significantly. These results illustrate that drought resistance at this site reflects population-level differences associated with climate of origin. Similar patterns have been observed in other conifer systems, where drought resistance shows stronger genetic differentiation than post-drought recovery, indicating that population-level adaptation may be most clearly expressed during the stress event itself (Sebastian-Azcona et al., 2025).

Recovery values indicated that all populations showed some capacity for increased post-drought growth, suggesting that once favorable moisture returned, southern lodgepole pine at FEF were able to resume growth regardless of provenance climate. However, resilience varied between climate clusters, with cooler and wetter populations returning more strongly to pre-drought growth levels than colder and drier populations. Notably, both extremes in resilience response (highest and lowest) occurred in clusters that were similarly cold but differed in precipitation. This illustrates that adaptation to provenance precipitation regime may play a more important role than temperature in shaping post-drought responses at this site. Nearly all trees returned to pre-drought growth levels following the drought, as seen in other studies (Bigler et al., 2007; Montwé et al., 2016).

While some studies of lodgepole pine and other conifers have found tradeoffs between growth and drought resistance, where faster-growing populations may exhibit greater drought sensitivity due to patterns in resource allocation (Bennett et al., 2015; Choat et al., 2012; McDowell et al., 2008), our findings do not support this pattern. Despite weak growth differences among provenance groups, populations from warmer and wetter climates exhibited greater drought resistance, suggesting that drought response strategies in southern lodgepole pine populations may not necessarily align with those previously observed in other populations. In northern lodgepole pine populations, Montwé et al. (2016) found that their southern populations (with latitudes spanning 42.30°N to 50.97°N compared to our populations spanning 37.6°N to 48.3°N) exhibited stronger growth-drought resistance tradeoffs, with greater growth under favorable conditions accompanied by greater drought sensitivity during the event. While some populations used in both studies overlapped in lodgepole pine climate space, in our study, populations from colder and drier climates showed lower resistance and resilience during drought, whereas recovery following drought was similar across climate clusters. This could mean that populations from less productive environments may reduce growth more readily during stress, resulting in overall lower growth rates. From a management perspective, these patterns suggest that while seed source might be less critical for maximizing growth under favorable conditions, it becomes increasingly important as drought frequency and intensity increase (Allen et al., 2010; Aitken et al., 2008; Isaac-Renton et al., 2018).

4.5. Management Implications

The results of our study support deliberate, climate-informed seed selection for climate adaptation and reforestation efforts in the western U.S. For sites with climate conditions comparable to FEF, managers may have flexibility in seed selection before facing maladaptation (i.e., reduced survival and growth). However, differences in drought resistance and resilience among provenances indicate that future reforestation efforts in the face of climate change might consider placing greater emphasis on selecting traits related to drought response rather than average growth alone (Aitken et al., 2008; Isaac-Renton et al., 2018). Our results indicate that seed sources from colder and drier climates relative to the planting site may suffer in the future due to their reduced growth resistance and resilience to drought. These traits may increase vulnerability to future disturbance events, particularly under increasingly variable climate conditions (Lloret et al., 2011).

These findings may also support seed sourcing strategies that incorporate a mixture of provenances to hedge uncertainty (Bucharova et al., 2019; Prakash et al., 2024). Mixing seed sources, or increasing heterogeneity, can enhance adaptive capacity by leveraging genetic diversity that is typical of natural forests (Bower et al., 2024; Ledig and Kitzmiller, 1992). Provenance climate clusters in this study were classified by climate rather than geography, highlighting the value of considering more than just geography alone when sourcing seeds for FAM plantings in order to sustain lodgepole pine forests under climate change. Finally, evidence that drought response traits exhibit genetic variation and can be used to identify more resilient genotypes further supports the potential for climate-informed seed selection in management strategies (Sebastian-Azcona et al., 2025).

