

THESIS

THE INFLUENCE OF PROVENANCE ON RADIAL GROWTH AND DROUGHT
RESILIENCE OF LODGEPOLE PINE IN FRASER EXPERIMENTAL FOREST,
COLORADO, U.S.A.

Submitted by

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ABSTRACT

THE INFLUENCE OF PROVENANCE ON RADIAL GROWTH AND DROUGHT RESILIENCE OF LODGEPOLE PINE IN FRASER EXPERIMENTAL FOREST, COLORADO, U.S.A.

Climate change poses unprecedented challenges to forested ecosystems, particularly in drought-affected areas in the western United States, where increased temperatures and shifting precipitation regimes are negatively impacting locally adapted tree species. In response, researchers and land managers are exploring innovative forest adaptation strategies to maintain forest resilience, such as assisted migration. This study examines the potential of lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) to be utilized in forest assisted migration efforts in western North America, drawing from the understanding that this widespread species displays intraspecies variation in growth-climate associations due to local adaptations across its extensive geographic range. We make use of a provenance study established in the early 1980s in Fraser Experimental Forest, Colorado, U.S.A. to examine the effect of seed source, or provenance, on growth-climate responses and drought resilience of lodgepole pine in its southernmost range. We investigate two primary research questions. First, does provenance climate influence the radial growth response of lodgepole pine trees? Second, do lodgepole pine trees from climatically drier provenances exhibit greater resilience to drought, as measured by annual radial growth before and after drought events? To address our first question, we employed dendrochronological methods and a generalized linear mixed-effects modeling approach utilizing climate data to analyze the variation in overall radial growth of trees explained by the difference in provenance

and study site climates during our study period, 1992-2021. In addressing our second question, we utilized the Standardized Precipitation Evapotranspiration Index (SPEI) and metrics of quantifying drought resilience to determine the impact of provenance site aridity on tolerance to drought during our selected drought period, 2001-2002.

Our analyses revealed significant differences in radial growth between trees from different provenances. Specifically, we found that trees originating from provenance sites with greater growing season average vapor pressure deficit, yet higher precipitation, exhibited increased radial growth. In analyzing drought resilience, we found that trees from provenances with higher average temperatures and greater evapotranspiration showed greater resilience to drought, aligning with previous research linking seed source climate aridity to drought tolerance. Interestingly, we also found that trees from sites with greater climate moisture index compared to their growing site exhibited greater radial growth resilience to drought, suggesting that certain populations may be less sensitive to moisture deficits.

Our research sheds light on the relationship between provenance climate with radial growth response and drought resilience in an assisted migration context. Our findings suggest that provenance climate aridity may confer resilience to trees during resource-limited events. More broadly, our study underscores the potential of utilizing local adaptations and intraspecies variability of tree species in climate adaptation efforts aimed at mitigating the impact of climate change in forested ecosystems.

ACKNOWLEDGEMENTS

Colorado State University acknowledges, with respect, that the land we are on today is the traditional and ancestral homelands of the Arapaho, Cheyenne, and Ute Nations and peoples. This was also a site of trade, gathering, and healing for numerous other Native tribes. We recognize the Indigenous peoples as original stewards of this land and all the relatives within it. As these words of acknowledgment are spoken and heard, the ties Nations have to their traditional homelands are renewed and reaffirmed. CSU is founded as a land-grant institution, and we accept that our mission must encompass access to education and inclusion. And, significantly, that our founding came at a dire cost to Native Nations and peoples whose land this University was built upon. This acknowledgment is the education and inclusion we must practice in recognizing our institutional history, responsibility, and commitment.

We recognize Indigenous people as not only the original stewards of this land, but also as the original foresters, ecologists, and scientists in their own right. The concepts explored in this paper, such as the human-assisted movement of seeds, or assisted migration, are not new ideas; rather they have been practiced for centuries. As we engage in these discussions, it is crucial to recognize that we are not reinventing the wheel but rather relearning and respecting the wisdom of those who came before us.

I would like to express my deepest gratitude to those who have supported me throughout my master's project and thesis. First and foremost, I extend my heartfelt thanks to my advisors, Sarah Hart and Wade Tinkham, for their valuable mentorship and encouragement. Their expertise and insights have been fundamental in shaping this research, and their unwavering support has been a constant source of motivation. I also wish to thank the members of my thesis

committee, Mike Battaglia and Jamie Dahl, for their thoughtful feedback and guidance. Their diverse perspectives have enriched my work in this project and have pushed me to achieve more than I thought possible. This thesis is a true testament to the contributions of my advisors and committee and their belief in my work and my abilities as a researcher.

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I would like to acknowledge and thank Musser B. Moore for his pivotal role in establishing the provenance experiment at Fraser Experimental Forest, which I had the privilege to study for this project. I deeply appreciate the hard work and dedication involved in creating this long-term field study, which has provided, and will continue to provide, valuable insights into forest climate adaptation management practices for decades to come.

Finally, thank you to the Department of Forest and Rangeland Stewardship at Colorado State University, Colorado Forest Restoration Institute, and Rocky Mountain Research Station at the U.S.D.A. Forest Service for making this project possible through support and funding.

DEDICATION

I dedicate this thesis to my loving family. A special feeling of gratitude to my mom, whose support and love have been my guiding light. My dad, whose expertise and guidance have been invaluable in my academic journey. My grandma, Stella, whose dedication to academia inspired me to pursue a life of learning. My aunt, Carolina, my godmother, whose memories and inspiration are forever cherished and remembered.

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CHAPTER 1: THE INFLUENCE OF PROVENANCE ON RADIAL GROWTH AND
DROUGHT RESILIENCE OF LODGEPOLE PINE IN FRASER EXPERIMENTAL FOREST,
COLORADO, U.S.A.

1.1 Introduction

Climate change is ushering in a period of unprecedented challenges in forested ecosystems (IPCC, 2023). In western North America, rising temperatures and shifting precipitation patterns have intensified drought conditions, reshaping disturbance regimes and negatively impacting the growth, survival, and regeneration of locally adapted tree species (Davis et al., 2019; Davis et al., 2023; Hof et al., 2017; Kerhoulas et al., 2013; Rodman et al., 2022). As the consequences of climate change unfold, there is growing concern that locally adapted tree species will continue to be negatively impacted and may struggle to adapt or migrate in time without intervention (Aitken et al., 2008; Beardmore and Winder, 2011; Nigro et al., 2022).

To address the many challenges that climate change presents, researchers and land management organizations are exploring adaptive silviculture strategies to enhance the resiliency and adaptability of North American forests to climate change (Nagel et al., 2017; Palik et al., 2022; Royo et al., 2023; Wellstead et al., 2017). One such strategy is forest assisted migration, or the movement of tree seeds from populations that are better suited for anticipated climate conditions (Koralewski et al., 2015; Leech et al., 2011; Palik et al., 2019; Pedlar et al., 2012; Sáenz-Romero et al., 2020; Williams and Dunroese 2013). Assisted migration efforts are rooted in two primary ideas. First, trees are locally adapted to the climate conditions at their growing site (Gray et al., 2016). Second, on their own, trees respond slowly to a changing climate (Nigro et al., 2022). Much of our knowledge surrounding the growth-climate relationships of trees is

generated from provenance experiments, the collection of seeds from diverse geographic and climatic locations, germination, out-planting at a study site, and subsequent measurement of growth over time (McLane et al., 2011a; Park and Rogers 2023; Rehfeldt et al., 1999; Risk et al., 2021). These studies aim to understand the influence of seed source, or provenance, on tree responses to climate and disturbance (McLane et al., 2011a). Findings from such provenance experiments, in addition to increased pressure and federal funding from recent legislation (Infrastructure Investment and Jobs Act, 2021), have operationalized assisted migration as a forest climate change mitigation strategy across the West (Risk et al., 2021), with large-scale seed sourcing and reforestation efforts occurring across the western U.S. (U.S.D.A. Forest Service, 2022).

Among North American conifer tree species, lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) is of particular interest in the realm of the utilization of provenance experiments to inform assisted migration efforts (Moore, 1981; Zhao and Wang, 2023). This species, due to its large geographic extent (Figure 1.1) displays wide variation in growth-climate relationships and disturbance-adaptive traits, such as cone serotiny, which allows for rapid site recolonization following severe wildfire, and resin duct production, which provides physical and chemical defense mechanisms against insect infestation (Anderson, 2003). Notably, provenance studies have shown that lodgepole pine traits vary extensively with seed source (Illingworth, 1978; Liepe et al., 2016; McLane et al., 2011a; McLane et al., 2011b). However, this focus on utilizing lodgepole pine in provenance studies to inform assisted migration efforts is largely limited to the species' northernmost extent, spanning British Columbia, Canada (Figure 1.1). This has resulted in a notable gap in scientific understanding of the species' capacity for use in these efforts in its southernmost region in the western U.S. (Gray et al., 2016; Illingworth, 1978;

Mahony et al., 2020; McLane et al., 2011a; McLane et al., 2011b). In this region, lodgepole pine is widespread (Anderson, 2003) and is already threatened by increased climate change-induced drought conditions, but its potential adaptability and plasticity, as seen in its northern range, may suggest that some populations are better adapted to these conditions and valuable for assisted migration in threatened forests (Halofsky et al., 2018).

