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Post-fire western larch reforestation success depends on interactions between site conditions and seed source

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Abstract

Background Wildfires are burning more area across the western US than they have in the recent past, driving an increased need for post-fire reforestation. At the same time, trees are struggling to keep up with climate change and post-fire tree planting may present an opportunity to plant seedlings from seed sources adapted to changing conditions. To better understand how reforestation outcomes for an ecologically and economically important conifer species in the northwestern US vary with seed source and site conditions, we conducted a post-fire western larch (*Larix occidentalis*) planting experiment in western Montana. We ask (1) what biophysical factors influence post-fire western larch planted seedling mortality and growth? and (2) does planting seedlings from a lower-elevation seed source decrease mortality at the driest and warmest sites and/or increase mortality at the coldest sites?

Results We planted western larch seedlings from a low-elevation and a high-elevation seed source across an elevation gradient and monitored seedling mortality and growth for 3 years. Overall seedling mortality 3 years post-planting was similar between seed sources with higher and more variable mortality in the low-elevation plots (ranging from 15 to 94% depending on seed source and plot combination; mean (sd) 60(28)%) and lower mortality in the mid-elevation and high-elevation plots (2–19%; mean (sd) 9(5.6)%). Planting seedlings from a lower-elevation seed source did not increase short-term mortality at the highest-elevation plots. Seedling mortality and growth were strongly related to site conditions, with higher mortality and lower growth associated with more southerly aspects, higher maximum temperatures, and lower soil moisture. Seedlings from the high-elevation seed source showed a stronger negative response to high maximum temperatures than seedlings from the low-elevation seed source for both mortality and growth.

Conclusions Biophysical conditions at the planting site were the stronger drivers of seedling mortality, with seed source acting as a secondary control. Interactive effects between microclimate and seed source suggest that seedlings from the low-elevation seed source may perform better under warming conditions. For western larch reforestation, site selection may have more impact on short-term survival than planting different seed sources, although we find some evidence that seed source may mediate responses to warming. Longer-term outcomes will require additional monitoring.

Keywords Reforestation, Western larch, Post-fire, Wildfire, Tree planting

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Resumen

Antecedentes Los incendios de vegetación están quemando más áreas en el oeste de los EEUU de lo que se había quemado en el pasado reciente, lo que lleva a incrementar la necesidad de la reforestación post-incendios. Al mismo tiempo, los árboles están luchando por sobrevivir en el contexto del Cambio Climático, y la plantación post incendios puede representar una oportunidad para plantar plántulas provenientes de fuentes de semillas adaptadas a esas condiciones cambiantes. Para entender mejor como los resultados de la reforestación ecológica y económica de importantes especies de coníferas en el noroeste de los EEUU varían debido a la fuente de las semillas y a las condiciones de sitio, condujimos un experimento de plantación de alerce americano occidental (*Larix occidentalis*) en el oeste de Montana. Nuestras preguntas fueron: 1) ¿qué factores biofísicos influyen en la mortalidad y el crecimiento de plántulas de alerce americano occidental en plantaciones realizadas en el post-fuego?; 2) En estas plantaciones, las plántulas provenientes de una fuente de semillas ubicadas a bajas elevaciones, ¿decrecen su mortalidad en sitios secos y más cálidos y/o incrementan su mortalidad en sitios más fríos?

Resultados Plantamos plántulas de alerces americanos occidentales provenientes de fuentes de semillas de rodales ubicados a bajas y altas altitudes a través de un gradiente de altitud, y monitoreamos su mortalidad y crecimiento por tres años. En general, la mortalidad de plántulas tres años post plantación fue similar entre las distintas fuentes de semillas, con una mortalidad más alta y variable en las parcelas ubicadas a bajas elevaciones (variando entre el 15 y el 94%) y dependiendo de la fuente de semillas y la combinación de las parcelas; el promedio (desviación estándar) de 60 (28%) y menor mortalidad en las parcelas ubicadas a elevaciones medias y altas (2-19%; promedio (desviación estándar) 9 (5,6). La plantación de plántulas provenientes de bajas elevaciones no incrementaron la mortalidad en el corto plazo en las parcelas ubicadas a altas elevaciones. La mortalidad y el crecimiento fue fuertemente relacionado con las condiciones de sitio, con una mayor mortalidad y menor crecimiento con orientaciones sur, mayores temperaturas máximas y más baja humedad del suelo. Las plántulas provenientes de fuentes de semillas de elevaciones altas mostraron una respuesta negativa más fuerte a las temperaturas máximas que las semillas provenientes de elevaciones bajas tanto en mortalidad como en crecimiento.