4.6. Limitations and Future Research

As with many long-term provenance trials, this study is constrained by the limitations of field studies. Provenance trials provide valuable insights into intraspecific variability and growth-climate relationships, however, they cannot fully separate genotypic or phenotypic responses from other factors such as microsite effects, soil variation, and competition from other trees (Risk et al., 2021). Additionally, this study is limited to a single, high-elevation planting site that sits solidly within lodgepole pine's climatic range and our analysis focused on a single

drought event. Further research evaluating the drought response of southern lodgepole pine under a more severe drought or at a more moisture-limited site could provide additional insights into the water stress responses of these populations. As climate projections indicate that droughts in the western U.S. will become more frequent and severe in the coming decades (Allen et al., 2010), the need to better understand how southern lodgepole pine populations respond under greater moisture limitations becomes imperative. Combining data from long-term field experiments with controlled growth experiments involving temperature and moisture manipulations could help clarify whether weak provenance effects (like those found in our study) persist under greater climatic stress and would help define drought tolerance thresholds across seed sources (Aitken and Bemmels, 2015). In addition, while this study focused on growth, survival, and drought response, successful FAM implementation ultimately depends upon successful reproduction and establishment of new generations. Future work evaluating reproductive success would improve our understanding of long-term FAM outcomes for southern populations of lodgepole pine.

5. Conclusions

Using a long-term provenance experiment, this study provides rare insight into how southern lodgepole pine survival, growth, and drought responses are shaped both by local climate and provenance climate. The weak influence of provenance climate on growth and survival observed here highlights the potential flexibility of southern lodgepole pine under favorable conditions. However, the provenance-level responses that emerged through assessing drought resistance and resilience underscore that climate-informed seed selection practices may become increasingly important under future climate scenarios characterized by increased drought frequency and intensity. As such, approaches based solely on geography or fixed seed zones are unlikely to remain effective as our climate continues to deviate from historical conditions. While mixing provenance seed sources may be appropriate for promoting growth and survival under current or mild conditions, our results highlight the risks of assuming that drought tolerance is uniform across southern lodgepole pine populations. Ultimately, this study contributes to an understudied area of lodgepole pine research by focusing on southern populations in the western U.S. More long-term studies that capture both mild and extreme climatic conditions may be necessary for guiding assisted migration strategies that increase forest resilience to current climate conditions, as well as to the increasingly variable climate conditions that await forests in the future.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank Dr. Musser B. Moore for creating and installing this valuable experiment. We would also like to thank Banning Starr for providing access to the site and for assistance with logistics related to field data collection. Thank you to Lydia Hoffman, Rick Grybko, George Woolsey, Gunnar Ohlson, and Lauren Lad for help with field data collection for this project. Thank you to the USDA Forest Service Rocky Mountain Research Station (20-JV−11221633–140) and Colorado Forest Restoration Institute Appropriations Funding for funding support. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.124026.

