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Long-term survival, growth, and reproduction responses of Engelmann spruce provenances to climate

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ABSTRACT

As changes in climate accelerate, mature forests experience different local conditions than those that they were established under and are likely adapted to. Tree regeneration is highly constrained by climatic conditions and as these conditions continue to change, it is important to understand how reforestation choices will affect future forests. Provenance studies have been used for more than a century to understand the influence of genetics and the environment on traits, and can now additionally provide information on provenance performance under the rapidly changing climate. Here we compare survival, growth, reproduction, and growth-climate relationships among 20 provenances of Engelmann spruce (*Picea engelmannii*) trees over 45 years in a provenance study. We found that the best surviving provenances were climatically similar to the plantation with dry climates and short growing seasons, but this did not apply to overall growth. Seedlings from provenances with higher summer to spring precipitation ratios were faster to reproduce and were taller at outplanting, which was advantageous for all but the tallest seedlings. Annual growth rings of provenances responded similarly to climate, with most having both high resistance and resilience to drought. Growth was positively correlated with high temperatures year-round and wet summers. This study reveals that many Engelmann spruce provenances from varying climates can be successful at relatively cold and dry high elevation sites, boding well for assisted population migration efforts. However, differences exist between provenances in their growth, survival, and reproduction potential, which will continue to influence how they perform in the future.

1. Introduction

Tree species have evolved to grow and survive under a particular set of climate conditions, which along with disturbance and competition dynamics, dictate where they exist on the landscape (Rehfeldt et al., 2006; Savolainen et al., 2007). For widely distributed species that exist in a variety of different environments, there is ample evidence of local adaptation, or genetic differentiation between populations that makes fitness higher at home sites than away sites (Aitken et al., 2008; Savolainen et al., 2007). Longer growing seasons, variable precipitation, and more frequent drought events due to climate change are predicted to shift species and population ranges (Svenning and Sandel, 2013). Changes in climate are likely to leave many tree populations vulnerable to conditions they are not adapted to, due to their long generation times and sessile nature. Therefore, they must migrate or have plasticity in their traits to survive long-term, but projections of climate change suggest trees will need to migrate quicker than they can in most cases (Zhu et al., 2012). Understanding how local adaptation varies across tree distributions is important for managing forests in the face of these changes.

Foresters have used provenance studies to investigate local adaptation in trees for over a century, helping them to select the best seed sources for timber production (Langlet, 1971). Provenance studies take seeds from various populations (i.e., provenances) and plant them in one location to compare the performance of individuals from different provenances in a common growing environment. They therefore isolate the effects of inherited growth characteristics from characteristics that arise from the growing environment. These studies revealed clines in genetic variation across the landscape which were used to establish seed zones and transfer distances that delineate how far a seed may be transferred without risking maladaptation (Johnson et al., 2004). A key assumption of the seed zone concept is that local climate conditions do not change over time and thus planting seed collected locally will ensure that future generations are adapted to the climate conditions of the local

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area. However, with climate rapidly changing, using seed matched to the future climate, rather than that of the past, is now expected to increase planting success (Vitt et al., 2010; Williams and Dumroese, 2013; O'Neill and Gómez-Pineda., 2021). Provenance studies that were established decades ago can be reanalyzed with this new goal in mind.

Several tree adaptations are likely to be favorable under projected future warmer and drier climates. Drought adaptation has been found to vary among provenances for some conifer species, but individual variation appears to be high even within provenances (Guy and Holowachuk, 2001; Kolb et al., 2016; Liepe et al., 2016; Montwé et al., 2016). Here, we consider drought resistance and resilience as two different adaptations to water stress. Resistance in relation to drought can be thought of as the individual's ability to continue growing even when water is scarce whereas resilience can be thought of as an initial reduction in growth during drought but a rapid return to pre-drought levels once water becomes more abundant (Lloret et al., 2011). The amount of resistance and resilience that a tree species displays can vary between provenances (Goodrich et al., 2016; Liu et al., 2023). Where water is abundant, a warmer climate may favor individuals that are more plastic in their growth and can take advantage of longer growing seasons by increasing growth and outcompeting others (Carroll et al., 2021; Yuan et al., 2018). An often-overlooked trait in provenance studies is the ability to tolerate climatic extremes, which although rare, can have an outsized impact on natural selection (Germain and Lutz, 2020). Especially under rapid change, trees planted in the current environment must be able to withstand a range of climatic extremes that are likely to continue shifting during their lifetimes. Therefore, adaptation to cold and frost may benefit seedlings that are being planted upslope in anticipation of warmer temperatures (Montwé et al., 2018).

Here we evaluate the survival and growth responses of 20 provenances of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) to climate over 45 years to determine how the climate of seed origin influences provenance sensitivity to climate and drought. Engelmann spruce is an important species for recreation, timber, and habitat (Devineau et al., 2010). Therefore, improving our understanding of the effects of climate on the survival and growth of this high elevation tree species can help inform future management decisions. Bioclimate modeling suggests that a warmer, drier climate will alter the range of Engelmann spruce in central and southwest Colorado by the year 2060 (Rehfeldt et al., 2015, 2006). Anticipated warming and drying will result in the driest locations that currently support Engelmann spruce-dominated forests to no longer be suitable for the species (Rehfeldt et al., 2006). Indeed, subalpine forests already have documented cases of increased mortality due to drought and heat (Allen et al., 2010; Bigler et al., 2007). High elevation forests also tend to take a long time to regenerate after disturbance (Stevens-Rumann et al., 2018) and with rapidly accelerating warming, they may miss their opportunity to establish. Therefore, reforesting high elevation forests with genetic material from provenances that possess adaptations to future conditions may allow these forests to persist and further adapt to climate change in the future. By examining the effects that climate has on Engelmann spruce from various seed sources, we hope to inform future management decisions regarding assisted migration and planting site-adapted trees.

Our main study questions are: 1) how do provenances of Engelmann spruce differ in their long-term survival, height, diameter, and cone production and is this related to climate of origin? and 2) how do provenances of Engelmann spruce differ in their annual growth ring response to climate, and is this related to climate of origin? Most provenance studies of Engelmann spruce to-date have focused on its northern range limit (i.e. Canada), where it readily hybridizes with *Picea glauca* (white spruce), sometimes referred to as the "interior spruce" complex (Degner, 2020). To our knowledge there are only two other range-wide provenance tests of Engelmann spruce that have been conducted south of the "interior spruce" zone (Rehfeldt, 2004, 1994), both of which were planted in Idaho, United States and assessed after 4 years in the field. Across the range they found that provenances from warmer climates had greater and a longer duration of shoot elongation, especially those from the Southwestern US. Therefore, we hypothesized that trees from warmer provenances would grow larger in our high elevation, Colorado Rocky Mountain study but may have lower survival due to frost damage. We were uncertain whether provenance climate would impact drought-tolerance in this study due to the lack of prior research on this subject but supposed that provenances from more arid climates would tolerate drought better than others, either through high resistance or greater resilience.

2. Methods

2.1. Study area

Our data comes from an Engelmann spruce provenance study established in 1970 on the White River National Forest in the Moniger Creek area of the Eagle-Holy Cross Ranger District (Shepperd, 1981). The study area just north of Vail, Colorado, sits at an elevation of 2930 m (Table 1) and is on a relatively flat north-eastern aspect. At the time of planting there was no vegetation due to logging and fire. The site received an average of 583 mm of precipitation annually during the study period of 1970–2015, with an average daily temperature of 3.5°C (PRISM Climate Group, 2024). From 1970 – 2015, mean and minimum temperatures at the plantation increased significantly for summer (mean – linear model, $t = 2.2$, $p < 0.05$; min – linear model, $t = 3.1$, $p < 0.01$) and fall (mean – linear model, $t = 2.2$, $p < 0.05$; min – linear model, $t = 3.3$, $p < 0.01$; Fig. 1). Precipitation did not display significant trends over time. A randomized, complete block design was used with 4 trees from each of the 20 provenances planted in 12 replicated blocks, for a total of 960 trees planted (Shepperd, 1981). The 20 provenances span a large range of latitude, elevation and climate (Table 1, Supplementary Figure 1, Supplementary Figure 2).

2.2. Sampling design

As described in Shepperd et al. (1981), survival, height, diameter at breast height (DBH), and the presence or absence of cones (prior year or older) on each tree were recorded. Survival was measured six times between 1974 and 2014, whereas height was measured from 1979 onward, DBH was measured from 1991 onward, and cone presence/absence was measured four times from 1985 – 2006. In the summer of 2016, we revisited the site and collected increment cores at a height of 30 cm from six to eight live trees from each provenance in eight randomly selected blocks. Some blocks sampled had no survivors from certain seed sources, resulting in the decreased number of cores for some provenances (Table 1).