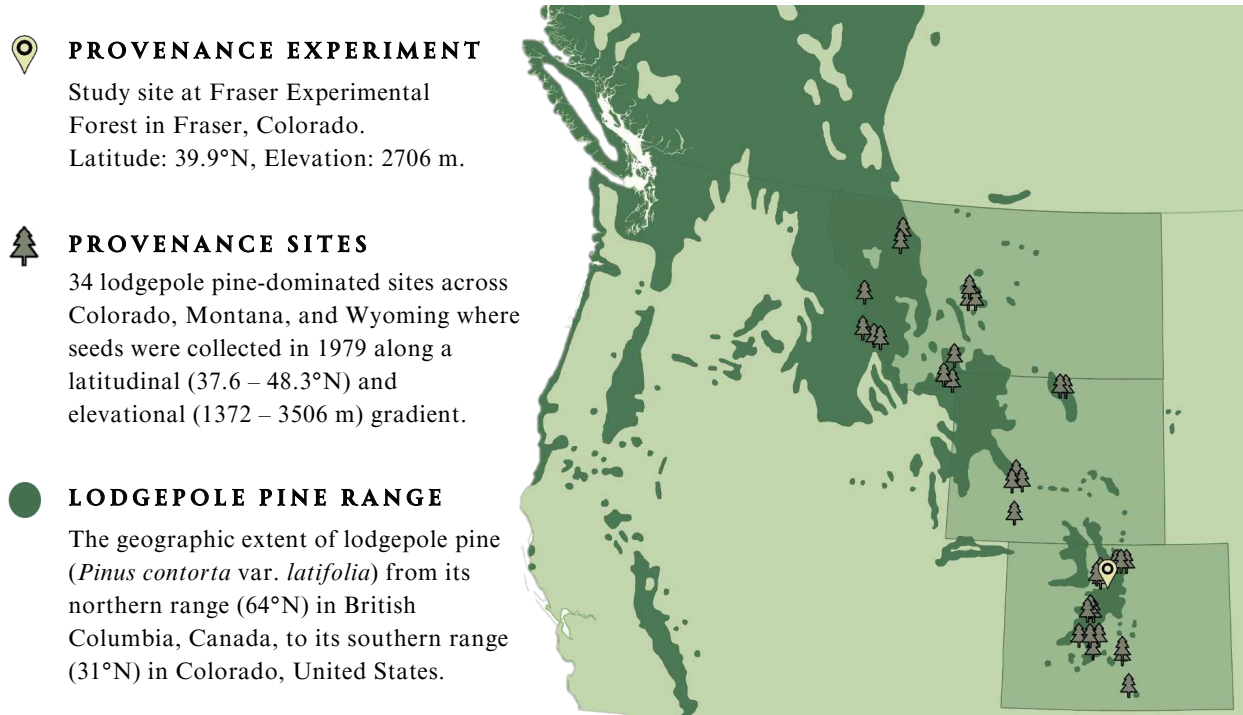


Figure 1.1. Study site at Fraser Experimental Forest in Fraser, Colorado in relation to 34 original seed source populations (provenances) across the native range of lodgepole pine and across the western United States in Colorado, Montana, and Wyoming. Lodgepole pine range data layer provided by Data Basin adapted from Little (1971).

Amid unprecedented wildfires, widespread insect outbreak events, and severe droughts, locally adapted tree species are experiencing widespread reductions in growth and increases in tree mortality (Aitken et al., 2008; Anderegg et al., 2015; DeSoto et al., 2020; Jarvis and Kulakowski 2015). This study aims to contribute insights into the adaptive potential of lodgepole pine in its southernmost growing range to inform assisted migration efforts aimed at enhancing forest resilience in the face of climate change by examining how seed source influences variation

in climate-growth responses of lodgepole pine. By shedding light on these relationships in the species' vulnerable southern range (Worrall and Rehfeldt, 2021), we can leverage the intraspecies variability that exists within this species to select for seeds from sources that are best suited to anticipated future climate conditions in forests. Using a nearly 40-year-old lodgepole pine provenance experiment, our research is driven by two primary research questions. First, does provenance (seed source) climate influence the radial growth response of lodgepole pine trees in the species' southernmost range? Second, do lodgepole pine trees from climatically drier provenances exhibit greater resilience to drought, as measured by annual radial growth before, during, and after drought events? For our first question, we hypothesize that lodgepole pine radial growth is influenced by provenance climate in the species' southernmost extent. For our second question, we hypothesize that lodgepole pine trees from drier climates will exhibit greater radial growth resilience to drought due to drought adaptations inherent to their provenance.

1.2 Methods

1.2.1 Study Site

To address our research questions, we sampled a 42-year-old provenance experiment in Fraser Experimental Forest (FEF) located in Fraser in north central Colorado. This is a subalpine and riparian, high-elevation ecosystem, at an elevation of approximately 2,791 m. Throughout our selected study period, 1992-2021, the site experienced an average temperature of 3°C and 59 cm of average precipitation, with most precipitation occurring during the late-winter and mid-spring months (Wang et al., 2016). To establish the provenance study, cone samples were collected from lodgepole pine trees along a latitudinal (37.6°N to 48.3°N) and elevational (1372 m to 3506 m) gradient spanning 34 populations from La Veta Pass, Colorado to Marias Pass, Montana (Moore, 1981) (Figure 1.1). Seeds were collected in summer (July-September) 1979

then germinated in the Colorado State Forest Service greenhouse in Fort Collins, Colorado in 1980. After two seasons of greenhouse growth, seedlings were planted in a clear-cut lodgepole pine stand in 1982 at the northern edge of FEF. The planting involved 45 seedlings from each of the 34 provenances, arranged randomly in three adjacent blocks measuring 84 m x 48 m each. Within each block, 447 seedlings were planted at a square spacing of 3.0 m with one empty space, totaling 1,341 trees across three blocks (Moore, 1981).

1.2.2 Field Sampling

Field data collection occurred in June-August 2022 and June-July 2023. In 2022, survival data and the majority of growth data were collected. In 2023, replacement measurements were collected (i.e., new tree core samples to replace broken or unclear cores, new growth measurements to replace missing data). We recorded the survival status (live/dead) of each planted individual ($n = 1,341$). If a tree was no longer present (i.e., did not survive after planting/past seedling stage), we recorded it as “NS” (“No Survival”). If there was evidence of mechanical removal of a tree, we recorded it as “CS” (“Cut Stump”). Both “NS” and “CS” trees were discarded from analysis. Radial growth 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. Though our initial intention was to sample radial growth from 7-8 trees from each provenance, this was not possible due to mechanical removal and differential mortality. Instead, our sample consisted of 2-6 trees per provenance. We extracted one increment core from each sample tree at approximately 0.30 m above ground level using a 5.15 mm diameter increment borer. Directionality was not considered when deciding the location of core sample extraction due to the flatness of slope at the site.

Cores were labeled with an individual tree code and stored inside of paper straws within well-ventilated plastic jars until sample processing occurred. For each sample tree, we recorded diameter at breast height (DBH), tree height, tree vigor, and competition. DBH was measured at 1.37 m above the base of each tree using a logger's tape. Tree height was measured using a laser rangefinder from a distance of at least 10 m from the sample tree. Tree vigor was assessed using a visual classification method (Appendix 1). Due to the presence of advanced volunteer regeneration within portions of the study area, competition data was collected by measuring the DBH of all volunteer trees taller than 1.37 m within a 1.8 m radius surrounding each sample tree. Competition plots were used to calculate local basal area per hectare (BA), trees per hectare (TPH), and Reineke's stand density index (SDI) (Reineke, 1933).

1.2.3 Lab Processing

Tree core sample processing occurred in fall 2022. Samples were prepared using standard dendrochronological techniques (Speer, 2010). Cores were mounted onto long strips of wood using glue and secured using string. Once the glue dried, the string was removed, and the core mounts were cut so that each core was mounted individually. The cores were sanded at the Field Sample Prep Lab at Colorado State University to within approximately 1 mm of being flush with the core mount using a belt sander with successive grits from coarse to fine. We used an EPSON (Epson America, Inc., Los Alamitos, CA, U.S.) color scanner to scan each core at a resolution of 1200 dots per square inch (dpi). If a core sample did not include the pith by more than three growth rings, or if knots were present and obscured any growth rings, a replacement core was collected in June 2023 and processed in July 2023. Cores that lacked distinguishable growth rings due to poor sampling or preparation were excluded. Cores were visually cross dated using a microscope. Cybis Coordinate Record (*CooRecorder*) software (Larsson, 2014) was utilized to

identify the age of each tree core by assigning either the year 2021 or 2022 to the most recent latewood ring if the sample was collected in 2022 or 2023, respectively. Following Maxwell and Larsson (2021), position points were created on each latewood ring from bark to pith, then ring widths were measured, and points were saved as position files. The Cybis Dendro Dating Program (*CDendro*) software (Larsson, 2003) was utilized to perform initial cross-dating (Maxwell and Larsson, 2021). The *dplR* package (Bunn, 2008, 2010; Bunn et al., 2023) was utilized in R Studio version 2023.9.1.494 (R Core Team, 2023) to cross-date ring width series. We excluded tree cores with poor cross-dating correlation, defined here as having an interseries residual correlation less than 0.4. Using this threshold, we aimed to retain cores that reflected inter-provenance growth variation while ensuring rings were accurately dated. The resulting, final data set included 160 trees, consisting of 73 trees from Colorado, 64 from Montana, and 23 from Wyoming (Table 1.1). We selected the years 1992-2021 as our study period, a decision motivated by the availability of clear annual ring-width data and the alignment of this 30-year window with the 30-year climate normal at the study site. Annual basal area increment (BAI) was calculated for each tree ($n = 160$) for each year of growth during the selected study time period (1992-2021) as a measure of annual radial growth for utilization in further analyses.

Table 1.1. Summary of spatial and elevational data of sampled trees (n = 160) at Fraser Experimental Forest listed by state (Colorado, Montana, Wyoming) and provenance.