Data availability

Research Link Provided: https://doi.org/10.2737/RDS-2024–0066

References

Aitken, S.N., Bemmels, J.B., 2015. Time to get moving: assisted gene flow of forest trees. Evol. Appl. 9, 271–290. https://doi.org/10.1111/eva.12293.
Aitken, S.N., Whitlock, M.C., 2013. Assisted Gene Flow to Facilitate Local Adaptation to Climate Change. Annu. Rev. Ecol. Evol. Syst. 44, 367–388. https://doi.org/10.1146/annurev-ecolsys-110512-135747.
Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., Curtis-McLane, S., 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evol. Appl. 1, 95–111. https://doi.org/10.1111/j.1752-4571.2007.00013.x.
Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manag. 259, 660–684. https://doi.org/10.1016/j.foreco.2009.09.001.
Anderegg, L.D.L., Anderegg, W.R.L., Abatzoglou, J., Hausladen, A.M., Berry, J.A., 2013. Drought characteristics' role in widespread aspen forest mortality across Colorado, USA. Glob. Change Biol. 19, 1526–1537. https://doi.org/10.1111/gcb.12146.
Anderson, M.D., 2003. *Pinus contorta* var. *latifolia*. Fire Effects Information System. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. ⟨https://www.fs.usda.gov/database/feis/plants/tree/pincontl/all.html⟩.
Andreadis, K.M., Clark, E.A., Wood, A.W., Hamlet, A.F., Lettenmaier, D.P., 2005. Twentieth-Century Drought in the Conterminous United States. J. Hydrometeor 6, 985–1001. https://doi.org/10.1175/JHM450.1.
Andrews, S.F., Flanagan, L.B., Sharp, E.J., Cai, T., 2012. Variation in water potential, hydraulic characteristics and water source use in montane Douglas-fir and lodgepole pine trees in southwestern Alberta and consequences for seasonal changes in photosynthetic capacity. Tree Physiol. 32 (2), 146–160. https://doi.org/10.1093/treephys/tpr136.
Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Softw. 67 (1), 1–48. https://doi.org/10.18637/jss.v067.i01.
Beguería, S., Vicente-Serrano, S.M., 2023. SPEI: Calculation of the Standardized Precipitation-Evapotranspiration Index. R package version 1.8.1. ⟨https://CRAN.Rproject.org/package=SPEI⟩.
Bennett, A.C., McDowell, N.G., Allen, C.D., Anderson-Teixeira, K.J., 2015. Larger trees suffer most during drought in forests worldwide. Nat. Plants 1, 15139. https://doi.org/10.1038/nplants.2015.139.
Bigler, C., Gavin, D.G., Gunning, C., Veblen, T.T., 2007. Drought induced lagged tree mortality in a subalpine forest in the Rocky Mountains. OIKOS 116 (12), 1983–1994. https://doi.org/10.1111/j.2007.0030-1299.16034.x.
Biondi, F., 1999. COMPARING TREE-RING CHRONOLOGIES AND REPEATED TIMBER INVENTORIES AS FOREST MONITORING TOOLS. Ecol. Appl. 9, 216–227. https://doi.org/10.1890/1051-0761(1999)009%255B0216:CTRCAR%255D2.0.CO;2.
Biondi, F., Qeadan, F., 2008. A Theory-Driven Approach to Tree-Ring Standardization: Defining the Biological Trend from Expected Basal Area Increment. Tree-Ring Res. 64 (2), 81–96.
Birdsey, R.A., Dugan, A.J., Healey, S.P., Dante-Wood, K., Zhang, F., Mo, G., Chen, J.M., Hernandez, A.J., Raymond, C.L., McCarter, J., 2019. Assessment of the influence of disturbance, management activities, and environmental factors on carbon stocks of U.S. national forests (No. RMRS-GTR-402). U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. https://doi.org/10.2737/RMRS-GTR-402.
Bottero, A., D'Amato, A.W., Palik, B.J., Bradford, J.B., Fraver, S., Battaglia, M.A., Asherin, L.A., 2017. Density-dependent vulnerability of forest ecosystems to drought. J. Appl. Ecol. 54, 1605–1614. https://doi.org/10.1111/1365-2664.12847.
Bower, A.D., Frerker, K.L., Pike, C.C., LaBonte, N.R., Palik, B.J., Royo, A.A., Anderson, S.M., Ferreira, A.R., Brandt, L.A., 2024. A practical framework for applied forestry assisted migration. Front. For. Glob. Change 7, 1454329. https://doi.org/10.3389/ffgc.2024.1454329.
Bucharova, A., Bossdorf, O., Holzel, N., Kollmann, J., Prasse, R., Durka, W., 2019. Mix and match: regional admixture provenancing strikes a balance among different seed-sourcing strategies for ecological restoration. Conserv. Genet. 20, 7–17. https://doi.org/10.1007/s10592-018-1067-6.
Bunn, A., Korpela, M., Biondi, F., Campelo, F., Mérian, P., Qeadan, F., Zang, C., 2023. dplR: Dendrochronology Program Library in R. R package version 1.7.6.⟨https://CRAN.R-project.org/package=dplR⟩.
Bunn, A.G., 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26, 115–124. https://doi.org/10.1016/j.dendro.2008.01.002.
Bunn, A.G., 2010. Statistical and visual crossdating in R using the dplR library. Dendrochronologia 28, 251–258. https://doi.org/10.1016/j.dendro.2009.12.001.
Burns, R.M., Honkala, B.H., 1990. Silvics Manual. In: Conifers, Agricultural Handbook, 1. U.S. Department of Agriculture, Washington, D.C.