Conclusiones Las condiciones biofísicas en el lugar de plantación fue el condicionante más importante en la mortalidad de las plántulas, con la fuente de semillas actuando como un control secundario. Los efectos interactivos entre el microclima y la fuente de semillas sugiere que las plántulas provenientes de elevaciones más bajas pueden desempeñarse mejor bajo condiciones más cálidas. Para la reforestación del alerce americano occidental, la selección del sitio puede tener un mayor impacto en la supervivencia a corto plazo que el plantar con diferentes fuentes de semilla, aunque encontramos alguna evidencia de que la fuente de semillas puede mediar las respuestas a condiciones más cálidas. Los resultados a más largo plazo requerirán de monitoreos adicionales.

Background

Wildfires are burning more area across the western US than they have in the recent past (Iglesias et al. 2022), driven partially by climate change producing warm and dry conditions that are conducive to burning (Abatzoglou and Williams 2016; Higuera and Abatzoglou 2021). At the same time, the area burning at high severity is also increasing (Parks et al. 2025) and short-interval fires are increasingly impacting western landscapes (Harvey et al. 2023), creating more area within wildfire perimeters that are far from surviving trees that can act as seed sources. The combination of limited seed sources and warm, dry post-fire conditions can drive post-fire conversion from forest to non-forest vegetation (Coop et al. 2020; Hill and Field 2021). Active post-fire reforestation may be required where natural regeneration is limited but recovery and persistence of conifer-dominated forests is desired.

While few studies have examined survival and growth of planted seedlings in post-fire environments in the western US (Rodman et al. 2024), those that have done so have found that seedling survival is highly variable (Ouzts et al. 2015; Crockett and Hurteau 2022; Marsh et al. 2022; Marshall et al. 2023, 2024; Rodman et al. 2024). Reforestation success depends on multiple steps in the reforestation pipeline, including matching seed collection, seedling production, and fine-scale planting practices with the expected environmental conditions at a site (Grossnickle 2012; Dumroese et al. 2016). Planted seedling survival varies with seedling size, microsite conditions, topoedaphic conditions, biotic interactions, and climate (Grossnickle 2012; Rother et al. 2015; Pinto et al. 2018; Hill and Ex 2020; Dixit et al. 2021; Crockett and Hurteau 2022; Marshall et al. 2023, 2024; Marsh et al. 2023; Villar-Salvador et al. 2026), with generally higher seedling survival under moister conditions created by macroclimate, microclimate, and/or microsite

conditions. To increase the success of post-fire reforestation efforts, it is critical to understand how these environmental conditions at the outplanting site interact with other aspects of the reforestation pipeline.

As climate conditions continue to change, challenging tree species' ability to keep pace (Allen et al. 2015; Hill et al. 2023; Crockett and Hurteau 2024; Nigro et al. 2025), post-fire tree planting may present an opportunity to plant seedlings adapted to future climate conditions through assisted population migration (Palik et al. 2022; Bower et al. 2024). Assisted population migration, also called assisted gene flow or assisted population expansion, is the movement of individuals or genotypes over relatively short distances, within the current distribution of the species (Williams and Dumroese 2013; Aitken and Whitlock 2013; Aitken and Bemmels 2016). Evidence of local adaptation to climate conditions, despite high gene flow, suggests selection for local adaptation to climate is strong for many conifer species, thus providing a basis for moving individuals to facilitate rapid adaptation to climate change (Aitken and Bemmels 2016; Leites and Benito Garzón 2023). Despite the opportunity that post-fire reforestation projects present to implement assisted population migration, few studies have examined the impact of assisted population migration on seedling survival and growth in an operational context (Palik et al. 2022), particularly following wildfire (Young et al. 2020; but see Moran et al. 2024). While assisted population migration may reduce maladaptation to future climate conditions, there are concerns that moving seedlings across large climate transfer distances (the difference in climate between source and planting sites) to better match future climate conditions could potentially reduce seedling performance in the short-term either directly (e.g., through frost damage) or indirectly through altered biotic interactions (Aitken and Whitlock 2013; Grady et al. 2015; Kranabetter et al. 2015). Although a long history of forestry provenance trials and genetic research exists which can inform assisted population migration (e.g., O'Neill et al. 2014; Rehfeldt et al. 2014; Aitken and Bemmels 2016; St. Clair et al. 2020), many practitioners still cite "uncertainty of outcomes" and "knowledge of seed sources suited to the future climate of the planting site" as major barriers to implementation (Agne and Slesak 2025).