State	Provenance	n	Latitude (°N)	Longitude (°W)	Elevation (m)
Colorado (CO)	CO-1	4	40.6	-105.4	2378
	CO-2	6	40.6	-105.5	2588
	CO-3	4	37.6	-105.2	2805
	CO-4	4	38.4	-105.4	2744
	CO-5	3	38.5	-105.4	3049
	CO-6	3	38.5	-106.3	3338
	CO-7	4	38.8	-106.3	3003
	CO-8	6	38.8	-106.4	3079
	CO-9	4	38.8	-106.4	3506
	CO-10	5	39.4	-106.3	3178
	CO-11	7	39.4	-106.3	3201
	CO-12	5	39.5	-106.4	2652
	CO-13	5	40.3	-106.1	2652
	CO-14	4	40.4	-106.1	2835
	CO-15	6	40.4	-106.1	2683
	CO-16	3	40.6	-105.5	2805
Total:	16	73			
Montana (MT)	MT-1	6	46.8	-110.8	1875
	MT-2	6	46.8	-110.7	2164
	MT-3	6	47.0	-110.8	1561
	MT-4	5	48.3	-113.4	1555
	MT-5	6	48.3	-113.4	1524
	MT-6	5	46.7	-114.5	1372
	MT-7	7	45.7	-114.0	2134
	MT-8	5	45.7	-114.0	2210
	MT-9	6	45.7	-113.9	1951
	MT-10	3	45.4	-111.2	1783
	MT-11	5	44.8	-111.2	2012
	MT-12	4	44.9	-111.4	2287
Total:	12	64			
Wyoming (WY)	WY-1	2	44.8	-107.4	2287
	WY-2	5	44.8	-107.5	2591
	WY-3	4	42.7	-108.9	2439
	WY-4	6	41.7	-108.9	2591
	WY-5	3	42.7	-108.9	2920
	WY-5A	3	42.6	-108.8	2668
Total:	6	23			

1.2.4 Climate Data and Window Selection

To address our first research question on whether differences in radial growth exist between trees from different provenances, we utilized two complementary approaches. First, we employed a generalized linear mixed-effects modeling approach (GLMM) to predict tree growth (BAI) as a function of climate at FEF. Second, we explored how moving the provenances across climate space impacted annual BAI trends using provenance climate data relative to FEF. To do this, we obtained climate data from ClimateNA for FEF for the period 1992-2021, corresponding to our selected study period. To characterize the climatic conditions experienced by the trees before seed collection, we also obtained 30-year normal period data (1951-1980) for each provenance site from ClimateNA (Wang et al., 2016). A total of 11 monthly climate variables were obtained for both FEF and the 34 provenance sites (Table 1.2). Guided by similar studies that describe growth-climate relationships for lodgepole pine (Parks et al., 2019), we calculated three additional variables from the ClimateNA data: average and maximum vapor pressure deficit (VPD_{ave} and VPD_{max}; calculated using relative humidity and air temperature), and evapotranspiration (ET; calculated as Hargreaves' reference evaporation [E_{ref}] – climatic moisture deficit [CMD]) (Hill et al., 2024; Parks et al., 2019) (Table 1.2).

Table 1.2. Summary of climate variables obtained from ClimateNA. Variables that were added and calculated using obtained ClimateNA variables are listed at the bottom of the table. Methods of calculation or derivation of variables are listed where applicable (Hogg et al., 2013; Wang et al., 2016).

Variable	Description	Calculation or Derivation
Tmin	Minimum temperature (°C)	
Tave	Mean temperature (°C)	
Tmax	Maximum temperature (°C)	
PPT	Precipitation (mm)	
Eref	Reference evaporation (mm)	Calculated using Tave
CMD	Hargreaves climatic moisture deficit (mm)	Calculated as Eref – PPT
RH	Relative humidity (%)	Calculated using Tmax, Tmin
CMI	Hogg’s climate moisture index (mm)	Calculated as PPT – PE*
DD18	January - December degree-days above 18°C	Derived using Tave
DD5	January - December degree-days above 5°C	Derived using Tave
NFFD	January - December number of frost-free days	Derived using Tmin
VPDave	Mean vapor pressure deficit (kPa)	Calculated using RH, Tave
VPDmax	Maximum vapor pressure deficit (kPa)	Calculated using RH, Tmax
ET	Evapotranspiration (mm)	Calculated as Eref – CMD

* *Potential evapotranspiration*

Given that radial growth of lodgepole pine is often correlated with monthly climate conditions of several months (Villalba et al., 1994), we performed a sliding window analysis for each FEF climate variable to identify the period of time with the highest correlation with the annual average BAI across all trees. We used the `monthly_response()` function from the *dendroTools* package (Jevsenak, 2020) in R to correlate BAI with climate variables using a sliding window from 1 to 24 months that included the climate of both the previous and current year based on the understanding that current year tree growth can be influenced by both the climate of the current year and of the previous year (Villalba et al., 1994).

To assess the performance of trees between provenances relative to the difference between provenance climate and transfer site, we relativized the provenance climate variables obtained for each provenance to the FEF climate variables. First, the 1951 to 1980 monthly climate for each provenance was summarized to the same climate windows identified during the

window analysis of FEF to obtain annual values for each provenance and for each variable. Then, these were averaged to describe the 30-year climate normal of each provenance. Finally, the FEF annual climate metrics were relativized against the 30-year climate normal values for each provenance using Equation 1.

$$FEF_{relative;i,j} = \frac{Provenance\ Norm_j - FEF_i}{FEF_i} \times 100 \quad [Equation\ 1]$$

In this equation, $FEF_{relative}$ is the relative percent difference in climate for each year (i) and provenance (j), $Provenance\ Norm$ is the 30-year climate normal for each provenance (j), and FEF is the climate metric for each year (i). A positive $FEF_{relative}$ value indicates a seed source site (provenance) with a climate normal greater than the observed climate at FEF in a given year, while a negative $FEF_{relative}$ value indicates a seed source site with a climate normal lower than the observed climate at FEF in a given year (Figure 1.2).

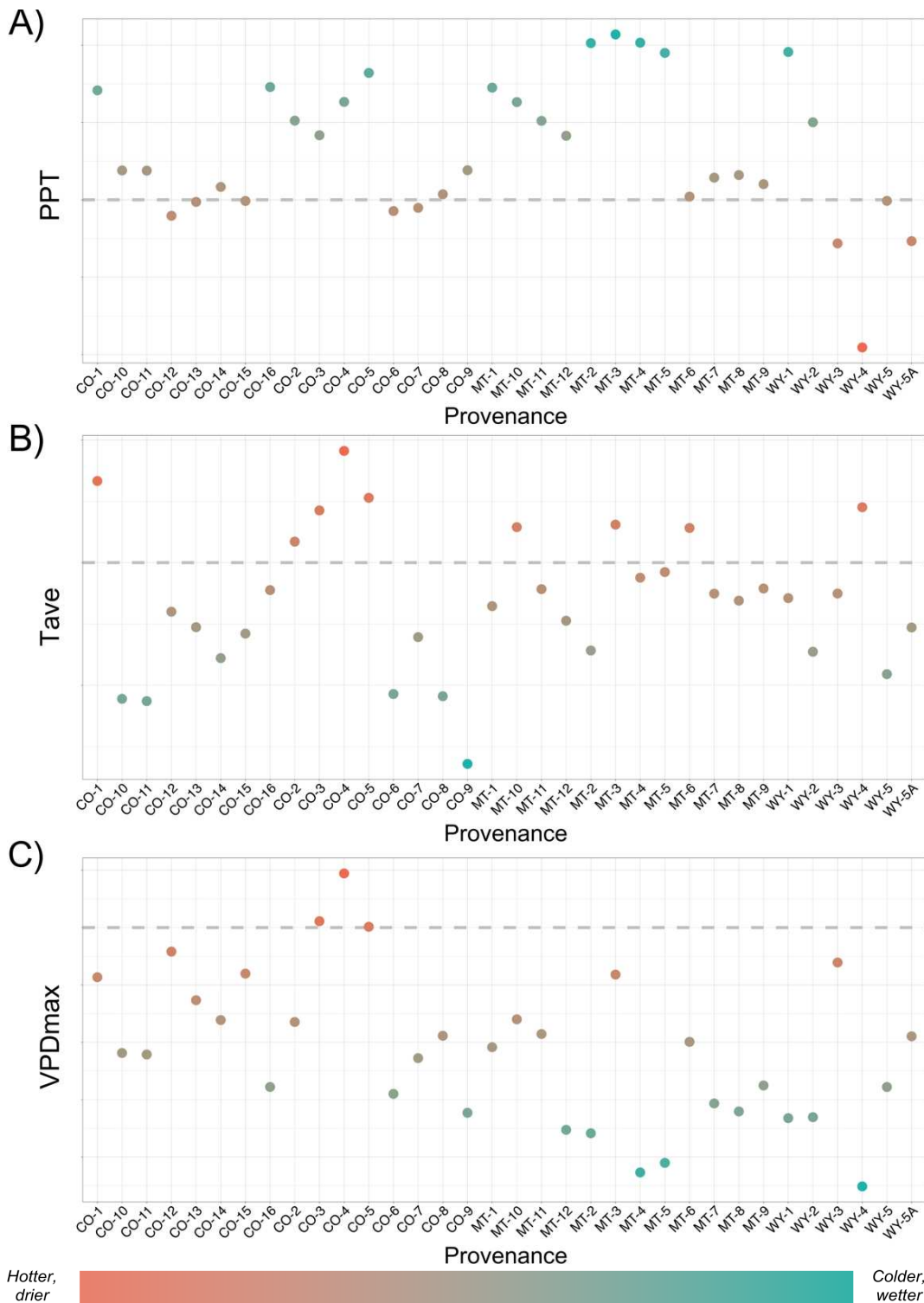


Figure 1.2. Provenance climates relative to the study site at Fraser Experimental Forest. Each panel displays one of three variables chosen for illustration: (A) precipitation (PPT), (B) average temperature (Tave), and (C) maximum vapor pressure deficit (VPDmax). Colored dots represent the average value of the corresponding variable of a provenance in a given year, with red values corresponding to relatively hotter, drier climates, and blue values corresponding to relatively colder, wetter climates. Grey dashed lines represent the climate at Fraser Experimental Forest.

1.2.5 Climate Modeling

We utilized GLMM to assess the influence of provenance climate on radial growth at FEF. We built two models: a baseline model using the FEF climate data, and a relative model using the relative provenance climate data. To overcome the uneven number of samples from each provenance (Table 1.1), we modeled radial growth as BAI from each individual tree, with an added random effect for provenance in each model.