Case, M.J., Peterson, D.L., 2007. Growth-climate Relations of Lodgepole Pine in the North Cascades National Park, Washington. Northwest. Sci. 81, 62–75. https://doi.org/10.3955/0029-344X-81.1.62.
Casmey, M., Hamann, A., Hacke, U.G., 2022. Adaptation of white spruce to climatic risk environments in spring: Implications for assisted migration. For. Ecol. Manag. 525, 120555. https://doi.org/10.1016/j.foreco.2022.120555.
Chhin, S., Hogg, E.H. (Ted), Lieffers, V.J., Huang, S., 2008. Influences of climate on the radial growth of lodgepole pine in Alberta. Botany 86, 167–178. https://doi.org/10.1139/B07-120.
Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J., Zanne, A.E., 2012. Global convergence in the vulnerability of forests to drought. Nature 491, 752–755. https://doi.org/10.1038/nature11688.
Dannenberg, M.P., Wise, E.K., Smith, W.K., 2019. Reduced tree growth in the semiarid United States due to asymmetric responses to intensifying precipitation extremes. Sci. Adv. 5 (10), eaaw0667. https://doi.org/10.1126/sciadv.aaw0667.
DeRose, J., 2023. Conserving lodgepole pine genetic diversity in the face of uncertainty. For. Ecol. Manag. 545, 121235. https://doi.org/10.1016/j.foreco.2023.121235.
Dye, L.A., Pearl, J.K., Smith, L., Coulthard, B.L., Butkiewicz, C., Cooper, Z., DeGrand, J., Friedman, J., Homfeld, I.K., Howard, H., Ironcloud, L., Wray, S., 2022. Co-Occurring Wyoming *Pinus* Species Exhibit Differing Climate-Growth Relationships. Tree-Ring Res. 78 (1), 13–24. https://doi.org/10.3959/TRR2021-5.
Fritts, H.C., 1974. Relationships of ring widths in arid-site conifers to variations in monthly temperature and precipitation. Ecol. Monogr. 44, 411–440.
Gleason, K.E., Bradford, J.B., D'Amato, A.W., Fraver, S., Palik, B.J., Battaglia, M.A., 2021. Forest density intensifies the importance of snowpack to growth in water-limited pine forests. Ecol. Appl. 31. https://doi.org/10.1002/eap.2211.
Gray, L.K., Hamann, A., 2013. Tracking suitable habitat for tree populations under climate change in western North America. Clim. Change 117, 289–303. https://doi.org/10.1007/s10584-012-0548-8.
Gray, L.K., Rweyongeza, D., Hamann, A., John, S., Thomas, B.R., 2016. Developing management strategies for tree improvement programs under climate change: Insights gained from long-term field trials with lodgepole pine. For. Ecol. Manag. 377, 128–138. https://doi.org/10.1016/j.foreco.2016.06.041.
Halofsky, J.E., Peterson, D.L., Ho, J.J., Little J., N., Joyce, L.A., 2018. Climate change vulnerability and adaptation in the Intermountain Region [Part 2]. Gen. Tech. Rep. RMRS-GTR-375. Fort Collins. CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, pp. 199–513.
Illingworth, K., 1978. Study of lodgepole pine genotype environment interaction in BC. International Union of Forestry Research Organizations (IUFRO) joint meeting of working parties: Douglas-fir provenances, lodgepole pine provenances, Sitka spruce provenances, and Abies provenances. British Columbia Ministry of Forests, Information Services Branch, Victoria, British Columbia, Canada, pp. 151–158.
IPCC, 2023. Summary for Policymakers. In: Core Writing Team, H.Lee, Romero., J. (Eds.), Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland, pp. 1–34.
Isaac-Renton, M., Montwé, D., Hamann, A., Spiecker, H., Cherubini, P., Treydte, K., 2018. Northern forest tree populations are physiologically maladapted to drought. Nat. Commun. 9, 5254. https://doi.org/10.1038/s41467-018-07701-0.
Jevšenak, J., 2020. New features in the dendroTools R package: Bootstrapped and partial correlation coefficients for monthly and daily climate data.