Western larch (*Larix occidentalis* Nutt.) is an ecologically, culturally, and economically important tree species in the Northern Rockies and interior Northwest (Schmidt et al. 1976). Given its high fire resistance and ability to regenerate well following wildfire, the species could become an increasingly important component of northwestern forests as fire activity increases, provided seed sources are available post-fire (Steed and Goeking 2020; Hoecker and Turner 2022; Vieira et al. 2024). However, western larch also has a relatively narrow climate niche relative to many of the co-occurring species in its range (Rehfeldt and Jaquish 2010). Adult presence depends on summer dryness, winter minimum temperatures, and summer maximum temperatures, and locations that meet these climatic tolerances are projected to shift significantly by mid-century (Rehfeldt and Jaquish 2010). Provenance tests and common garden experiments with western larch suggest that there is weak to moderate genetic differentiation for traits related to seedling growth, survival, spring frost tolerance, and pathogen resistance, with the proportion of phenotypic variance explained by population or provenance ranging from 0 to 0.16 depending on trait (Rehfeldt 1995; Roskilly and Aitken 2024). Geographic location, elevation, and climate variables were mostly strongly associated with traits such as bud flush, growth, bud set, and pathogen resistance ($R^2 = 0.08–0.34$, depending on study and variables), while spring and fall frost damage were not related to these variables (Rehfeldt 1995; Rehfeldt and Jaquish 2010; Roskilly and Aitken 2024). Planted western larch seedling survival has been studied in post-timber harvest areas, with higher seedling survival associated with higher light availability, larger initial seedling size, less vegetative competition, and lower maximum summer temperature (Chen and Klinka 1998; Pinto et al. 2018; Chen and Nelson 2020). Fewer studies have investigated the survival or growth of planted western larch seedlings in post-wildfire environments (Rodman et al. 2024).

To better understand the biophysical drivers of planted western larch seedling mortality and growth in post-fire landscapes and how these interact with seed source, we leveraged an operational post-fire planting effort conducted in western Montana, USA. We planted western larch seedlings from a low-elevation and a high-elevation seed source across an elevation gradient (1446–1888 m) and monitored seedling mortality and growth for 3 years to ask (1) what biophysical factors influence post-fire western larch planted seedling mortality and growth? and (2) does planting seedlings from a lower-elevation seed source decrease mortality and increase growth at the driest and warmest sites and/or increase mortality and decrease growth at the coldest sites? We expected that microclimate conditions at planting sites would interact with seed source such that seedlings from the low-elevation seed source would perform better at the warmer and drier sites, while seedlings from the high-elevation seed source would perform better at cooler and wetter sites.

Methods

Study site

The study site was located on Black Mountain 30 km northeast of Missoula, MT, USA (−113° 41′, 47° 02′) on land owned by The Nature Conservancy (TNC), previously managed as industrial timber land, and in the aboriginal territories of the Salish and Kalispel people. Across the elevation gradient at the site (1446–1888 m), mean annual temperature ranges from 5.6 °C to 3.8 °C, mean minimum temperature of the coldest month from − 8.4 °C to − 9.8 °C, mean maximum temperature of the warmest month from 26.4 °C to 23.7 °C, and mean annual precipitation from 678 to 1179 mm (30-year normals from 1991 to 2020; 800-m resolution; PRISM Climate Group, Oregon State University, 2025). The soils at the low-elevation plots are Lamellic Eutrudepts and Haplustepts, whereas the mid-and high-elevation plots are Andic Haplocryalfs (NRCS, US Soil Survey). Soil texture showed little variation across all plots with an average loam texture comprised of 38% sand, 43% silt, and 19% clay. Lower elevations of the study site are dominated by *Pinus ponderosa* Lawson & C. Lawson, *Pseudotsuga menziesii* (Mirb.) Franco, and *L. occidentalis* with an understory of *Ceanothus velutinus* Douglas ex Hook, *Mahonia repens* (Lindl.) G. Don, and *Symphoricarpos albus* (L.) S.F. Blake. Mid- and high-elevation areas are dominated by *P. menziesii* and *L. occidentalis*, with components of *Pinus contorta* Douglas ex Loudon, *Abies lasiocarpa* (Hook.) Nutt., and *Picea engelmanii* Parry ex Engelm. The understory of higher elevation sites is predominantly *Epilobium angustifolium* L., *Xerophyllum tenax* (Pursh) Nutt., *Spiraea betulifolia* Pall., and *Vaccinium membranaceum* Douglas ex Torr. The study site burned in the Liberty Fire which started on July 15, 2017 and burned over 11,000 ha.