We built the baseline generalized linear mixed-effects model for how tree growth (BAI) responds to variations in site climate using the *lme4* package (Bates et al., 2015) in R. The model included radial growth (BAI) as the outcome variable with two random effects for year (tree age) and tree nested within site (provenance) and the 14 FEF climate variables as fixed effects, as well as basal area as an additional fixed effect to account for competition. We employed a Gamma distribution with a log-link to account for the zero truncation and long upper-tailed distribution that is common for tree growth data of this nature. Due to varied scales across model variables, all fixed effects were centered and scaled such that the mean value was set to zero with other values representing standard deviations above and below the mean. Variables were removed for collinearity using Pearson correlation analysis with a threshold of 0.7. After collinear variable removal, we performed stepwise Akaike Information Criterion (AIC) for model goodness-of-fit selection and assessed the Variance Inflation Factor (VIF) for independent variable multicollinearity using a predefined threshold of 2.0. Effect size of variables in the final model were assessed using Cohen's f from the *sjstats* package (Lüdtke, 2022) in R. The *performance* package (Lüdtke et al., 2021) in R was used to calculate marginal and conditional R^2 values (Nakagawa et al., 2017). Model performance was assessed through interpretation of R^2 values, where marginal R^2 (R^2_m) measures the variance of the fixed effects in a model, and

conditional R^2 (R^2c) measures the variance of both fixed and random effects (Nakagawa and Schielzeth, 2013). The final model was tested for residual spatial autocorrelation using Moran's I from the *ape* package (Paradis and Schliep, 2019) in R to determine any potential impacts of tree planting location on individual tree growth.

A similar approach was utilized to develop a second climate model using the 14 provenance relative metrics as fixed effects, as well as an additional fixed effect for BA to account for competition. Because the climate metrics in this model represent a percent departure for each provenance from the FEF climate, only BA was scaled in this model. The model used a Gamma distribution with log link and year (tree age) as a random effect. This model utilized the same steps for variable reduction as the baseline model.

1.2.6 SPEI and Timescale Selection

We addressed our second research question surrounding how provenance climate influences drought resilience by utilizing a method proposed by Lloret et al. (2011) to measure drought response using BAI. We used a resilience metric that evaluates the ratio of BAI after a drought against BAI before a drought, with greater values showing stronger resilience to the drought's effects. To describe drought at FEF, we calculated the Standardized Precipitation Evapotranspiration Index (SPEI) at temporal scales ranging from 1 to 24 months for the period 1992-2021 using the *SPEI* package (Beguería and Vicente-Serrano, 2023) in R. SPEI, a widely used drought index, provides a standardized measure of drought severity by incorporating both precipitation and potential evapotranspiration (Vicente-Serrano et al., 2010). We utilized the window selection method employed in our analysis of climate to identify the most relevant SPEI timescale from 1 to 24 months that best corresponded with BAI growth using *dendroTools* (Jevsenak, 2020) in R. We utilized the resulting time scale selection to identify drought periods

using a threshold of ≤ -0.6 SPEI. Our threshold selection was informed by the SPEI classification outlined by Wang et al. (2018) in which SPEI values ranging from -0.5 to -1.0 indicate mild drought. Additionally, this selection represented a natural break within our data. Our study site did not experience severe droughts, making a lower threshold more appropriate for capturing relevant drought periods. Applying this threshold resulted in the identification of four distinct drought periods spanning one- to two-years in length across our study period. We selected the 2001-2002 drought period for analysis based on the availability of sufficient data to calculate drought resilience, which requires at least five years of BAI data before and after the drought period.

1.2.7 Drought Resilience Modeling

We calculated resilience (R) for each tree (i) using average BAI at varying intervals (j) from one to five years before (BAI_{pre}) and after (BAI_{post}) the selected drought period using Equation 2 (Lloret et al., 2011).

$$R_{i,j} = \frac{BAI_{post,i,j}}{BAI_{pre,i,j}} \quad [\text{Equation 2}]$$

To examine the relationship between resilience and relative climate, we used multiple linear regression analysis and fit a multiple linear model using the $lm()$ function in the *stats* package (R Core Team, 2023) in R. The model included resilience (R) as the outcome variable and the 14 relative climate variables and trees per hectare to account for competition as the predictor variables. Variables were removed for collinearity using Pearson correlation analysis with a threshold of 0.7. Stepwise AIC methods was performed for model goodness-of-fit selection, and VIF was assessed to test for independent variable multicollinearity using a predefined threshold of 2.0. Model performance was assessed using the R^2 value that was adjusted for the number of predictors in the final model ($Adj R^2$).

1.3 Results

1.3.1 Overall Growth and Competition

Tree survival was 66% across the study but varied between provenances, with survival ranging from 40% to 88% (Figure 1.3.A). Within the different states, mean (standard deviation) provenance survival was 72% (11%), 63% (13%), and 62% (8%) for Montana, Wyoming, and Colorado, respectively. Across the study, the mean DBH and height were 14.7 cm and 7.7 m, respectively (Figure 1.3.B & C). Of the Montana provenance sites, nine of the 12 had mean DBH values and 10 of 12 had mean height values greater than the overall mean, with the largest mean DBH and height from Montana-10 (MT-10). While Colorado had DBH and height values more distributed across the observed range, the Wyoming provenances consistently displayed mean DBH and height values beneath the overall mean (Figure 1.3.B & C; Appendix 3).

Across competition plots at each individual sample tree at the study site, basal area (BA) values per hectare ranged from 26.58 to 261.66. Trees per hectare (TPH) values spanned 397.78 - 2784.48. Stand density index (SDI) ranged from 74.16 - 579.70 (Appendix 2).

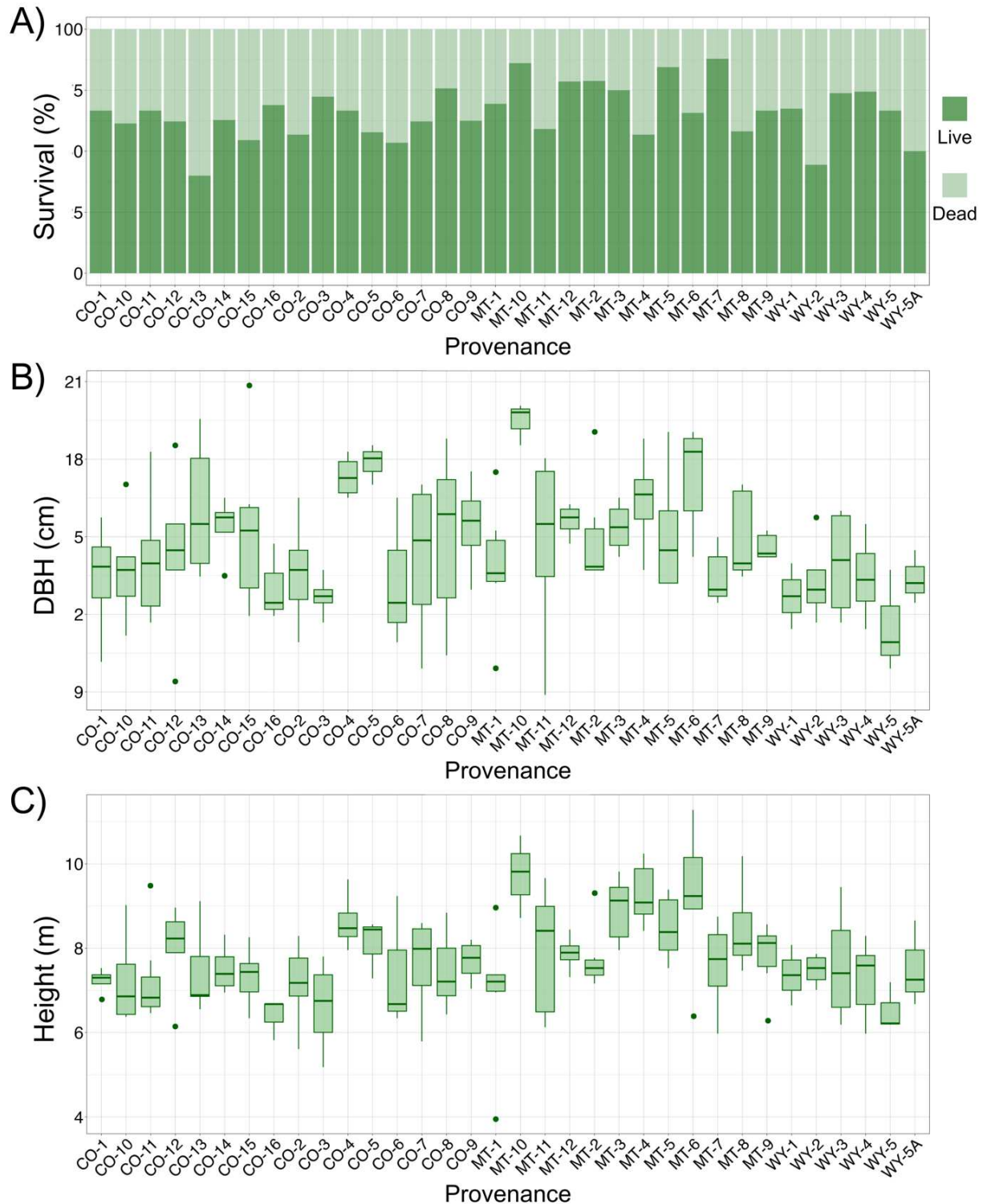


Figure 1.3. Fraser Experimental Forest tree provenance differences in (A) survival, (B) diameter at breast height, and (C) tree height in 2022, 2023. Survival data was collected on all study trees ($n = 1,341$), while diameter at breast height and tree height were collected from the sample of trees ($n = 160$). Boxplots denote the median, 25th and 75th percentiles, and either the minimum of or maximum value or 1.5 times the interquartile range (dependent on closest proximity to the mean). Outliers beyond 1.5 times the interquartile range from the median are shown as points.

1.3.2 Climate Analysis

From the linear regression analysis of mean annual BAI as a function of FEF climate, we obtained an optimal window width providing the largest R^2 for each climate variable, indicating the highest variance explained by the FEF climate data from 1992-2021 (Table 1.3). Optimal windows varied between variables, with lengths spanning 1- to 18-months. Optimal windows of three variables, PPT, CMD, and VPDave, aligned closely with FEF’s typical growing season period of May through October. The strength of variation explained by the linear relationships between BAI and climate variables varied greatly, with the strongest corresponding to 17-month intervals of the number of frost-free days (NFFD; $R^2 = 0.85$) followed by the minimum mean temperature (Tmin; $R^2 = 0.83$) (Table 1.3).