Kuhn, M., Wickham, H. Tidymodels: a collection of packages for modeling and machine learning using tidyverse principles.
Lázaro-Nogal, A., Matesanz, S., Godoy, A., Pérez-Trautman, F., Gianoli, E., Valladares, F., 2015. Environmental heterogeneity leads to higher plasticity in dry-edge populations of a semi-arid Chilean shrub: insights into climate change responses. J. Ecol. 103, 338–350. https://doi.org/10.1111/1365-2745.12372.
Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., Makowski, D., 2021. performance: An R Package for Assessment, Comparison and Testing of Statistical Models. J. Open. Source Softw. 6, 3139. https://doi.org/10.21105/joss.03139.
Langlet, O., 1971. Two Hundred Years Genecology. Taxon 20, 653–721. https://doi.org/10.2307/1218596.
Larsson, L.A., 2003. CDendro: Cybis Dendro dating program.
Ledig, F.T., Kitzmiller, J.H., 1992. Genetic strategies for reforestation in the face of global climate change. For. Ecol. Manag. 50, 153–169. https://doi.org/10.1016/0378-1127(92)90321-Y.
Leech, S.M., Lara Almuedo, P., O'Neill, G., 2011. Assisted Migration: Adapting Forest Management to a Changing Climate. J. Ecosyst. Manag. 12. https://doi.org/10.22230/jem.2011v12n3a91.
Lenth, R., 2025. emmeans: Estimated Marginal Means, aka Least-Squares Means. R. Package Version 1 (11), 2–8. https://doi.org/10.32614/CRAN.package.emmeans.
Liepe, K.J., Hamann, A., Smets, P., Fitzpatrick, C.R., Aitken, S.N., 2016. Adaptation of lodgepole pine and interior spruce to climate: implications for reforestation in a warming world. Evol. Appl. 9, 409–419. https://doi.org/10.1111/eva.12345.
Little Jr., E.L., 1971. Atlas of United States trees, volume 1, conifers and important hardwoods. U.S. Department of Agriculture Miscellaneous Publication, p. 1146, 9 p., 200 maps.
Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. Oikos 120, 1909–1920. https://doi.org/10.1111/j.1600-0706.2011.19372.x.
Lowery, D.P., 1984. Lodgepole Pine (No. FS-253), An American Wood. Forest Service United States Department of Agriculture.
Mathys, A., Coops, N.C., Waring, R.H., 2014. Soil water availability effects on the distribution of 20 tree species in western North America. For. Ecol. Manag. 313, 144–152.
Maxwell, R.S., Larsson, L.A., 2021. Measuring tree-ring widths using the CooRecorder software application. Dendrochronologia 67, 125841. https://doi.org/10.1016/j.dendro.2021.125841.
Maxwell, S., Wixom, J., Hessl, A., 2011. A comparison of two techniques for measuring and crossdating tree rings. Dendrochronologia 29, 237–243. https://doi.org/10.1016/j.dendro.2010.12.002.
McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New. Phytol. 178, 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x.
McLane, S.C., Daniels, L.D., Aitken, S.N., 2011. Climate impacts on lodgepole pine (*Pinus contorta*) radial growth in a provenance experiment. For. Ecol. Manag. 262, 115–123. https://doi.org/10.1016/j.foreco.2011.03.007.
Montwé, D., Isaac-Renton, M., Hamann, A., Spiecker, H., 2016. Drought tolerance and growth in populations of a wide-ranging tree species indicate climate change risks for the boreal north. Glob. Change Biol. 22, 806–815. https://doi.org/10.1111/gcb.13123.
Moore, M.B., 1981. Geographic variation in lodgepole pine in the Central Rocky Mountains 201.
Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x.
Nakagawa, S., Johnson, P.C.D., Schielzeth, H., 2017. The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. J. R. Soc. Interface 14 (134), 20170213. https://doi.org/10.1098/rsif.2017.0213.
Nemani, R.R., Keeling, C.D., Hashimoto, H., Jolly, W.M., Piper, S.C., Tucker, C.J., Myneni, R.B., Running, S.W., 2003. Climate-Driven Increases in Global Terrestrial Net Primary Production from 1982 to 1999. Science 300, 1560–1563. https://doi.org/10.1126/science.1082750.