2.3. Lab analysis

Cores were mounted and sanded using progressively finer grit sandpaper until the annual rings were clearly visible under a microscope. Each core was measured under a microscope using the program MeasureJ2X to create a chronology of ring widths by year. The tree-ring program COFECHA was used to check for potential inaccuracies by checking for correlations between chronologies (Holmes, 1983). Some cores were eliminated due to poor quality, resulting in 4–8 trees from each provenance being sampled (Table 1).

2.4. Statistical analysis

2.4.1. Principal components analysis

We performed a principal components analysis (PCA) to compare the climates of the 20 provenances and one plantation site to each other, and to the climatic range of Engelmann spruce. The average for 1961–1990 of 29 climate variables (AdaptWest Project, 2022) were considered and 13 were selected to be used in the PCA to limit the number of highly

Table 1
Location, elevation, average 1961–1990 mean annual temperature (MAT), mean annual precipitation (MAP), number of frost-free days (NFFD), precipitation as snow (PAS), and sample size of all provenances and the plantation. Climate values extracted from ClimateNA (AdaptWest Project, 2022). The plantation information is bolded.

Provenance	Code	Lat (°)	Long (°)	Elevation (m)	MAT (°C)	MAP (mm)	NFFD	PAS (mm)	# of cores	# trees in 2014
Cutting Permit 31	CP31	50.475	−120.006	1562	2.1	586	143	280	5	31
Inlet Creek	IC	50.133	−116.267	1402	2.4	670	141	338	7	30
Powers Creek	PC	49.917	−119.767	1249	4.4	699	182	304	5	34
Kidd Creek	KC	49.185	−116.158	1432	3.4	826	162	385	7	29
Okanogan NF	ONF	48.186	−121.001	1280	4.2	1964	162	898	6	39
Wenatchee NF	WNF	48.154	−120.475	777	8.3	327	215	87	4	27
Wallowa-Whitman NF	WWNF	45.036	−118.39	1417	5.5	644	163	222	7	41
Payette NF	PaNF	44.985	−116.03	1889	2.8	1105	118	612	8	39
Cache NF	CaNF	42.298	−111.573	2590	2.7	1083	140	631	6	35
Larimer 1	L1	40.995	−105.5	2407	4.5	446	142	113	8	29
Larimer 2	L2	40.88	−105.68	2865	2.0	541	108	261	6	45
Roosevelt NF	RoNF	39.979	−105.537	2743	3.4	592	131	210	8	40
Plantation	**P**	**39.730**	**−106.496**	**2926**	**1.8**	**655**	**112**	**349**	-	-
Pike NF	PiNF	39.033	−104.977	2712	4.6	611	149	139	8	37
Gunnison NF	GuNF	39.03	−107.18	3169	2.3	858	121	478	7	42
Grand Mesa-Uncompahgre NF	GMUNF	39.028	−108.02	3200	0.5	920	105	572	8	34
Dixie NF	DNF	37.75	−111.88	3017	2.8	673	122	333	7	41
San Juan NF	SJNF	37.251	−106.81	3230	2.0	993	118	521	8	35
Santa Fe NF	SFNF	36.08	−105.67	2895	4.1	640	137	205	8	38
Coconino NF	CoNF	35.31	−111.7	2865	4.3	805	123	312	7	34
Gila NF	GiNF	32.999	−107.797	2499	9.6	672	217	29	6	21

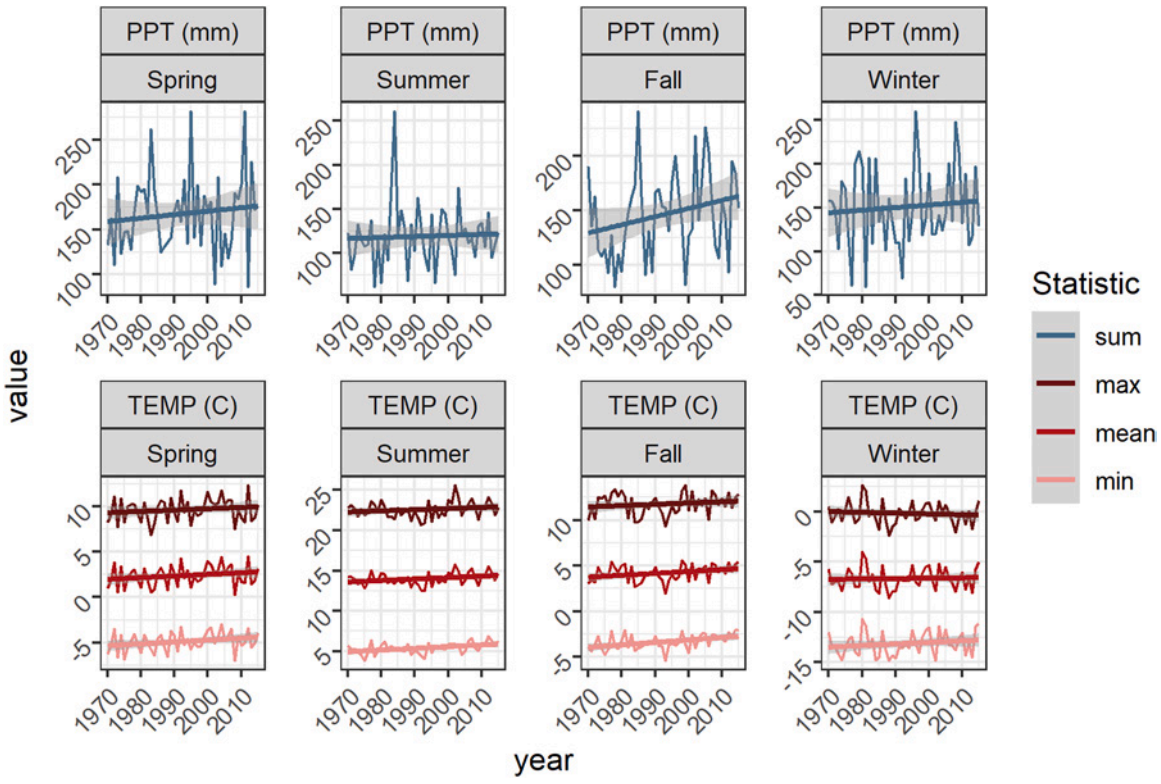

Fig. 1. Trends in seasonal precipitation and temperature from 1970 – 2015 at the plantation site. Lines with grey shading show linear model predictions with 95 % confidence intervals.

correlated variables (Supplementary Table 1; Supplementary Figure 3). Climate variables were extracted from the geographic coordinates of all provenances, plus 200,000 points uniformly sampled from within the geographic range of Engelmann spruce in the US and Canada (Mathys et al., 2014; USDA Forest Service, 2013). Principal components with eigenvalues greater than 2 were retained for analysis.

2.4.2. Climatic transfer

Principal components 1 and 2 were transformed to represent the climatic transfer between the provenance of tree origin and the plantation by subtracting the plantation position on PC1/PC2 from the provenance position; these variables were named $PC_x transfer$ where x equals 1 or 2, depending on the principal component of interest (Eq.1).

$$PC_x transfer = provenance\_PC_x - plantation\_PC_x \quad (1)$$

The Euclidean distances between each provenance and the plantation in the 2-dimensional PCA space were calculated using Pythagorean's theorem and called PCAdist (Eq.2).

$$PCAdist = \sqrt{PC1transfer^2 + PC2transfer^2} \quad (2)$$

In some cases, individual climate variable transfers were also calculated to investigate the effect of multivariate climate vs. specific influential climate variables. These transfers were calculated for all climate variables that went into the PCA (Supplementary Table 1) by subtracting the plantation value from the provenance value (Eq.3).

$$Climate\ variable\ transfer = provenance\ climate - plantation\ climate \quad (3)$$

Therefore, transfers greater than zero indicate the provenance climate variable was greater than that of the plantation whereas transfers less than zero indicate the plantation climate variable was greater than that of the provenance.

2.4.3. How do provenances of Engelmann spruce differ in their long-term survival, height, diameter, and cone production and is this related to climate of origin?

The tree traits analyzed were survival to 2014, nursery height, absolute field height, relativized height growth rate (Eq.4), absolute DBH, relativized basal area growth rate (Eq.5), and cone presence in each of the years these traits were measured.

$$Relativized\ height\ growth\ rate\ \left(\frac{\%}{yr}\right) = \frac{\frac{Ht_t - Ht_{t-1}}{Ht_{t-1}} \times 100}{n_{years}} \quad (4)$$

$$Relativized\ basal\ area\ growth\ rate\left(\frac{\%}{yr}\right) = \frac{\frac{\pi\left(\frac{DBH_t}{2}\right)^2 - \pi\left(\frac{DBH_{t-1}}{2}\right)^2}{\pi\left(\frac{DBH_{t-1}}{2}\right)^2} \times 100}{n_{years}} \quad (5)$$

HT_t and DBH_t represent the height and DBH at time t, HT_{t-1} and DBH_{t-1} represent the height and DBH in the prior survey, and n_{years} represents the number of years between the two surveys. Therefore, the relativized values indicate the % per year that each tree grew between surveys. Absolute height was log-transformed to meet linear model assumptions.