Table 1.3. Results of the sliding window analysis showing optimal climate variable windows for each climate variable obtained from ClimateNA. Asterisks (*) denote to previous growing season.

Variable	Window Width	Window Selection	R^2
Tmin	17 months	May* – September	0.83
Tave	17 months	May* – September	0.68
Tmax	7 months	July* – January	0.41
PPT	3 months	June – August	0.36
Eref	11 months	June* – April	0.27
CMD	4 months	June – September	0.29
RH	6 months	Nov* – April	0.72
CMI	1 month	November*	0.23
DD18	18 months	May* – October	0.52
DD5	17 months	June* – October	0.68
NFFD	17 months	May* – September	0.85
VPDave	4 months	June – September	0.44
VPDmax	1 month	July*	0.26
ET	4 months	June – September	0.44

In the FEF base model, the variable reduction process of the generalized linear mixed-effects model of radial growth, measured in the model as BAI, resulted in June through August precipitation (PPT), the previous November’s Hogg’s climate moisture index (CMI), and degree

days above 18°C from the previous May to current October (DD18) had the strongest climatic effects on annual radial growth (Table 1.4). Annual BAI increased in years with greater PPT and DD18 (Figure 1.4), indicating that higher moisture availability and warmer conditions lead to greater annual radial growth. Conversely, the model shows a negative relationship between BAI and CMI, suggesting that higher moisture levels during the previous fall were associated with reduced growth ($p < 0.001$; Figure 1.4). Additionally, BAI exhibited a positive relationship with basal area (hereafter BA), indicating that growth increases as competition increases at the site (Figure 1.4). Testing of model spatial residuals using Moran’s I revealed no significant spatial autocorrelation ($p = 0.406$).

Table 1.4. Summary of generalized linear mixed-effects models describing tree growth as a function of either the climate at Fraser Experimental Forest or using the relativized climate from the 34 provenances. Model performance was assessed through the interpretation of both marginal and conditional r-squared values (R^2m and R^2c , respectively).

		Est	SE	<i>t</i>	<i>p</i>	Cohen’s <i>f</i>	R^2m	R^2c
<i>BAI ~ FEF Climate + (1 Year) + (1 Tree:Provenance)</i>							0.46	0.62
Fixed	Intercept	6.077	0.08	76.468	< 0.001			
Effects	PPT	0.29	0.069	4.184	< 0.001	0.122		
	CMI	-0.188	0.074	-2.534	0.011	0.126		
	DD18	0.212	0.075	2.843	0.004	0.093		
	BA	0.129	0.034	3.51	< 0.001	0.107		
		Est	SE	<i>t</i>	<i>p</i>	Cohen’s <i>f</i>	R^2m	R^2c
<i>BAI ~ Relative Climate + (1 Year)</i>							0.14	0.38
Fixed	Intercept	6.175	0.112	55.003	< 0.001			
Effects	PPT	0.272	0.031	8.669	< 0.001	0.124		
	VPDave	1.468	0.108	13.513	< 0.001	0.179		
	VPDmax	-0.784	0.093	-8.396	< 0.001	0.116		
	BA	0.12	0.008	14.882	< 0.001	0.227		

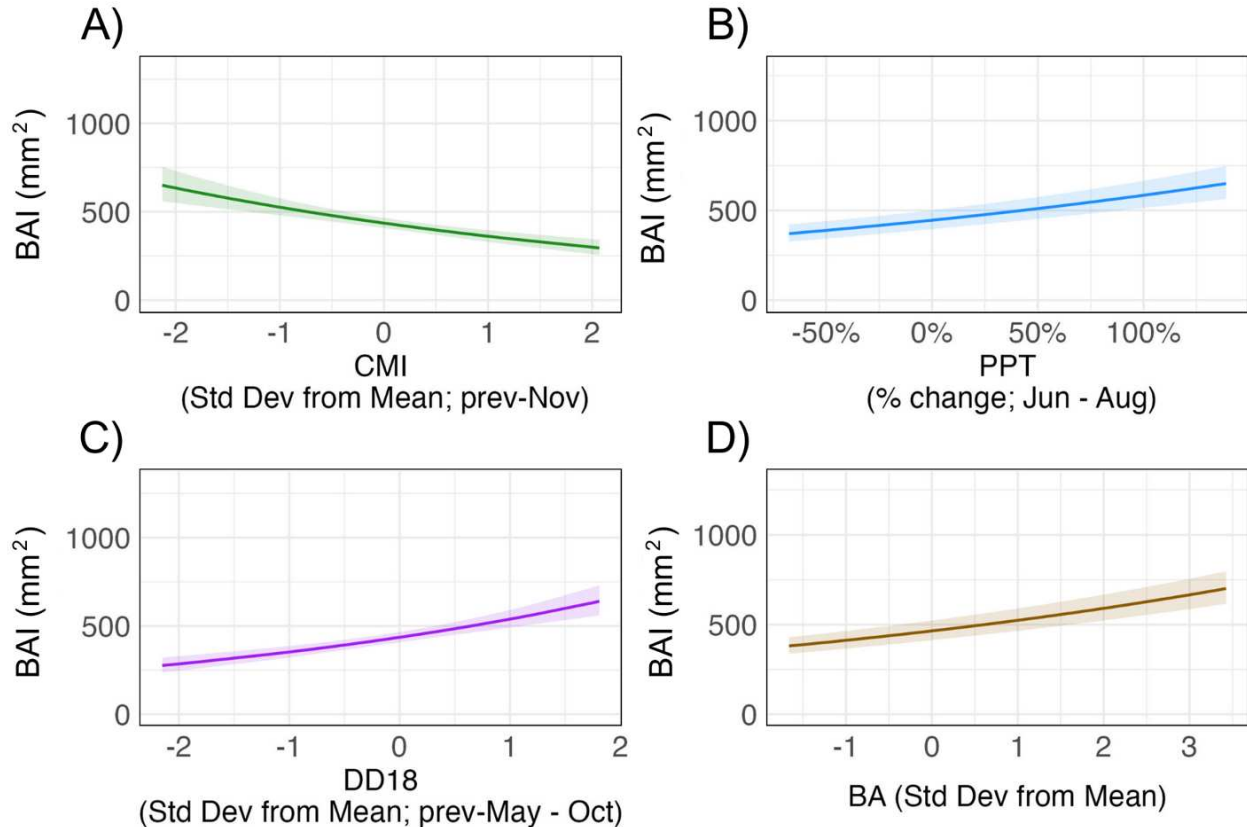


Figure 1.4. Effects plots from the generalized linear mixed model of lodgepole pine provenance radial growth at Fraser Experimental Forest during 1992-2021. The four plots illustrate the effect on the response variable, basal area increment (mm^2), of the four final predictor variables in the model: (A) Hogg's climate moisture index from the previous November, (B) precipitation from June through August, (C) degree days above 18°C in the previous May through current October, and (D) basal area as a metric for competition. Each predictor is expressed in standard deviations from the mean. Shaded areas around each line represent the 95% confidence interval of the model predictions.

The final generalized linear mixed-effects model of tree radial growth as a function of relative provenance climate showed that June through August PPT, the previous July's mean vapor pressure deficit (VPD_{ave}), and maximum vapor pressure deficit in February through May (VPD_{max}) had the greatest climatic effect on growth (Table 1.4). In the model, the relativized climate variables represent the percent difference between the FEF annual climate and each provenance's climate normal for that variable (Equation 1), with both metrics summarized using the optimal climate windows. BAI had a positive relationship to PPT, suggesting that trees from sites with greater growing season moisture experienced greater growth (Figure 1.5). Increases in

relative VPDave are associated with greater BAI, indicating that trees from sites with greater previous-summer atmospheric moisture deficit exhibited greater growth at their transplanted growing site that has less deficit (i.e. FEF has lower VPDave). Conversely, higher VPDmax correlates with reduced BAI, suggesting that seed sources from locations with greater February through May, or early spring, atmospheric moisture deficits are performing worse. Similar to the FEF base model, BAI is positively related to BA, signifying some level of growth facilitation through competition (Figure 1.5). Testing of model spatial residuals using Moran's I revealed no significant spatial autocorrelation ($p = 0.502$).