Paradis, E., Schliep, K., 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35, 526–528. https://doi.org/10.1093/bioinformatics/bty633.
Park, A., Rodgers, J.L., 2023. Provenance trials in the service of forestry assisted migration: A review of North American field trials and experiments. For. Ecol. Manag. 537, 120854. https://doi.org/10.1016/j.foreco.2023.120854.
Park, A., Talbot, C., 2018. Information Underload: Ecological Complexity, Incomplete Knowledge, and Data Deficits Create Challenges for the Assisted Migration of Forest Trees. BioScience 68, 251–263. https://doi.org/10.1093/biosci/biy001.
Pedlar, J.H., McKenney, D.W., Aubin, I., Beardmore, T., Beaulieu, J., Iverson, L., O'Neill, G.A., Winder, R.S., Ste-Marie, C., 2012. Placing Forestry in the Assisted Migration Debate. BioScience 62, 835–842. https://doi.org/10.1525/bio.2012.62.9.10.
Prakash, A., Capblancq, T., Shallows, K., Saville, D., Landau, D., Landress, C., Jacobs, T., Keller, S., 2024. Bringing genomics to the field: An integrative approach to seed sourcing for forest restoration. e11600 Appl. Plant. Sci. 12 (3), 20. https://doi.org/10.1002/aps3.11600.
R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ⟨https://www.R-project.org/⟩.
Rehfeldt, G.E., 1983. Adaptation of *Pinus contorta* populations to heterogeneous environments in northern Idaho. Can. J. For. Res. 13, 405–411.
Rehfeldt, G.E., 1988. Ecological genetics of *Pinus contorta* from the Rocky Mountains (USA): a synthesis. Silvae Genet. 37, 131–135.
Rehfeldt, G.E., Ying, C.C., Spittlehouse, D.L., Hamilton Jr., D.A., 1999. Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. Ecol. Monogr. 69 (3), 375–407.
Rehfeldt, G.E., Tchebakova, N.M., Parfenova, Y.I., Wykoff, W.R., Kuzmina, N.A., Milyutin, L.I., 2002. Intraspecific responses to climate in *Pinus sylvestris*. Glob. Change Biol. 8, 912–929. https://doi.org/10.1046/j.1365-2486.2002.00516.x.
Reinhardt, K., Castanha, C., Germino, M.J., Kueppers, L.M., 2011. Ecophysiological variation in two provenances of *Pinus flexilis* seedlings across an elevation gradient from forest to alpine. Tree Physiol. 31 (6), 615–625.
Renwick, K.M., Rocca, M.E., 2015. Temporal context affects the observed rate of climate-driven range shifts in tree species. Glob. Ecol. Biogeogr. 24, 44–51. https://doi.org/10.1111/geb.12240.
Rhoades, C.C., Fegel, T.S., Hubbard, R.M., Chambers, M.E., 2022. Limited seed viability in long-dead serotinous lodgepole pine trees in the Southern Rockies, USA. For. Ecol. Manag. 526, 120565. https://doi.org/10.1016/j.foreco.2022.120565.
Rhoades, C.C., Fegel, T.S., Schneider, C., Vorster, A.G., 2025. Post-fire seedling recruitment across a range of stand age in bark-beetle impacted lodgepole pine forests: informing reforestation needs. For. Ecol. Manag. 596, 123048. https://doi.org/10.1016/j.foreco.2025.123048.
Risk, C., McKenney, D.W., Pedlar, J., Lu, P., 2021. A compilation of North American tree provenance trials and relevant historical climate data for seven species. Sci. Data 8, 29. https://doi.org/10.1038/s41597-021-00820-2.
Royo, A.A., Raymond, P., Kern, C.C., Adams, B.T., Bronson, D., Champagne, E., Dumais, D., Gustafson, E., Marquardt, P.E., McGraw, A.M., Miesel, J.R., Munson, A. D., Périé, C., Moreira, F.J.T., Ola, A., Bouchard, M., Bissonnette, J.F., 2023. Desired REgeneration through Assisted Migration (DREAM): Implementing a research framework for climate-adaptive silviculture. For. Ecol. Manag. 546, 121298. https://doi.org/10.1016/j.foreco.2023.121298.