Experiment

We used a split-plot design with three plots located in each of three elevation bands (low: 1446–1477 m; mid: 1621–1663 m; high: 1746–1888 m) for a total of nine plots and two seed sources planted in each plot (Table S1). We selected plot locations to maximize the elevation difference in planting locations. Because our experiment was part of an operational reforestation effort being conducted by TNC, plot placement was constrained to within planned planting units which were areas burned at high severity according to Monitoring Trends in Burn Severity data (Eidenshink et al. 2007) and confirmed by tree mortality estimates in the field (all plots had 100% mortality). Within the planned planting units, we maximized the distance between the plots (the minimum distance between plots was 180 m). All plots were at least 30 m from the edge of the planting unit. Each plot was 40 by 40 m and was split parallel to the slope to create two subplots that were each planted with 55 seedlings from one of two seed sources (110 seedlings per plot/990 total seedlings planted).

We selected two local western larch seed sources that would typically be planted by the U.S. Forest Service in this region at sites between approximately 1036–1463 meters above sea level ("low-elevation" seed source; "MTLM 3401–4800" breed zone) or at sites > 1463 meters above sea level ("high-elevation" seed source; "MTHI 4800+" breed zone), although exact planting guidelines will vary with the geographic location of the seed source. For this study, the low-elevation seed source was wild collected from a site on the Lolo National Forest in western Montana at 1,375 m elevation. Based on the elevations and geographic locations of the low-elevation seed source and experimental planting sites, more detailed guidelines for planting western larch in western Montana (Rehfeldt 1982, 1983) suggest that the low-elevation seed source be planted at the low-elevation plots but not at the mid-elevation or high-elevation plots. However, when comparing climate transfer distances under recent climate conditions (Table 1), the mid-elevation plots more closely match the climate conditions that the low-elevation seed source is adapted to. When considering future climate conditions under a scenario of a global mean increase in temperature of 2 °C (Hoecker et al. 2024), the low-elevation seed source would be the most suited for the mid-elevation and high-elevation plots (Table 1). Under future climate conditions, the low-elevation plots exceed suggested climate transfer limits of 2 °C (St.Clair et al. 2022) for mean maximum July temperature. All plots exceed this transfer limit for mean minimum January temperature under the future climate scenario. The high-elevation seed source was from a seed orchard and was genetically improved for growth potential. The parent trees for the seed source came from the western MT breeding zone above 1463 m, but we do not know the exact location of the parent trees and therefore cannot calculate exact climate transfer distances. Recent work suggests that selective breeding for growth in western larch has not compromised seedling drought resistance (Roskilly et al. 2025) and has maintained genetic variation in bud flush phenology and cold hardiness but did delay bud set (Roskilly and Aitken 2024).

Seedlings from the two seed sources were donated by the Lolo National Forest who obtained them from the USDA Forest Service Coeur D'Alene Nursery. The seedlings were 2-year-old bareroot stock that were thawed and transported from the nursery with the same methods the Lolo National Forest uses for their reforestation projects. The seedlings for this project were treated and

Table 1 Climatic transfer distances for the planted plots and the low-elevation seed source. Transfer distances are calculated as the past (1961–1990), current (1985–2015), or future (+ 2 °C increase in global mean temperature) climate of the planting site minus the climate to which the seed source is adapted (1961–1990 at the seed collection location). Climate data is from Topoterra at 220 m resolution (Hoecker et al. 2024). Suggested climate transfer limits are ± 2° C for temperature and ± 200 mm (0.5*deficit at seed source location) for water deficit (St. Clair et al. 2022). Units for annual water deficit ("Def") are mm and for mean minimum January temperature ("Tmin") and mean maximum July temperature ("Tmax") are °C