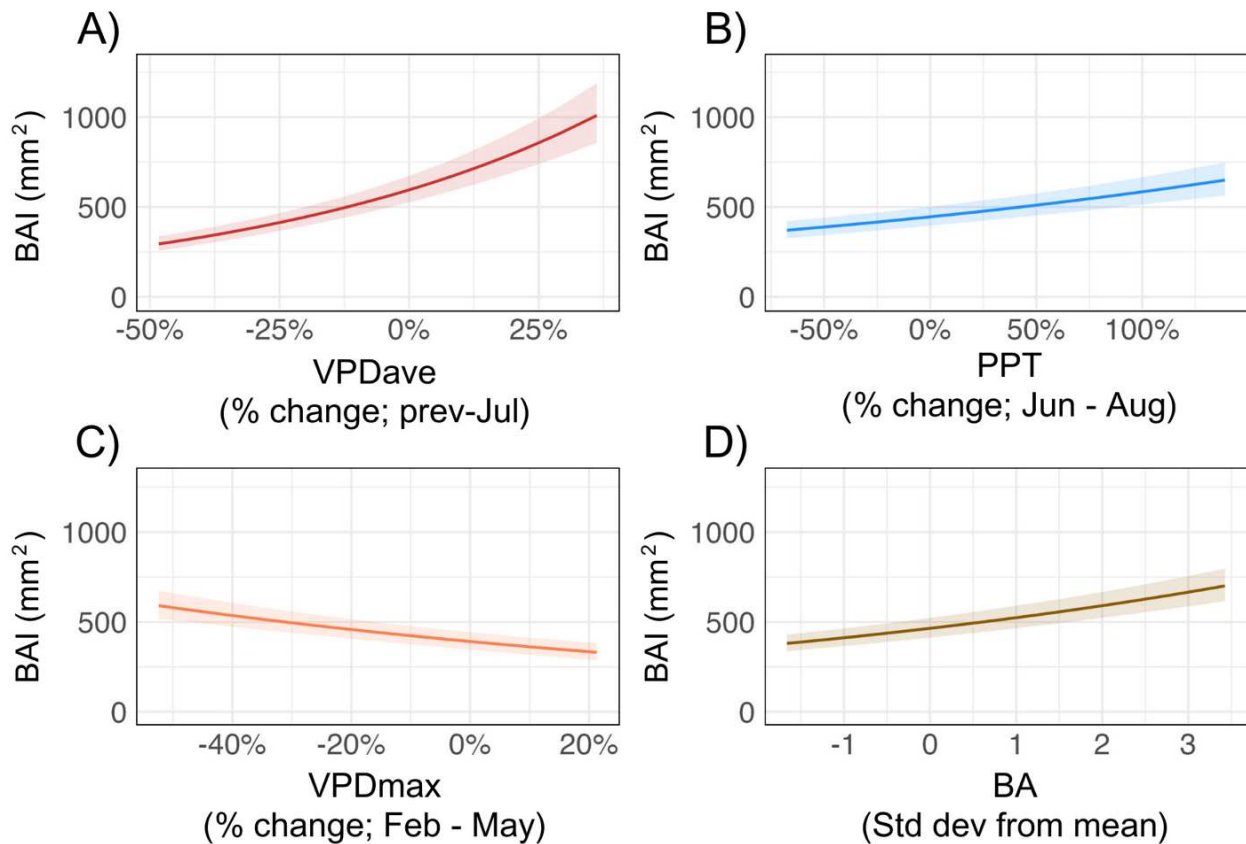


Figure 1.5. Effects plots from the generalized linear mixed model of relative provenance climate to the Fraser Experimental Forest study site. The four plots illustrate the effect on the response variable, basal area increment (mm^2), of the four final predictor variables in the model: (A) average vapor pressure deficit in the previous July, (B) precipitation in June through August, (C) maximum vapor pressure deficit in February through May (early spring), and (D) basal area expressed in standard deviations from the mean. Provenance climate predictors are expressed as percent change from the Fraser Experimental Forest climate. Shaded areas around each line represent the 95% confidence interval of the model predictions.

1.3.3 Drought Resilience Analysis

SPEI window analysis determined that a one-month interval spanning June through September of each year of the study period displayed the strongest relationship with BAI ($R^2 = 0.424$) (Appendix 4). Utilizing this timescale and a threshold of ≤ -0.3 SPEI, we identified one drought event occurring in 2001 and 2002 to use in further analysis. This choice is substantiated by the well-documented and extensively studied period of drought conditions in Colorado during that time, attributed to rising temperatures and accompanied by severe wildfire activity (Coop et al., 2020; Fornwalt et al., 2016; Romme et al., 2003; Seager et al., 2015).

Variable reduction of the multiple linear model of drought resilience determined that the relative climate variables most predictive of drought resilience are evapotranspiration from the current year's June through September (ET), late-fall CMI, and mean monthly temperature from the previous May through current September (Tave) (Table 1.5). There is a positive association between resilience and relative ET and CMI (Figure 1.6). Although weaker, the relationship between resilience and Tave was also positive, showing that trees from provenances with higher temperatures show more drought resilience at FEF during drought conditions. Conversely, resilience displayed a negative correlation with TPH, suggesting a potential adverse effect of higher tree density on drought resilience (Figure 1.6). Similar to the other models, Moran's I revealed no significant spatial autocorrelation ($p = 0.482$).

Table 1.5. Summary of the linear model describing drought resilience as a function of the relativized climate from the 34 provenance sources at Fraser Experimental Forest.

		Est	SE	<i>t</i>	<i>p</i>	Cohen's <i>f</i>	<i>Adj R</i> ²
<i>Resilience ~ Relative Climate</i>							0.20
Predictors	Intercept	1.156	0.072	16.054	< 0.001		
	ET	0.297	0.082	3.61	< 0.001	0.422	
	CMI	0.045	0.017	2.594	0.01	0.173	
	Tave	0.11	0.089	1.234	0.219	0.106	
	TPH	-0.0001	0.00002	-3.089	0.002	0.249	

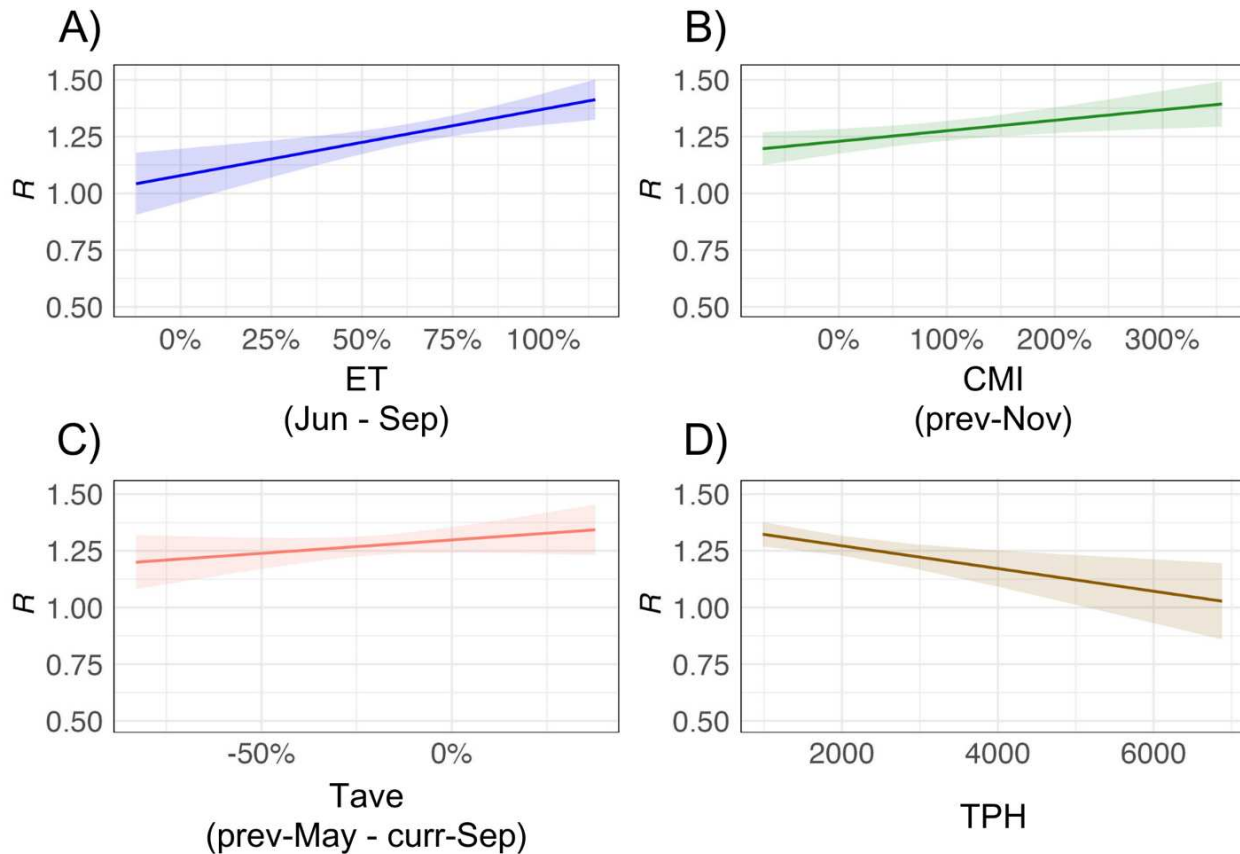


Figure 1.6 Effects plots from the multiple linear model of drought resilience as a function of relative provenance climate to the Fraser Experimental Forest study site. The four plots illustrate the effect on the response variable, drought resilience, of the four final predictor variables in the final model: (A) evapotranspiration in June through September (growing season), (B) Hogg's climatic moisture index for the previous November, (C) mean temperature for the previous May through the current September, and (D) trees per hectare. Shaded areas around each line represent the 95% confidence interval of the model predictions. High resilience values reflect greater drought resilience, and low resilience values reflect lower drought resilience.

1.4 Discussion

This study examined how the difference between growing site climate and provenance climate influences the annual radial growth and drought resilience of the southernmost populations of lodgepole pine, offering insights into the species' adaptive potential in forest assisted migration efforts to combat climate change.

1.4.1 Overall Growth

The field data results revealed that tree survival varied significantly across the study site, with notable differences between provenances (Figure 1.3.A). The mean (standard deviation) provenance survival rates were highest in Montana at 72% (11%), followed by Wyoming at 63% (13%), and Colorado at 62% (8%). Montana also demonstrated greater growth (DBH and height) performance across the site (Figure 1.3.B & C). Nine of 12 sites exhibited mean DBH values that exceeded overall study averages, and 10 of 12 sites exhibited mean height values that exceeded overall study averages. By contrast, DBH and height values of Colorado provenances displayed a more even spread across the observed range. Wyoming provenances consistently exhibited mean DBH and height values below the overall observed means (Figure 1.3.B & C; Appendix 3). These findings demonstrate that sourcing seeds for similar experiments should not adhere to state or arbitrary boundaries, but rather be collected to represent the dynamic climate of a species' range. However, it is also important to note that the field growth data presented here represent a snapshot in time, and the relationships between provenance climate and radial growth are further elucidated in our analyses of BAI, which provide insights into growth trends over a longer period of time.

1.4.2 Climate Response at FEF

The baseline assessment of radial growth at the FEF study site supports established knowledge that years with increased precipitation and longer growing seasons support greater growth (Table 1.4). Our results show that lodgepole pine growth exhibits variability in growth and drought response based on seed source, a relationship previously observed in cooler and wetter regions of the species' range (McLane et al., 2011a; McLane et al., 2011b) and now shown in the warmer and drier regions of the species' range. Consistent with previous research findings and in support of our first hypothesis, we found that provenance climate has an impact on the radial growth response of lodgepole pine (Aitken et al., 2008; McLane et al., 2011a; McLane et al., 2011b), with significant differences in BAI growth between trees from different provenances planted at FEF during our study period (Table 1.4). We also found that provenance climate impacted resilience of trees during the 2001-2002 drought period (Table 1.5), supporting previous findings examining the impact of seed source on lodgepole pine drought response (McLane et al., 2011a; McLane et al., 2011b; Wang et al., 2006). Additionally, our findings partially support our second hypothesis that trees from more arid provenances will exhibit greater resilience to drought due to local adaptations that confer drought tolerance. Overall, the climatic mechanisms and seasonality driving both climate-growth response between provenances and drought resilience are more nuanced than expected.