Tree traits were compared using type-3 ANOVA with year and provenance as interacting predictor variables and block as a random effect. If the interaction was not significant, type-2 ANOVA with the interaction excluded was used to obtain the result. Height and DBH models were linear whereas models for survival and cone presence were binomial mixed effects models since the response was either 0 (died/no cones present) or 1 (survived/cones present). Cone presence models also included an additional fixed effect of tree height, as tree size is known to influence cone production (Alexander and Shepperd, 1990) and thus we wanted to eliminate the difference between provenances in cone production that were conflated with their differences in size. Linear mixed effects models with field height as the response variable, nursery height as a fixed effect and provenance as a random effect were run for each year heights were measured in the field to determine whether seedling height at outplanting affected long-term field height. The effects of provenance climate on tree traits were investigated through mixed effects models consisting of the predictor variables PC1transfer, PC2transfer, their interaction, their quadratic effects, and PCAdist, with random effects of provenance, block, and year.

If there were no significant effects of the PCA transfer distance metrics on tree traits, univariate linear (n = 33) and quadratic (n = 33) models for all individual climate variable transfer distances were run to test whether single climate variables may be influencing certain traits more than overall climatic distance as measured with the PCA. In these models, the tree trait was the response variable, the climate variable transfer (Eq.3) was the predictor, and random effects of provenance, block and year were included.

2.4.4. How do provenances of Engelmann spruce differ in their annual growth ring response to climate, and is this related to climate of origin?

Seasonal climate at the plantation was calculated for the years 1970 – 2015, with the year of ring formation considered the "current year". Seasons included prior summer (June – Aug in the year before the current year), prior fall (Sept – Nov of the prior year), prior winter (Dec of the prior year and Jan – Feb of the current year), spring (Mar – May of the current year), and summer (June – Aug of the current year). Climate variables included actual evapotranspiration (AET), climatic water deficit (CWD), maximum vapor pressure deficit (VPDmax), precipitation, minimum, average, and maximum temperature, day of the first fall frost (DOFFF) in the prior and current years and day of the last spring frost (DOLSF) in the current year (Supplementary Table 2). Temperature and VPDmax were averaged across seasons in each year while CWD, AET and precipitation were summed. The 2.5th and 97.5th quantiles were calculated for each of the seasonal climate variables from 1970 – 2015 and years with values falling outside of this interval in a way that indicated worsening drought (i.e., high temperatures, VPDmax, CWD and low precipitation and AET) were considered "extreme". We tallied the number of climate variables in each year that indicated extremely droughty climates and picked the year with the most indicators of extreme drought as the targeted "drought year", which was 2002 (Supplementary Figure 4). This drought is estimated to be among the most severe of the last 500 years (Andreadis et al., 2005).

Ring width measurements from 1985 – 2015 were detrended using a smoothing spline with a stiffness of 35 years, producing ring width index (RWI) values. The first 15 years of growth were removed to eliminate any young tree "growth spurts" not due to climate anomalies. To summarize overall RWI variability, the bias-corrected Gini coefficient was calculated with the DescTools package (Signorell, 2024) for each tree's RWI series, which gives a measurement of data heterogeneity on a scale from 0 (least heterogeneous) to 1 (most heterogeneous) (Biondi and Qeadan, 2008). Only the common period (for which we had records for all trees) of 1991 – 2010 was used for these calculations. We then used ANOVA with block as a random effect to test whether provenances had significantly different Gini coefficients. The response variable was log-transformed to conform to the assumptions of ANOVA.

Pearson's product-moment correlations were calculated between annual RWI and each seasonal plantation climate variable (Supplementary Table 2). Correlations within each provenance were tested with a T-test using a null hypothesis of the true correlation being equal to zero. The growth-climate correlation for each tree was used as a response variable in an ANOVA to test whether growth-climate correlations significantly differed between provenances. For those that significantly differed, linear mixed effects models were run to identify whether the correlation was influenced by provenance climate (Supplementary Table 1). Provenance and block were included as random effects in these models, with the growth-climate correlation as the response variable and provenance climate transfer as the predictor variable.

Drought indices were calculated using a pre-drought period of 1985–2001, drought period of 2002–2003, and post-drought period of 2004 – 2015. This used all RWI data collected (except for the first 15 years) to get the most unbiased metric of average growth at the site pre- and post-drought. The drought period included 2002 and 2003 to account for lag-effects of the 2002 drought on 2003 growth. Resistance was calculated as the average RWI in the drought period divided by the average RWI during the pre-drought period (Lloret et al., 2011). Resilience was calculated as the average RWI of the post-drought period divided by the average RWI of the pre-drought period. ANOVA was used to test whether provenances had significantly different resistance and resilience values and if they did, we used post-hoc Tukey HSD tests to determine which pairs of provenances were significantly different from each other. Recovery time of trees that reduced RWI in 2002, 2003 or both was calculated as the number of years after 2003 that it took for the RWI to meet or exceed the long-term pre-drought average RWI. The

maximum and cumulative amount of RWI reduction experienced in the years before recovery were also calculated to assess the severity of the impact of drought on RWI reduction (Thurm et al., 2016). Differences between provenances in log-transformed recovery time, maximum growth reduction, and cumulative growth reduction were tested with ANOVA.

2.4.5. Outlier exclusion

Given that the Gila NF provenance was an outlier in terms of DBH, height, survival and cone production, in addition to coming from a provenance with a very dissimilar climate from the rest of the provenances, it often had very high leverage in models. Therefore, all models that included tree traits (other than RWI) as response variables and provenance climate as predictor variables were run without the inclusion of the Gila NF provenance to reduce the possibility of Type 1 errors. Analyses related to annual ring growth (described in Section 2.4.4) include Gila NF as RWI values were scaled to each tree individually and therefore Gila was not an outlier for RWI.

3. Results

3.1. Principal components analysis

The first two principal components had eigenvalues greater than 2 and together explained 68.5 % of the variation in climate space across Engelmann spruce's geographic range (Fig. 2B). PC1 was most correlated with precipitation variables (PAS, autumn, winter, and spring precipitation, and monsoonality). Provenances with wetter fall, winter, and springs fell toward the upper end of PC1 whereas provenances with wetter summers fell toward the lower end of PC1 (Fig. 2B&C). PC2 was most correlated with temperature variables (MCMT, MWMT, and NFFD, with hotter provenances falling toward the upper end of PC2 (Fig. 2B&C).

3.2. How do provenances of Engelmann spruce differ in their long-term survival, height, diameter, and cone production and is this related to climate of origin?

Survival to 2014 (long-term survival) across all provenances ranged from 44 – 94 % (Fig. 3). Transfer distance in the PCA space did not significantly predict survival; however, several individual climate variable transfers were significant. Provenances from climates with shorter growing seasons (low NFFD; logistic mixed-effects model, $z = -2.3$, $p < 0.05$) and lower summer-to-spring precipitation ratios (logistic mixed-effects model, $z = -2.1$, $p < 0.05$) had significantly greater survival at the plantation (Fig. 4). In addition, provenances with intermediate to high CMD (hotter and drier) had the best survival (quadratic logistic mixed-effects model, $z = -2.7$, $p < 0.01$).