Sáenz-Romero, C., O'Neill, G., Aitken, S.N., Lindig-Cisneros, R., 2020. Assisted Migration Field Tests in Canada and Mexico: Lessons, Limitations, and Challenges. Forests 12, 9. https://doi.org/10.3390/f12010009.

Savva, Y., Denneler, B., Koubaa, A., Tremblay, F., Bergeron, Y., Tjoelker, M.G., 2007. Seed transfer and climate change effects on radial growth of jack pine populations in a common garden in Petawawa, Ontario, Canada. For. Ecol. Manag. 242, 636–647. https://doi.org/10.1016/j.foreco.2007.01.073.

Sebastian-Azcona, J., Cappa, E.P., Da Ros, L., Ratcliffe, B., Chen, C., Wei, X., Liu, Y., Mansfield, S.D., Hamann, A., El-Kassaby, Y.A., Thomas, B.R., 2025. Short- and Long-Term Growth Response to Multiple Drought Episodes: Evidence of Genetic Adaptation in a Conifer Species. Ecol. Evol. 15, e71398. https://doi.org/10.1002/ece3.71398.

Sebastian-Azcona, J., Hamann, A., Hacke, U.G., Rweyongeza, D., 2019. Survival, growth and cold hardiness tradeoffs in white spruce populations: Implications for assisted migration. For. Ecol. Manag. 433, 544–552. https://doi.org/10.1016/j.foreco.2018.10.046.

Speer, J.H., 2010. Fundamentals of Tree-Ring Research. The University of Arizona Press.

Ste-Marie, C., A. Nelson, E., Dabros, A., Bonneau, M.E., 2011. Assisted migration: Introduction to a multifaceted concept. For. Chron. 87, 724–730. https://doi.org/10.5558/tfc2011-089.

Teets, A., Moore, D.J.P., Alexander, M.R., Blanken, P.D., Bohrer, G., Burns, S.P., Carbone, M.S., Ducey, M.J., Fraver, S., Gough, C.M., Hollinger, D.Y., Koch, G., Kolb, T., Munger, J.W., Novick, K.A., Ollinger, S.V., Ouimette, A.P., Pederson, N., Ricciuto, D.M., Seyednasrollah, B., Vogel, C.S., Richardson, A.D., 2022. Coupling of tree growth and photosynthetic carbon uptake across six North American forests. J. Geophys. Res. Biogeosci 127, e2021JG006690. https://doi.org/10.1029/2021JG006690.

Twardek, W.M., Taylor, J.J., Rytwinski, T., Aitken, S.N., MacDonald, A.L., Van Bogaert, R., Cooke, S.J., 2023. The application of assisted migration as a climate change adaptation tactic: An evidence map and synthesis. Biol. Conserv. 280, 109932. https://doi.org/10.1016/j.biocon.2023.109932.

Ukrainetz, N.K., Yanchuk, A.D., Mansfield, S.D., 2018. Climatic drivers of genotype-environment interactions in lodgepole pine based on multi-environment trial data and a factor analytic model of additive covariance. Can. J. For. Res. 48, 835–854. https://doi.org/10.1139/cjfr-2017-0367.

Villalba, R., Veblen, T.T., Ogden, J., 1994. Climatic Influences on the Growth of Subalpine Trees in the Colorado Front Range. Ecology 75, 1450–1462. https://doi.org/10.2307/1937468.

Wang, T., Hamann, A., Yanchuk, A., O'Neill, G.A., Aitken, S.N., 2006. Use of response functions in selecting lodgepole pine populations for future climates. Glob. Change Biol. 12, 2404–2416. https://doi.org/10.1111/j.1365-2486.2006.01271.x.

Wang, T., Hamann, A., Spittlehouse, D., Carroll, C., 2016. Locally Downscaled and Spatially Customizable Climate Data for Historical and Future Periods for North America. PLoS. ONE 11, e0156720. https://doi.org/10.1371/journal.pone.0156720.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and Earlier Spring Increase Western U.S. Forest Wildfire Activity. Science 313, 940–943. https://doi.org/10.1126/science.1128834.

Williams, M.I., Dumroese, R.K., 2013. Preparing for Climate Change: Forestry and Assisted Migration. J. For. 111, 287–297. https://doi.org/10.5849/jof.13-016.

Worrall, J.J., Rehfeldt, G.E., 2021. Strategic Application of Topoclimatic Niche Models in Managing Forest Change. Forests 12, 1780. https://doi.org/10.3390/f12121780.

Yamaguchi, D.K., 1991. A simple method for cross-dating increment cores from living trees. Can. J. For. Res. 21 (3), 414–416. https://doi.org/10.1139/x91-053.

Zhao, Y., Wang, T., 2023. Predicting the global fundamental climate niche of lodgepole pine for climate change adaptation. Front. For. Glob. Change 6, 1084797. https://doi.org/10.3389/ffgc.2023.1084797.