Analysis of overall growth-climate relationships at the FEF study site over the study period 1992-2021, found that tree growth increased with increased growing season (June through August) precipitation. This aligns with previous research findings that link increased growing season precipitation to increased lodgepole pine growth (Case and Peterson, 2007; Chhin et al., 2008; Seely et al., 2015).

Interestingly, tree growth responded negatively to greater CMI in the previous November. The optimal seasonal window selection of the previous November aligns with previous research examining the lagged growth effect of lodgepole pine in response to climatic conditions from the previous year (Chhin et al., 2008; Cortini et al., 2011; Villalba et al., 1994). However, the observed directionality of this relationship contradicts these findings. CMI can be described as a measure of overall moisture availability at a site (Wang et al., 2014). Seely et al. (2015) highlighted that limited moisture availability largely controlled lodgepole pine biomass growth in their study of North American montane forest ecosystems. Moreover, in their meta-analysis of drought impacts on global forests, Allen et al. (2010) found that moisture stress (i.e., low moisture levels) generally reduces tree growth and can lead to mortality in many forest ecosystems worldwide. The unexpected result of lowered radial growth in response to heightened previous late-fall CMI, observed in this study, was similarly observed in a study by Finley and Zhang (2019). In that study, a negative correlation was found between November CMI and radial growth in ponderosa pine, suggesting that late-season moisture might interfere with the trees' acclimation processes. Although their study focused on ponderosa pine and the correlation was of the current-year CMI (not the previous year, as in this study) the findings may highlight a broader pattern in which late fall moisture could alter normal tree growth cycles (Finley and Zhang, 2019), thus highlighting the importance of considering seasonality and timing when considering growth-climate responses of lodgepole pine.

The positive relationship between DD18 from the previous May to the current October and tree growth further points to the influence of climate of the previous year on growth of the current year (Chhin et al., 2008; Cortini et al., 2011; Villalba et al., 1994). DD18, similar to the more widely used growing degree days (GDD), serves as a proxy for optimal plant growth

conditions, where higher values correspond to longer periods of favorable growing conditions (Wang et al., 2010; Wang et al., 2016). Liu and El-Kassaby (2018) found DD18 to be a key variable in predicting growth and productivity of conifer adaptive specialists including lodgepole pine, showing a positive correlation between DD18 and growth. Our results support this finding, as well as broader findings that reflect the relationship between plant growth and optimal growing conditions (Hankin et al., 2019; Sands and Mulligan, 1990).

1.4.3 Provenance Influence on Climate Response

In our analysis of the influence of provenance climate on radial growth, we found that trees from sites with greater mean vapor pressure deficit (VPD) in the previous summer (previous July) experienced greater radial growth at FEF than trees from sites with less VPD in the previous summer (Figure 1.5) when grown at FEF. VPD, or the average difference between the amount of moisture in the air and the amount of moisture it could hold when saturated, is an indicator of atmospheric dryness and is commonly used in measuring drought-stress in plants (Seager et al., 2015; Yuan et al., 2019). This positive correlation aligns with previous research indicating that trees respond positively in growth to decreased atmospheric moisture deficit (Davis et al., 2019; Novick et al., 2016; Seager et al., 2015) and could indicate an adaptive advantage in which trees from drier sites maintain photosynthetic adaptations that enable higher water-use efficiency when experiencing less atmospheric moisture stress at their growing site (Groissord et al., 2020; Ramírez-Valiente et al., 2022). This adaptation to dry conditions was found in a study by Wei et al., (2021) in western Canada, in which lodgepole pine displayed varying responses to drought based on provenance, and those responses were accompanied by varying physiological and morphological traits.

Maximum VPD showed the opposite effect on radial growth, contradicting our first finding and previous research (Novick et al., 2016; Seager et al., 2015; Yuan et al., 2019). We found that trees from sites with greater maximum VPD in early spring exhibited reduced radial growth (Figure 1.5), meaning that trees will experience less annual radial growth when moved to a site with less early spring VPD (deficit), than their seed source site. Massmann et al. (2019) observed that the impacts of VPD on tree growth vary with seasonality, and that lower VPD may even reduce stomatal conductance and transpiration. This has the capacity to ultimately curb growth in early spring, a time during which trees resume growth after winter, and when water demand is typically high (Massmann et al., 2019).

Growing season precipitation had a positive association with radial growth, indicating that trees originating from sites with greater June through August precipitation than their current growing site exhibited increased growth. This finding challenges the well-established understanding that precipitation drives tree growth (Anderson-Teixeira et al., 2022; Heilman et al., 2021), and, more specifically, increased growing season precipitation is associated with increased radial growth in lodgepole pine (Case and Peterson, 2007; Chhin et al., 2008). Our counterintuitive finding may be explained by a study by McLane et al. (2011a), which shows that trees from wetter sites may maintain adaptations that support higher water use efficiency, ultimately aiding in greater growth when moved to drier sites.

In both climate models, the positive association between Basal Area and BAI challenges previous findings that demonstrate the limiting effect of competition on tree growth and productivity (Bottero et al., 2017; Castagneri et al., 2022; Danyagari et al., 2023; Knapp et al., 2021). However, our result does align with recent findings that show that moderate competition

levels can facilitate tree growth at early development stages in ponderosa pine (Tinkham et al., 2021).

1.4.4 Provenance Influence on Drought Resilience

Our modeling of growth during the 2001-2002 drought period shows that trees originating from sites characterized by higher evapotranspiration exhibited greater resilience to drought (Figure 1.6). ET represents the combined process of water evaporation from the soil surface and transpiration from plant leaves, serving as a proxy for ecosystem water loss and drought-induced mortality (Parks et al., 2019; Stephenson, 1998; Yang et al., 2021). It is a complex climatic variable that connects water, energy, and carbon cycles, making it a multifaceted representation of both land- and atmospheric-moisture dynamics reflecting broader ecosystem functioning (Liu and El-Kassaby, 2018; Yang et al., 2021). Trees from sites with higher ET may develop traits such as enhanced water use efficiency, deeper root systems, and greater stomatal regulation, which may confer resilience during water-limited periods (Liu and El-Kassaby, 2018; McDowell et al., 2008). High ET sites can be environments with readily available water, which can prompt adaptive traits, whereas low ET sites can have limited moisture availability, which can lead to reduced growth and greater drought susceptibility (Anderegg et al., 2013; Yang et al., 2021). Adaptations conferred from high ET sites may help trees to withstand and recover from drought when transplanted to other sites. Findings from Liu et al. (2018) support this idea that trees from high ET sites may develop traits that promote drought resilience.

The positive relationship between May (previous year) through September (current year) mean temperature (T_{ave}) and growth resilience to drought indicates that trees from sites with higher T_{ave} exhibit greater drought resilience. This means that trees that are growing at a site

with lower average temperatures in a given year than their source site will exhibit greater resilience to drought. This aligns with previous research that found that trees respond negatively to increased temperatures, likely due to the increased atmospheric demand that often accompanies increased temperatures (Anderson-Teixeira et al., 2022; Restaino et al., 2016). This result may also point to a relationship between drought resilience and provenance climate aridity, as postulated in our second hypothesis. This potential link has not, to our knowledge, been thoroughly investigated in lodgepole pine, however, findings in a study of whitebark pine by McLane et al. (2012) discuss the potential of warmer temperatures to confer drought tolerance to trees, allowing establishment of the species outside its native range.

The positive association between November (previous year) climate moisture index (CMI) and resilience indicates that trees from provenances with greater average CMI in late-fall of the previous year exhibited increased drought resilience at their planted site. This means that the trees that show the greatest resilience to drought conditions are those that are currently growing under a moisture deficit at their growing site, as compared to their seed source site. A meta-analysis by Anderegg et al. (2016) found that hydraulic traits, such as hydraulic safety margin and xylem vulnerability to embolism, are critical determinants of drought-induced tree mortality across tree species globally. Trees with a lower hydraulic safety margin and higher xylem vulnerability are more prone to drought-induced mortality, suggesting that trees from sites with high ET may possess more robust hydraulic traits, contributing to their resilience during water-limited events. The amount and form of moisture received can alter these dynamics. The form of moisture (rain, snow, or air moisture) received by trees in the meta-analysis by Anderegg et al. (2016) is not specified, thus the moisture conditions may not fully align with the moisture conditions of our study. Additionally, given that the meta-analysis aggregates data

across diverse ecosystems, further research specific to our study area is warranted to glean the impacts of different forms of moisture on drought resilience.

Competition exhibited a negative effect on resilience, which indicates that as local stand density increases, radial growth resilience decreases. This is the opposite effect of competition on radial growth in the climate models, which can be attributed to the fact that this model analyzes a period of disturbance causing resource limitation, rather than a period of years as a whole as in the climate models. Studies have shown that competition can exacerbate tree stress during periods of disturbance or when resources are limited (Bottero et al., 2017; Gleason et al., 2017; Gleason et al., 2021; Sohn et al., 2016). However, the density of our study area is lower than the moderate- to high-density stands in the supporting studies. Thus, while this result aligns with established research, further research that includes analysis of a greater number of drought periods is warranted to further elucidate these dynamics.

1.4.5 Management Implications

As climate change continues to reshape temperature and precipitation patterns in the western U.S., understanding how provenance impacts the growth-climate responses of widespread tree species such as lodgepole pine is crucial. We can utilize information gleaned from both this research and similar research to guide forest management decisions aimed at enhancing the resilience of forested ecosystems in the western U.S. As such, several implications for management emerge from the findings of our research.