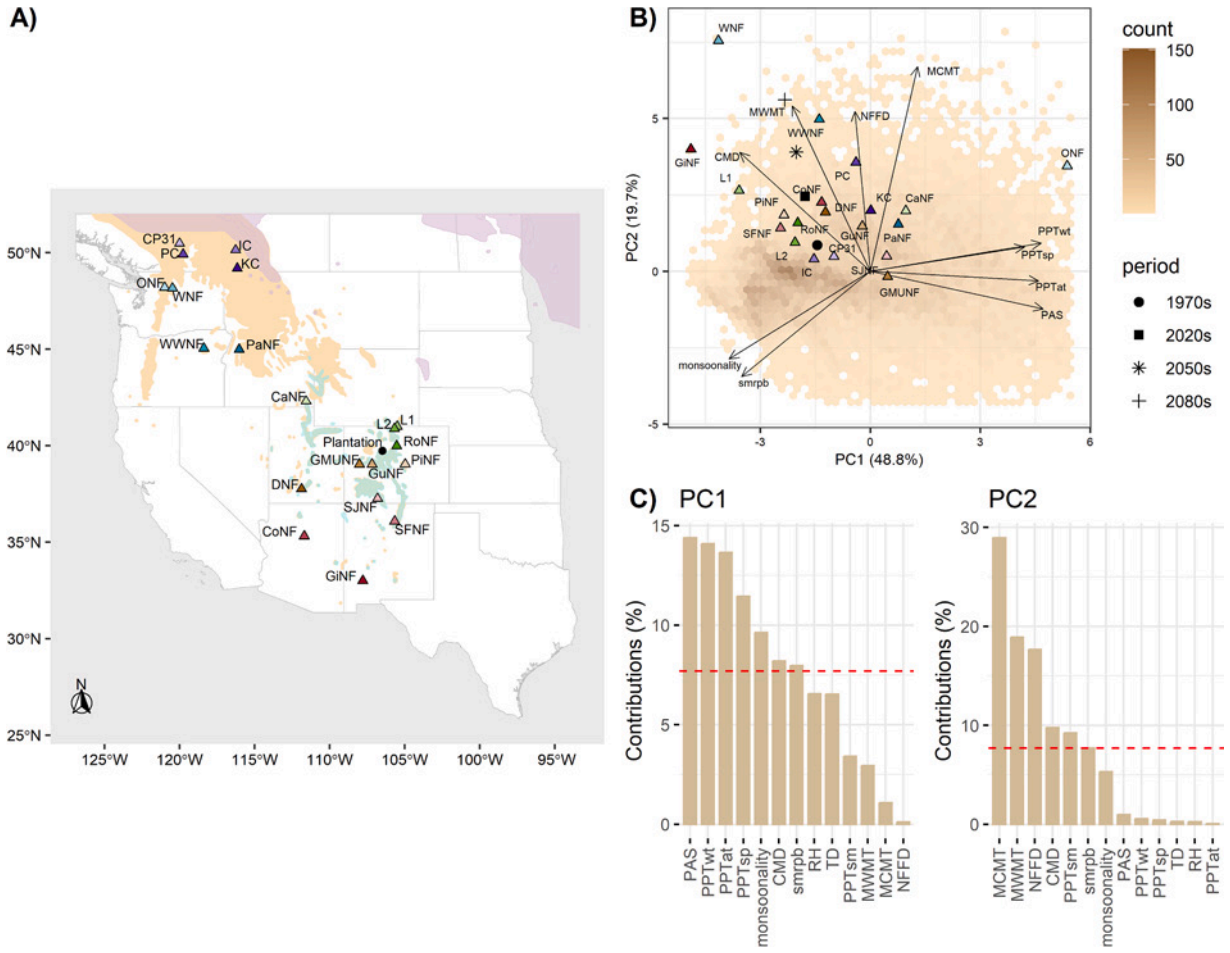

Fig. 2. Climate of provenances and plantation. A) provenance and plantation locations in the Western US, overlayed on the geographic range of Engelmann spruce (Little, 1971; beige shading), blue spruce (Little, 1971; blue shading), and white spruce (Little, 1971; purple shading). B) Biplot of PC1 vs. PC2 where percent variance explained is shown on axis titles in parentheses, climate variables are shown as black vectors and indicate which climate variables are most correlated with which PC. PCA scores for provenance 1970's climate and the plantation 1970's and projected 2020's, 2050's and 2080's climate are shown as points in the plots, with symbols indicating time period. Background shading indicates the relative frequency of Engelmann spruce across the bivariate climate space. C) The relative contributions of climate variables to PC1 and PC2. The red dashed line shows the theoretical contribution if all climate variables contributed uniformly.

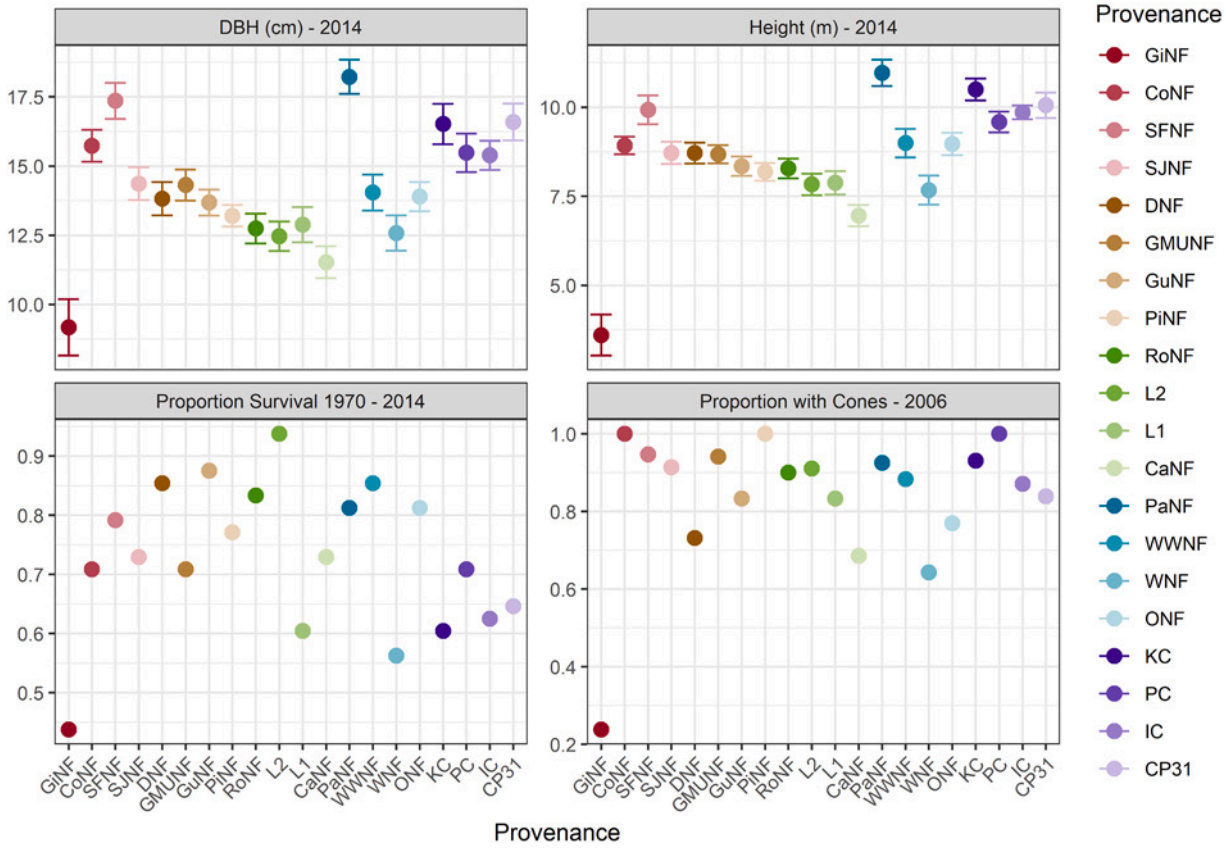

Fig. 3. Provenance mean diameter at breast height (DBH), mean height, survival and cone presence for the most recent measurement year. Provenances are ordered and colored by latitude (GiNF = lowest). Error bars show the standard error around the mean for each provenance in DBH and height.

Average provenance height in 2014 ranged from 3.6 – 11.0 m and DBH ranged from 9.2 – 18.2 cm (Fig. 3). There were significant effects of year, provenance and the year by provenance interaction on absolute tree height (type-3 ANOVA, df=19, $\chi^2 = 210.5$, $p < 0.0001$), indicating that the relative order of provenances in terms of height varied from year to year (Supplementary Figure 5). Both year (type-2 ANOVA, df = 3, X2 = 6262, $p < 0.0001$) and provenance (type-2 ANOVA, df = 19, X2 = 811, $p < 0.0001$) were statistically significant in predicting absolute DBH, but they did not significantly interact, indicating that the relative differences between provenances in DBH stayed the same over time (Supplementary Figure 5).

Summer precipitation ratio was significant in predicting nursery height (linear model, df = 17, t = 3.2, $p < 0.01$), where provenances from areas with greater summer precipitation ratios grew taller in the nursery, and thus were taller at outplanting. Nursery height had a significant positive effect on height in the field in all years except 2014, which was only marginally significant (Supplementary Figure 6). Provenance climate was not influential in absolute DBH, relative DBH growth rate, nor absolute height. Relative height growth rate was highest for provenances with overall climates most similar to that of the plantation (linear mixed-effects model, df = 17.2, t = -2.3, $p < 0.05$; Fig. 4).

Year, provenance and their interaction were significant in predicting probability of cone presence (type-3 ANOVA, df = 19, $\chi^2 = 31.7$, $p < 0.05$). Probability of cones was not significantly predicted by transfer distance in the PCA, but was predicted by height, with taller trees having a greater probability of cones (linear mixed-effects model, z = 14.6, $p < 0.0001$; Fig. 5). According to the model, trees across all provenances have a 50 % chance of having cones when they are 3.9 m tall and a 95 % chance of cones when they are 7.1 m tall. Provenances with greater summer precipitation transfer distances had a higher probability of having cones at a given height, with the probability plateauing for provenances with lower summer precipitation values (quadratic mixed-effects model, z = 2.2, $p < 0.05$; Fig. 5). Provenance temperature differential had a significant interaction with height (linear mixed effects model, z = 2.2, $p < 0.05$) where when trees were shorter, provenances with lower temperature differentials had a greater probability of having cones, but this effect went away when trees got taller (Fig. 5).

3.3. How do provenances of Engelmann spruce differ in their annual growth ring response to climate, and is this related to climate of origin?

The ring width series included 136 individuals, with an average series length of 36 years, mean series intercorrelation of 0.42 (0.17 SD) and mean AR1 of 0.61 (0.15 SD). The mean Gini coefficient across all trees from all provenances was 0.13 (SD = 0.04), indicating little variability in RWI between years from 1991 – 2010 (Fig. 6, Supplementary Figure 7). According to ANOVA, there was only a marginally significant difference between provenances in average Gini coefficient (ANOVA, df = 19, F = 1.6, p = 0.06).

Most trees (73 % of 137 trees) had at least one significant correlation between their RWI and seasonal climate at the plantation, although the climate variables of importance, strength, and direction of these correlations varied both between and within provenances. The plantation climate variable with the largest average correlation with RWI was prior winter VPDmax, which averaged 0.2 (± 0.16) across all trees from all provenances (Fig. 7, Supplementary Figure 8), indicating trees grew more than average when the winter preceding the growing season had a relatively high VPD (i.e. less moisture). This response was significantly different from zero for 16 of the 20 provenances (Supplementary Figure 8). There were many other significant climate-growth

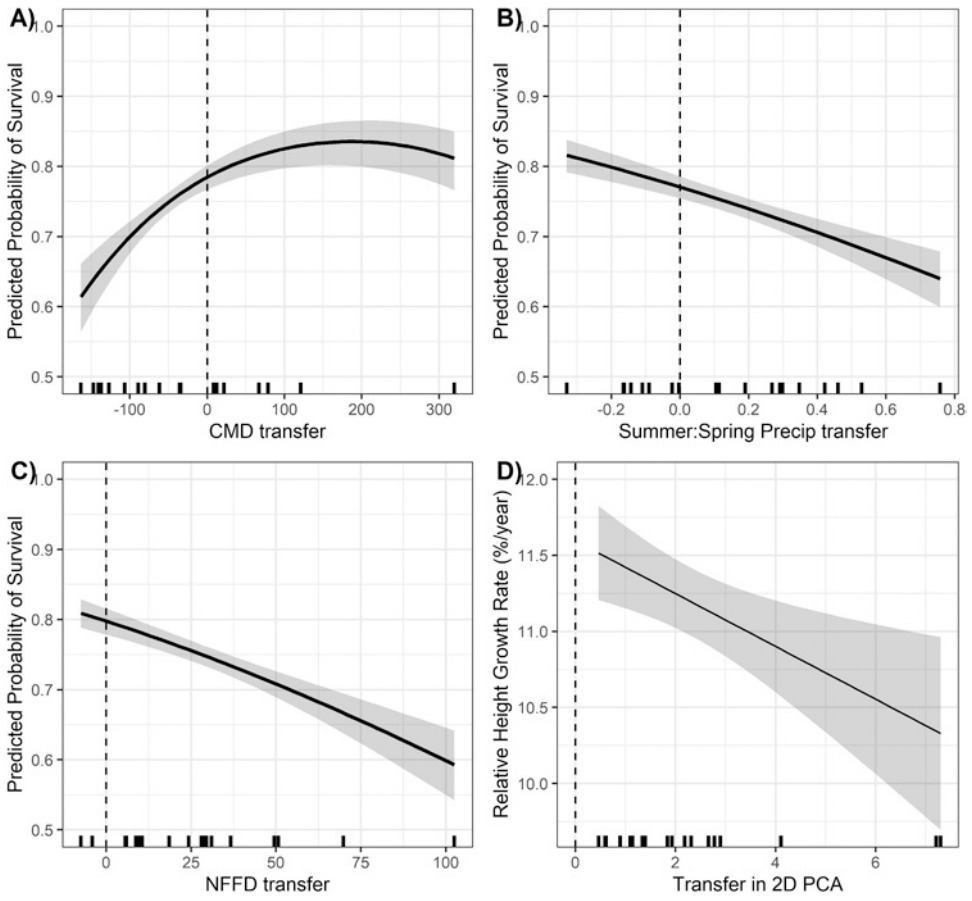

Fig. 4. Predicted probability of survival to 2014 (A-C) and relative height growth rate (D) predicted by the transfer from provenance to plantation in terms of climatic moisture deficit (CMD), summer to spring precipitation ratio, number of frost-free days (NFFD), and overall climate distance (2D PCA transfer). Positive transfer values indicate the provenance climate value was greater than that of the plantation whereas negative values show provenances with lower climate values than the plantation. The dashed vertical line shows where the provenance and plantation values are the same (transfer = 0).

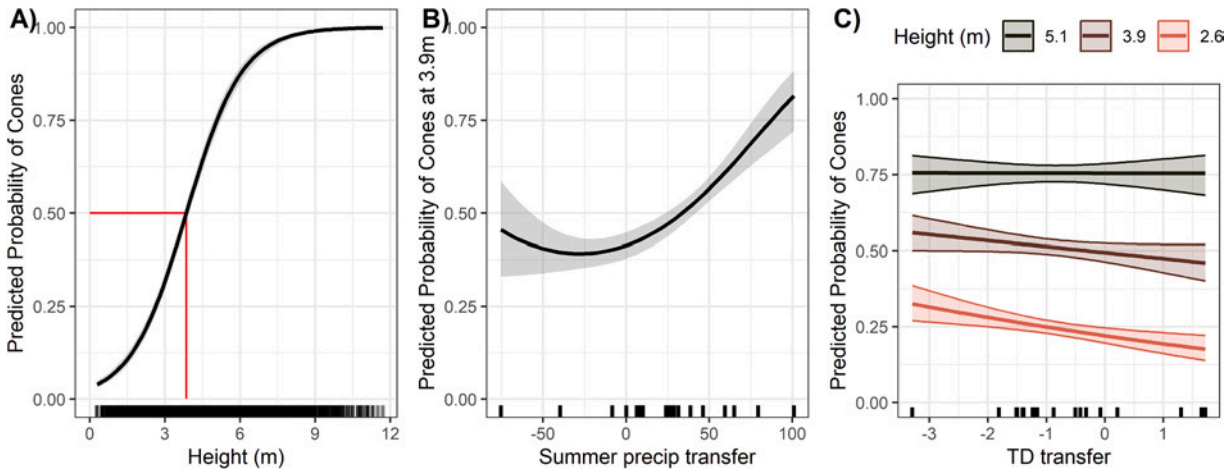

Fig. 5. Model results for A) the effect of tree height (m), B) the effect of summer precipitation transfer distance at 3.9-m height, and C) the effect of the interaction between temperature differential (TD) transfer distance and height on the predicted probability of cones. Lines show model predictions and shading shows 95 % confidence intervals around those predictions. Red lines in A) show the height at which trees have a 50 % chance of having cones (~3.9 m). Rugs show the distribution of provenances across each x-axis. Transfer distances greater than zero indicate the provenance climate value was greater than that of the plantation.

correlations that were relatively consistent across trees from different provenances (Fig. 7). Temperature in all seasons was positively correlated to growth at the site, as was AET. A later first fall frost date during the current and prior growing season was significantly positively related to growth whereas a later last spring frost date was negatively correlated with growth, indicating that longer growing seasons were generally beneficial for the trees at the plantation. Precipitation, VPDmax and climatic water deficit (CWD) had different effects on growth depending on the season (Fig. 7). In general, drier winters and springs were beneficial to ring growth whereas drier summers were detrimental to ring

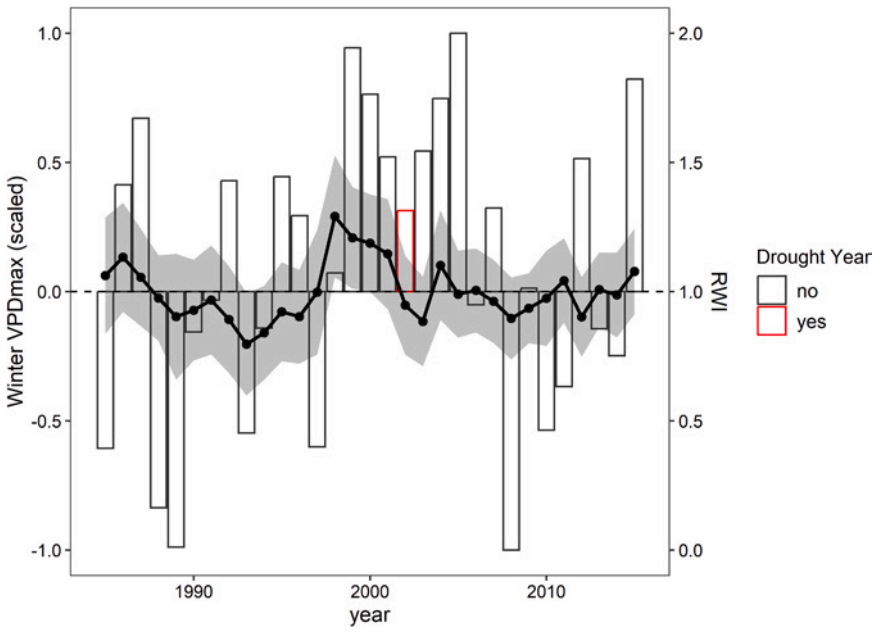

Fig. 6. Average ring width index (RWI, points) across all individuals from all provenances from 1985 to 2015. Shading represents standard deviation. Bars display the maximum vapor pressure deficit (VPDmax) for the winter immediately preceding the growing season, normalized to the range of −1 (minimum winter VPDmax during the period) to 1 (maximum winter VPDmax during the period), with the drought year of 2002 outlined in red.