Broad climate-growth relationships of lodgepole pine illustrated in our results highlight the pivotal role that growing season moisture availability and the accumulation of previous- and current-year growing degree days have on tree radial growth. These findings emphasize the importance of considering lagged growth-climate responses of lodgepole pine when formulating

management decisions (Chhin et al., 2008; Palik et al., 2022). Further, some observed results resonate with established knowledge surrounding moisture and optimal growing degree days and increased growth (Liu and El-Kassaby, 2018, Yang et al., 2021). However, it is crucial to consider the nuance observed in our findings when making informed climate adaptive management decisions. First, some provenances exhibited a lagged growth sensitivity response to late-fall moisture increases. This is important to consider, as climate change is expected to alter precipitation regimes (Trenberth, 2011), which could lead to increased precipitation during non-growing season months (Anderegg et al., 2016). Thus, seeds may be selected for adaptations to conditions of excess moisture during these periods (Anderegg et al., 2016). Second, when comparing the climate of the provenance site to the growing site, trees demonstrated complex relationships with vapor pressure deficit (VPD) at different seasonal scales. VPD is particularly relevant in the context of climate change, as rising VPD levels are anticipated in the western U.S. as climate change accelerates (Grossoird et al., 2020; Millar et al., 2007). The process of seed selection must account for tree responses to VPD, and more specifically from our study, that greater spring VPD in a provenance site promotes greater tree growth upon transplantation, and greater maximum summer VPD inhibits growth. These varied responses may suggest that lodgepole pine trees possess the capacity to adapt to growing conditions at varying atmospheric deficits, signifying that certain populations may be well-adapted to projected future climate conditions. Our observation that less growing season precipitation at the growing site compared to the provenance site did not inherently inhibit tree growth further suggests the adaptive potential for lodgepole pine to maintain growth even in the face of moisture deficits (McLane et al., 2011a; Montwé et al., 2016). Both of these findings point towards a greater flexibility in

sourcing of seeds, indicating that it may not be as site-limited as observed in other areas of the range of lodgepole pine (Aitken, 2004; Aitken and Whitlock, 2013).

Competition may benefit early tree growth initially by stimulating radial growth up to a certain threshold (Tinkham et al., 2021). However, this positive effect is observed only in the absence of drought or other disturbance events, based on our findings and previous research (Bottero et al., 2017; Castagneri et al., 2022; D'Amato et al., 2011;). During these resource-limited events, competition negatively impacts tree growth (Bottero et al., 2017; D'Amato et al., 2011; D'Amato et al., 2013), which highlights the need to carefully consider tree planting and stand density management, especially in anticipation of increased drought conditions due to climate change (Kerhoulas et al., 2013; Strzepek et al., 2010). Further, in planning for projected increased drought conditions, prioritizing tree species adapted to higher average growing season temperatures ensures higher drought resilience, as confirmed by our findings in this study. These implications emphasize the importance of considering seed source variability in forest management decision-making to optimize tree growth and resilience amidst changing environmental conditions.

Broadly, in selecting the optimal seed sources for forest climate adaptation, our findings suggest that while there are intricacies in the relationships between climate, growth, and drought response that must be carefully considered, there is also notable variation observed among seed sources, illustrating the potential of adaptation or maladaptation of lodgepole pine. Our findings suggest that while selecting source populations best suited for anticipated climatic changes may not be as straightforward as selecting warmer and drier populations with the guarantee of higher drought resilience, the selection process may not be as restrictive as previously assumed (Aitken, 2004).

1.4.6 Limitations and Future Work

There are several limitations in this study that point to avenues of future directions for research. Future research could benefit from examining the relationship between prior drought exposure and resilience, as demonstrated in a similar study focusing on Scots pine conducted by Bose et al., 2020. This study found that resilience of trees during extreme drought events was influenced by whether trees had previously experienced low- to moderate-severity droughts. Exploring the potential role that provenance drought history has on lodgepole pine drought tolerance constitutes a future direction for studies that could help to unravel the intricacies of provenance climate influence on drought resilience.

Additionally, in our analyses, we conducted window selection linear regression on all climate data for FEF and each of the 34 provenances using optimal window selections obtained from the window analysis performed on FEF climate data. In order to better account for the broader western range of lodgepole and its varying correlations with climate variables, it would be useful to conduct separate window selection analyses using the climate data from each provenance. This would result in correlations based on each provenance climate, rather than utilizing the window selections from the FEF window selection analysis and applying those to the provenance variables. This could result in climate windows that more effectively explain variation in growth associated with provenance climate conditions (Camarero et al., 2021).

A greater number of studies focusing on the physiological mechanisms that drive the relationships observed in this study, specifically surrounding climate impacts on photosynthesis, stomatal conductance, and vapor pressure deficit, would provide insight into the processes that drive growth and resilience under varying climate conditions.

Finally, considering current and projected increases in fire frequency due to climate change, understanding the impact of provenance on seed viability and serotiny prevalence of lodgepole pine cones could help guide seed source selection aimed at enhancing forest resilience (Rhoades et al., 2022). Future research can build on the findings in this study to develop a more complete understanding of lodgepole pine growth dynamics in the face of climate change.

1.5 Conclusion

This study sheds light on the relationship between lodgepole pine seed source (provenance) and radial growth and drought resilience in the species' vulnerable southern extent in the western United States. Through the examination of three decades of lodgepole pine growth data from a long-term provenance experiment in Fraser Experimental Forest in Colorado, we explore the adaptive potential of this species in the context of assisted migration for the purpose of forest climate adaptation. Our analysis demonstrates significant variation in growth-climate responses and drought resilience in southern lodgepole populations, a geographic range that remains largely understudied (Aitken and Bemmels, 2016; Aitken and Whitlock, 2013; McLane et al., 2011a).

Our study contributes to advancing the understanding of the adaptive potential of lodgepole pine and provides practical insights for forest managers and researchers grappling with the challenges of climate change. Our results underline the critical role of leveraging local adaptations and intraspecies variability in forest climate adaptation efforts. Further, lodgepole pine exhibits the potential to serve as a demonstrative species for assisted migration in the western U.S. in this era of forest climate adaptation. Implications of this research take on a broader context and serve as a crucial blueprint for climate adaptation efforts across forested ecosystems in the western U.S. and beyond.

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APPENDICES

Appendix 1. Methodology used for the classification of tree vigor of live trees used during field sampling at the provenance experiment study site at Fraser Experimental Forest in Fraser, Colorado in 2022 and 2023.

Class	Description
Excellent	Tree is healthy, needles green, canopy full, branching, upright, robust, no signs of insect pathogen or disease
Good	Tree is mostly upright, majority of needles green/canopy full, little sign of insect pathogen or disease
Fair	Tree is neither healthy nor dying, 20-30% needles yellow or brown, few signs of insect pathogen or disease
Poor	Tree is unhealthy, needles yellow or brown, signs of insect pathogen or disease
Dying	Tree is gnarled, poor stature, presence of insect pathogen or disease

Appendix 2. Summary statistics of competition metrics from competition data collected within a 1.8 m radius of each sampled tree (n = 160) at the provenance experiment study site in Fraser Experimental Forest in Fraser, Colorado in 2022.

Block	n	BA (per hectare)		TPH		SDI	
		Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
1	46	102.8	43.2	1003.1	648.2	259.3	116.1
2	58	100.9	45.1	658.4	398.1	236.1	107.3
3	56	106.5	50.5	752.9	495.5	252.8	122
Total:	160	103.4	46.3	790.6	529.7	248.6	114.8

Appendix 3. Summary statistics of survival, growth, height data of sampled trees at the provenance experiment study site at Fraser Experimental Forest in Fraser, Colorado.

Provenance	DBH (cm)		Height (m)	
	Mean	Std Dev	Mean	Std Dev
CO-1	13.4	2.4	7.2	0.3
CO-10	13.8	2.2	7.3	1.1
CO-11	14	2.3	7.2	1.1
CO-12	14.3	3.3	8	1.1
CO-13	16.1	2.6	7.4	1
CO-14	15.4	1.3	7.5	0.6
CO-15	15.3	3.2	7.3	0.7
CO-16	13	1.5	6.4	0.5
CO-2	13.6	1.9	7.2	0.9
CO-3	12.7	0.8	6.6	1.1
CO-4	17.3	0.8	8.6	0.7
CO-5	17.9	0.8	8.1	0.7
CO-6	13.3	2.9	7.4	1.6
CO-7	14.2	3.3	7.6	1.3
CO-8	15	3.3	7.5	0.9
CO-9	15.4	1.9	7.7	0.5
MT-1	13.8	2.5	6.9	1.6
MT-10	19.5	0.8	9.7	1
MT-11	14.7	3.7	7.9	1.6
MT-12	15.6	0.7	7.9	0.5
MT-2	15	2.1	7.8	0.8
MT-3	15.4	0.9	8.9	0.8
MT-4	16.4	1.7	9.3	0.7
MT-5	15.2	2.4	8.5	0.8
MT-6	17.3	2.1	9.2	1.8
MT-7	13.5	1	7.6	1
MT-8	15	1.8	8.5	1.1
MT-9	14.6	0.5	7.8	0.8
WY-1	12.7	1.8	7.4	1
WY-2	13.3	1.6	7.5	0.4
WY-3	14	2.2	7.6	1.5
WY-4	13.4	1.5	7.3	0.9
WY-5	11.5	2	6.5	0.6
WY-5A	13.4	1	7.5	1
All:	14.7	1.7	7.7	0.8

Appendix 4. Results of the sliding window analysis to determine the optimal timescale and window of the Standardized Precipitation Evapotranspiration Index. Window analysis was performed on monthly window intervals from 1- to 24- months. Results shown here are amended for length to only include results of 1- to 12-month timescale selection analysis. Asterisks (*) denote to previous growing season.

SPEI Length	Window Length	Starting Month	R^2
1 month	4 months	June – September	0.424
2 months	3 months	July – September	0.304
3 months	3 months	August – October	0.346
4 months	1 month	September	0.352
5 months	1 month	October	0.26
6 months	1 month	November	0.24
7 months	2 months	November – December	0.129
8 months	3 months	October – December	0.063
9 months	2 months	November – December	0.057
10 months	23 months	January* – November	-0.051
11 months	1 month	December	-0.032
12 months	1 month	June*	-0.031