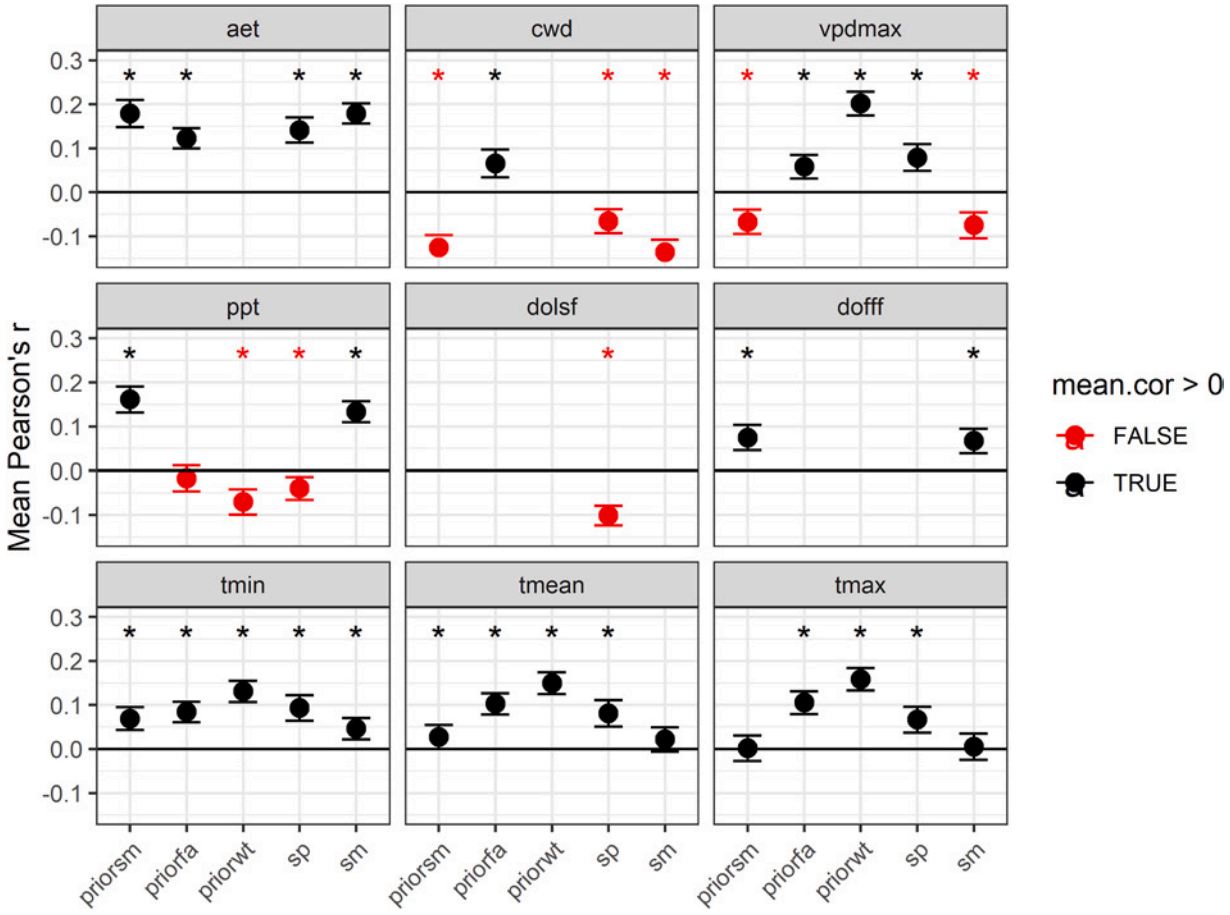

Fig. 7. Average RWI-climate correlation (Pearson's r) across all trees at the plantation for each seasonal variable investigated. Asterisks indicate correlations significantly different from zero, as detected by a two-sided *t*-test, and error bars display 95 % confidence intervals around the model estimates. Negative correlations are shown in red (mean correlation > 0 = FALSE) while positive ones are shown in black (mean correlation > 0 = TRUE).

growth.

Provenances were similar in their RWI response to climate, in part due to high intra-provenance variation in climate-growth responses (Supplementary Figure 8). Out of the 36 seasonal plantation climate variables tested, more than half (n = 19) had more variable growth responses within provenances than between them. Only two plantation climate variables influenced RWI in ways that significantly differed between provenances (ANOVA, winter precipitation: df = 19, F = 2.0, $p < 0.05$; spring CWD: df = 19, F = 2.1, $p < 0.01$). Trends with provenance climate revealed that provenances with overall climate more similar to the plantation were more negatively impacted by spring climatic water deficit (df = 21.6, t = 2.6, $p < 0.05$), specifically those with lower winter temperatures and from cooler and wetter climates (Fig. 8).

Long-term drought resistance averaged 0.91 (± 0.16) and did not significantly differ between provenances (ANOVA, df = 19, F = 0.80, p = 0.7), whereas long-term resilience averaged 0.98 (± 0.08) and did differ between provenances (ANOVA, df = 19, F = 3.3, $p < 0.001$), mostly due to the high average resilience of Gila NF (Table 2). In fact, trees from Gila NF had a greater average RWI after the drought than before it (mean resilience = 1.2). There were 17 out of 137 trees (12 %) that did not reduce RWI below the 1985 – 2001 average in either 2002 or 2003 (the drought period). Of the trees that did reduce RWI, there were no significant differences between provenances in how many years it took before RWI reached at or above the 1985 – 2001 average (recovery time; ANOVA, df=19, F=0.6, p = 0.9). All trees had at least one year after 2003 with the same or higher RWI as the 1985 – 2001 average, indicating a "full recovery". There were no significant differences between provenances in the maximum and cumulative growth reduction (ANOVA, df = 19, F = 0.5, p = 0.9 for both) post-2002 and before recovery.

Table 2
Mean and standard deviation (SD) of long-term resistance and resilience scores for each provenance. The drought period was 2002–2003, with a pre-drought period of 1985–2001 and a post-drought period of 2004–2015. Scores above 1 indicate higher average RWI during (resistance) or after (resilience) the drought period than before it. The asterisk indicates that Gila NF was significantly different from all other provenances in its mean resilience score.

Provenance	Code	Mean (SD) Resistance	Mean (SD) Resilience
Cutting Permit 31	CP31	0.84 (0.18)	0.98 (0.04)
Inlet Creek	IC	0.78 (0.21)	0.92 (0.08)
Powers Creek	PC	0.92 (0.09)	0.99 (0.04)
Kidd Creek	KC	0.96 (0.13)	0.97 (0.04)
Okanogan NF	ONF	0.88 (0.25)	0.97 (0.08)
Wenatchee NF	WNF	0.94 (0.04)	0.99 (0.06)
Wallowa-Whitman NF	WWNF	0.93 (0.18)	0.97 (0.05)
Payette NF	PaNF	0.86 (0.14)	0.98 (0.05)
Cache NF	CaNF	0.93 (0.2)	0.98 (0.03)
Larimer 1	L1	0.88 (0.1)	0.97 (0.05)
Larimer 2	L2	1.00 (0.16)	1.00 (0.05)
Roosevelt NF	RoNF	0.94 (0.12)	0.99 (0.06)
Pike NF	PiNF	0.98 (0.19)	1.01 (0.05)
Gunnison NF	GuNF	0.88 (0.16)	0.97 (0.05)
Grand Mesa-Uncompahgre NF	GMUNF	0.88 (0.1)	0.96 (0.03)
Dixie NF	DNF	0.93 (0.14)	0.95 (0.02)
San Juan NF	SJNF	0.97 (0.28)	0.97 (0.05)
Santa Fe NF	SFNF	0.82 (0.08)	0.98 (0.03)
Coconino NF	CoNF	0.94 (0.15)	0.96 (0.04)
Gila NF	GiNF	0.91 (0.12)	1.18 (0.25)*

4. Discussion

Engelmann spruce provenances at our study site largely responded to drought and climate in similar ways despite spanning 17 degrees of latitude in North America. There were differences between provenances in their reproductive maturity, survival, height and DBH after 45 years in the field, with one provenance (Gila NF) especially maladapted to the site. All other provenances had survival rates of over 55 % after 45 years and grew to average heights of 7–11 m and average diameters of 11–18 cm, with high intra-provenance variation. Therefore, it is likely that seedlings from various provenances may be planted without deleterious consequences in colder sites like the plantation studied here. However, there may be a threshold in provenance summer precipitation ratio that if crossed, results in maladaptation. Further testing of provenances with various degrees of summer precipitation ratios is needed to better define where this threshold lies.

4.1. Growth responses to plantation climate

High variation within provenances was a common occurrence for the responses analyzed here. There was substantial overlap between provenances in average height, DBH and survival (Fig. 3). Growth-climate relationships were also more variable within provenances than between them for 53 % of the climate variables tested (Supplementary Table 3). Trees have high gene flow between provenances (Savolainen

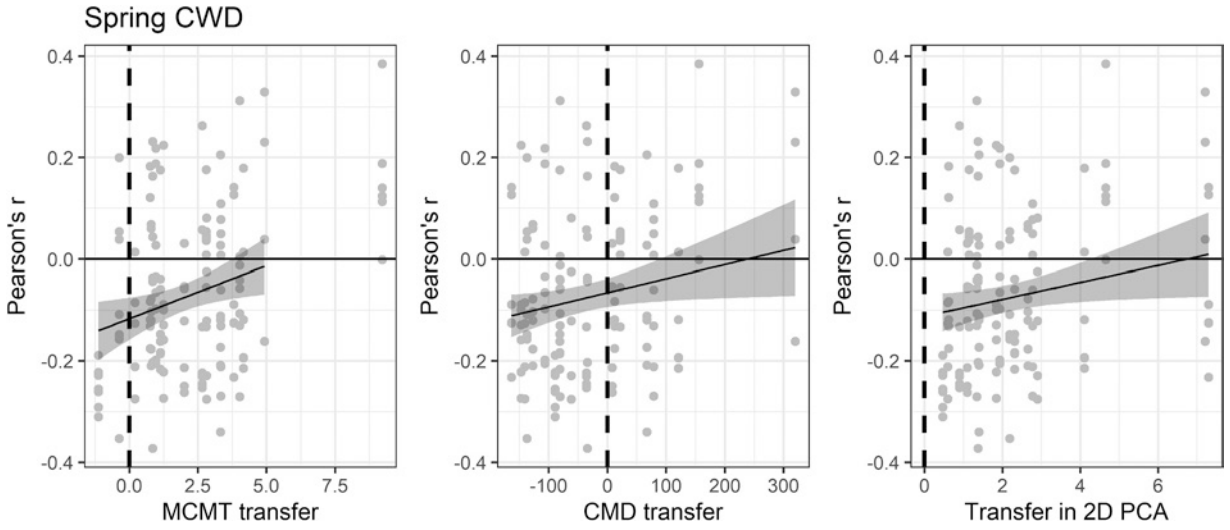

Fig. 8. Relationship between climate transfer (mean temperature of the coldest month [MCMT], climatic moisture deficit [CMD] and distance in the 2-dimensional PCA space [2D PCA]) and the correlation (Pearson's r) between plantation spring climatic water deficit (CWD) and ring width index (RWI). Lines show model predictions with shaded 95 % confidence intervals. Dashed vertical lines show where the climate transfer is equal to zero.

et al., 2007), and this, combined with 45 years of natural selection (i.e. mortality) at the plantation, likely led to low trait differentiation among provenances. Therefore, it may be important to collect seed from a wide variety of trees within a provenance to account for the high variation between individuals if certain provenance characteristics are desired. Engelmann spruce has also been found in previous studies to display less local adaptation and higher individual variation across the landscape than other sympatric conifer species, making acceptable seed transfer limits quite long (O'Neill et al., 2014; Rehfeldt, 1994; Sáenz-Romero et al., 2021).

Trees at the plantation, regardless of provenance origin, responded similarly in their growth to climate fluctuations at the site. In general, trees grew more when winters were dry, summers were wet and long, and temperatures were warm throughout the year, especially in winter. This indicates that growth at this site was largely limited by cold winter temperatures and dry summers from 1970 to 2015. Prior studies of Engelmann spruce *in situ* growth-climate correlations have also found reduced growth in years with dry summers (Birch et al., 2024; Rinaldi et al., 2021), but this can vary depending on the local conditions at the site being monitored (Adams and Kolb, 2005; Villalba et al., 1994). Compared to the provenances tested, the plantation climate is relatively cold and dry (Table 1, Supplementary Figure 9), so it makes sense that there was a positive effect of temperature on tree ring growth in this study. Other studies have found positive effects of temperature on tree ring growth in Engelmann spruce, usually at high elevations and latitudes where it is colder (Torbenson et al., 2025; Billah and Goldblum, 2019). On the other hand, trees growing in sites that are at the warmer and drier end of Engelmann spruce's climatic niche tend to show negative correlations with temperature and drought-related variables (Rinaldi et al., 2021; Griesbauer et al., 2021; Adams and Kolb, 2005; Villalba et al., 1994).

Despite the negative correlation between RWI and summer climatic moisture deficit, the drought of 2002, which had the highest summer moisture deficit during the study period (Supplementary Figure 4), did not appear to have large or long-lasting effects on ring growth in individuals from any of the provenances. We propose three hypotheses to why this may have been the case. First, even though 2002 was anomalously dry for the period studied at the plantation, the moisture conditions may have been well within the tolerable range for Engelmann spruce as a species. Droughts tend to affect tree growth most severely at the hottest and driest portions of species climatic niches (Rinaldi et al., 2021; Griesbauer et al., 2021; Adams and Kolb, 2005; Villalba et al., 1994). The plantation sits solidly in the center of Engelmann spruce's climatic niche (Fig. 2 & Supplementary Figure 9) and therefore may have been shielded from the worst of the drought impacts. Second, the years leading up to the drought of 2002 had relatively good growing conditions for the trees at the plantation (Fig. 6). In fact, the 4 highest average RWI values across provenances occurred during 1998–2001. This high growth before the drought may have left trees with carbon reserves they could rely on during the 2002 drought. Third, we found trees across provenances to be relatively insensitive to climate fluctuations, as other studies have also found for Engelmann spruce (Biondi and Qeadan, 2008; Birch et al., 2024; Kelsey et al., 2018).

It is important to note that the 2002 drought occurred 32 years after the trees were planted and therefore individuals more sensitive to drought may have already died before 2002 and those that remained may have been pre-conditioned by prior drought years, as found in Montwé (2024). RWI did tend to decrease when summers were drier than average, and as droughts are exacerbated by future warming, the trees at this site may become more impacted by hot and dry summers. There is evidence that conifers that don't fully recover from drought in terms of ring width are more likely to die from future droughts (DeSoto et al., 2020; Sterck et al., 2024). In this study, all trees eventually recovered to the average long-term pre-drought ring width; therefore, they do not seem to be in imminent danger of mortality from droughts of the magnitude experienced in 2002.

4.2. Provenance climate effects on performance

Several provenance studies have identified clines in provenance climate that correspond to survival, growth and other phenotypic traits of Engelmann and interior spruce (Grubinger et al., 2023; Liepe et al., 2016; Luo et al., 2025; MacLachlan et al., 2018; O'Neill et al., 2014; Rehfeldt, 2004; Roche, 1969; Ukrainetz et al., 2011; Ye et al., 2023). In general, clines for growth, phenology, and cold hardiness traits tend to be steeper than those for survival among Engelmann and interior spruce (Degner, 2020; O'Neill et al., 2014), though long-term survival is understudied. Studies that have assessed survival in interior spruce common gardens after 6 and 20 years indicate that provenances most climatically similar to the plantation have the highest survival (O'Neill et al., 2014; De La Torre et al., 2014). Our study indicates this is generally true for Engelmann spruce as well, with the most important climate variables being related to the length of the growing season, summer precipitation, and annual hot/dryness (Fig. 4). In the case of the plantation in this study, survival was therefore highest for provenances from climates with short frost-free periods that were relatively dry, likely due to their superior stress adaptations. Indeed, Shepperd (1981) noted that many of the seedlings from the Gila NF, a region with long growing seasons and high summer precipitation, were showing signs of frost damage in the 10-year analysis of this provenance study.

Cold adaptation in trees can be conferred through several traits including the timing of growth initiation and cessation, bud set and break, and the cold hardiness of the plant tissue (Aitken and Hannerz, 2001). Engelmann spruce provenances from areas with colder and more severe winter climates tend have shorter periods of shoot elongation, even when grown in mild environments (MacLachlan et al., 2018; Rehfeldt, 2004). This allows them to avoid frost damage in the spring and fall, which may be what led to greater survival of colder provenances in this study. There are often strong negative correlations between growth and cold adaptation, due to the tradeoff between growing later into the season and risking damage from early fall frost (Howe et al., 2003). Our results provide some evidence for this tradeoff as the best growing provenances did not tend to be the best surviving, especially those from northern latitudes (Fig. 3). In addition, cooler provenances tended to have more severe negative growth impacts from hot and dry spring conditions than those from warmer areas (Fig. 8), despite being better survivors overall.

Provenance studies of Engelmann and the interior spruce complex have found that provenances from lower elevations and latitudes tend to outgrow those from higher elevations and latitudes (Kueppers et al., 2017; Lazarus et al., 2018; Rehfeldt, 1994; Roche, 1969; Xie et al., 1998). Studies that have investigated provenance climate indicate that this is likely because provenances with longer growing seasons and higher temperatures tend to grow more than those from cooler areas (Grubinger et al., 2023; Liepe et al., 2016; MacLachlan et al., 2018; Rehfeldt, 2004; Roche, 1969; Ukrainetz et al., 2011; Ye et al., 2023). Differences due to provenance precipitation are less consistent (Degner, 2020), with studies of the interior spruce complex finding greater growth for provenances from areas of higher precipitation (Ukrainetz et al., 2011), greater aridity tolerance for provenances from more arid climates (Grubinger et al., 2023), and little importance of provenance precipitation (Ye et al., 2023). Here, we did not find any correlations between provenance climate and DBH nor height growth. This may be due to the length of our study (45 years) compared to other studies that only evaluate seedlings or young trees.

Provenances from climates with higher summer vs. spring precipitation ratios tended to grow tallest in the nursery and nursery height was a significant predictor of height in the field. The exception to this trend was the Gila NF provenance, which was tallest in the greenhouse, but shortest in the field. Trees from provenances with high summer precipitation were also more likely to produce cones at a given height, indicating that these trees are likely to have the speediest time to reproduction after outplanting, regardless of height. Assisted migration

often involves using seeds from lower latitudes (Williams and Dumroese, 2013) and our results suggest that this may also reduce the time to reproduction for Engelmann spruce trees, which could help accelerate natural selection to changing climatic conditions (Jump and Peñuelas, 2005). However, faster development of reproductive maturity could also be a stress response. More information regarding cone quality, quantity, and seed viability would be needed to fully assess the reproductive potential of these trees.

Differences between provenances in this study were relatively minor, apart from the one provenance (Gila NF) that had excessive mortality and extremely low growth. This indicates that there is some threshold that Gila NF exceeded which made it maladapted to the plantation site. Since it was the only provenance that experienced obvious maladaptation, it is impossible to know whether this threshold is related to the provenance climate, mishandling of seeds/seedlings or some other idiosyncrasy in the establishment of the plantation. However, Gila NF seedlings in the nursery were the tallest of all provenances, indicating that they were relatively healthy to begin with. The 10-year analysis of this plantation also noted the dramatic difference between Gila NF's initial height ranking and its ranking after 10 years, which was attributed to severe and repeated winter top damage that could reverse the height gains achieved during the growing season if a new lateral shoot has to take over as the leader the next year (Shepperd et al., 1981). Although these trends were starting to appear after 10 years, the data after 45 years shows that trees from Gila NF continued to decline while others did not, demonstrating the value of long-term field trials (St. Clair et al., 2020). Surveys from 1985 – 2006 reported dead tops on all but 8 individuals from Gila (17 % of the planted total), while other provenances had between 46 – 92 % of trees with no documentation of dead tops (Supplementary Figure 10). Gila NF was an outlier in several provenance climate variables as well, the most obvious being its high summer precipitation ratio and high mean temperature of the coldest month (Supplementary Figure 2). Gila NF had a ratio of summer to spring precipitation exceeding 4 whereas all other provenances had a ratio below 1.5. Clearly, more provenances with summer to spring precipitation ratios falling between these two extremes need to be tested to determine whether a trend exists. Rehfeldt (2004) found steeper clines in growth potential for Engelmann spruce in the southwestern United States than further north, suggesting that more provenances in the southwestern region would need to be tested to understand these clines. However, it is telling that a negative trend between survival and summer precipitation ratio was found even when Gila NF was excluded (Fig. 4).

Engelmann spruce provenances from the southwest (Arizona and New Mexico) have been found in other studies to differ significantly from provenances throughout the rest of the range, so much so that they have sometimes been considered a separate taxonomic group (Rehfeldt, 2004, 1994). In addition, Ledig et al. (2006) found evidence of recent genetic bottlenecks for the three southernmost provenances of Engelmann spruce that they sampled, which were all from latitudes lower than 35°N, like Gila NF in this study. Therefore the Gila NF provenance may have had lower genetic diversity than Engelmann spruce from the north, which have been found to have exceptionally high genetic diversity, likely due to hybridization with white spruce (Ledig et al., 2006). It is possible that Engelmann-white spruce hybrids were included in the provenances from British Columbia investigated here, given that they are near the hybridization zone and at relatively low elevations (Fig. 2A, Table 1). Studies that investigate the interior spruce complex have found that hybrids are able to grow quickly but also set bud early making them both fast growers and frost-tolerant (Liepe et al., 2016; MacLachlan et al., 2018; De La Torre et al., 2014; Xie et al., 1998). Our results indicate that the northern provenances tested here were fast growers, but they tended to have lower survival than more southern sources. It is possible that including all provenances in our analysis may have dampened effects of climate variables that are specific to one region or another, given that clines in growth potential have been shown to vary by region (Rehfeldt, 2004).

4.3. Implications for future change

We are limited in what we can predict for future climate based on the findings of this study, since the plantation was in a cooler location than most of the provenances came from (Supplementary Figure 2). Therefore, it is uncertain how seedlings from these provenances may react *in situ* to warming conditions or how transfers of provenances to warmer plantation sites may perform. However, one of the climate adaptation techniques gaining traction in forestry is assisted population migration, or the transfer of seeds from warmer climates to cooler areas in anticipation of future warming (Bower et al., 2024). Although not the original intent, this study is an assisted population migration trial established in 1970, as many of the historic climates of the provenances are better aligned with the 2020's and 2050's projections of temperature for the plantation than they are with the 1970's average (Fig. 2B). One of the outstanding questions about forestry assisted migration is whether seedlings from warmer climates will be able to initially survive harsh winters at the planting site, since seedlings are planted in anticipation of future warmer temperatures. This study shows that for Engelmann spruce, survival is likely to be reduced for seedlings from areas with longer growing seasons, but growth remains relatively unchanged at a cold and dry plantation site, similar to the findings of a long-term study of Douglas-fir in the Pacific Northwest (St. Clair et al., 2020). However, the modeled decline in survival for provenances with long growing seasons is from around 80–60 %, which is still relatively high. Depending on site goals, planting density could be adjusted to account for higher mortality, but the trees that survive are likely to grow well.

The main impediment to survival and growth at our site seemed to be the short growing season and cold temperatures. Trees from Gila NF had high initial mortality and still are way behind other provenances in terms of height and DBH, but their RWI values after 2002 have been much higher than early in the study (Supplementary Figure 7). This indicates that the remaining Gila NF trees may be able to take advantage of future warmer temperatures at the site. The future projected climate at the site is much hotter and slightly drier than the climate experienced over the past 45 years (Fig. 2B) and should more closely match the climates of the hotter and drier provenances tested here in the future. Continued monitoring will reveal if the relative success of the provenances at this site shift as these changes play out. As for current reforestation efforts, planted seedlings now are more likely to be limited by drought, and it remains to be seen if the conservative growth strategies of provenances with short frost-free periods in this study will confer an advantage under growing seasons shortened by drought instead of frost. Further testing of Engelmann spruce provenances in warm and dry environments is needed.

5. Conclusions

This provenance study, now established 55 years ago, is a valuable resource that will continue to provide insights on Engelmann spruce provenance adaptation to climate, and how these adaptations impact growth and survival as climate continues to change. This study shows that a wide variety of Engelmann spruce provenances are relatively well suited to the planting site. Differences between provenances in survival, growth and reproduction indicate that different seed sources may be selected for different management goals (e.g., fast growth, early reproduction, high survival, etc.). Future work at this site could include understanding the mechanisms driving differences between populations via studies of physiology, phenology, and other functional traits. Although this study gives us a long-term view of how these provenances performed over the past 55 years, the climate now is much different than it was when the seedlings in this study were planted. In addition, these provenances were only established at one site that is relatively cold and dry compared to the provenances tested. Therefore, additional

provenance studies that establish a similarly wide range of provenances at climatically variable planting sites will provide more information on how seed source may affect early planting success under current and future climate.

CRediT authorship contribution statement

Mike A. Battaglia: Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Nigro Katherine M:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization.

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123138.

Data availability

The data is published in Mendeley Data under doi: 10.17632/69z6jmpryw.1

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