	1961–1990			1985–2015			+ 2 °C future		
Plot	**Def**	**Tmax**	**Tmin**	**Def**	**Tmax**	**Tmin**	**Def**	**Tmax**	**Tmin**
Low 1	12.73	− 0.26	0.35	35.15	0.39	2.22	81.96	2.40	4.12
Low 2	12.93	− 0.10	0.36	35.35	0.55	2.23	82.06	2.56	4.12
Low 3	− 5.13	− 0.19	0.46	16.48	0.47	2.33	63.54	2.48	4.22
Mid 1	− 25.13	− 0.99	0.03	− 4.33	− 0.33	1.90	43.44	1.67	3.80
Mid 2	− 14.03	− 1.23	0.03	6.96	− 0.58	1.90	54.22	1.43	3.80
Mid 3	− 28.47	− 1.39	0.11	− 7.85	− 0.74	1.99	39.57	1.27	3.89
High 1	− 41.27	− 1.63	0.05	− 21.17	− 0.98	1.92	26.51	1.02	3.82
High 2	− 56.60	− 2.19	− 0.14	− 37.20	− 1.54	1.73	10.96	0.47	3.62
High 3	− 48.57	− 2.43	− 0.34	− 28.88	− 1.78	1.53	18.96	0.23	3.43

planted in the same way on the same days as the seedlings for the rest of the planting units by the contracted crew. Seedlings were kept in a cooler on the day of planting until they were placed in tree bags for immediate planting. All seedlings were planted by a single individual with over 10 years of professional tree planting experience to minimize differential survival due to planting technique. Each seedling was placed on the north side of a microsite object (e.g., snag, log, stump, or rock) to provide some shade and received an 18-inch scalp (removal of herbaceous vegetation surrounding the seedling), following common planting procedures in this region. All microsite objects shaded the soil surface; however, some (e.g., standing snags) may have provided more direct shading of the seedlings than others (e.g., fallen logs), which would be accounted for in the canopy cover metric described below. Seedlings were planted at least 4-m apart in a roughly grid pattern, with some variability due to microsite availability. Seedlings were planted between May 4 and 6, 2021 and then individually tagged.

We measured root collar diameter and height on each seedling following planting in 2021 and in late September/early October of 2021, 2022, and 2023. Seedling mortality was also assessed at each fall survey and in late May/early June 2022, 2023, and 2024. Note that because seedlings were planted in early May and mortality was not assessed until September in 2021, the summer 2021 interval included the month of May, which had low minimum temperatures, while the first 3 to 4 weeks of May were included in the winter survey periods for the following years. Seedlings were considered dead if no green needles remained, which was confirmed during subsequent surveys. In spring 2021, we used a spherical densiometer to measure canopy cover over each seedling (including dead trees and branches) by taking and averaging four readings, one in each cardinal direction. While we refer to this metric as "canopy cover" throughout, it is largely representative of cover from dead branches and snags. In October 2021, five random seedlings from each seed source in each plot were excavated, ensuring all roots were collected regardless of depth and lateral spread to the best of our ability. Seedlings were then dried to a constant weight and the roots and shoots of each seedling were weighed separately to calculate the root to shoot ratio.

To characterize site conditions, we installed microclimate sensors (TOMST buriable TMS unit (Wild et al. 2019)) before the planting date to measure temperature 15 cm above the ground surface and soil moisture at 20 cm depth (approximate rooting depth of planted seedlings) at the center of each plot. Microclimate data for 1 month at one plot and 5 months at a second plot were missing, and we filled in missing data based on modeled relationships to microclimate conditions at nearby plots (see supplemental methods). Six mineral-soil samples for texture analysis were collected from each plot at a 0–10 cm depth using a 2.5 cm diameter sampling probe. These six samples were then composited into a single plot sample and transferred back to the lab. The samples were sent to Agvise laboratories (Northwood, ND) for soil texture analysis using the hydrometer method. We also extracted fire severity as the differenced normalized burn ratio (dNBR) from the Monitoring Trends in Burn Severity database (30-m resolution; Eidenshink et al. 2007) at the center of each plot.

Given observations of potential frost damage to seedlings in spring 2022, we decided to test the frost tolerance of seedlings from each seed source and plot using an electrolyte-leakage test (Burr et al. 1990; Mabaso 2017). On May 30, 2023 we clipped 6–10 cm long branch tips from the top half (L'Hirondelle et al. 2006) of three random seedlings from each plot, with the exception of one low-elevation plot, which had very few surviving seedlings. Branch tips were stored in moist cheesecloth wrapped in aluminum foil and placed in a plastic bag that was kept in a cooler while sampling other plots. Within 6 h, all samples were in a growth chamber (Percival Scientific LT-36VLC8) set to 4 °C. The growth chamber was cooled at a rate of 2 °C per hour down to − 10 °C, kept at − 10 °C for 3 h and then warmed at a rate of 2 °C per hour back to 4 °C. Two additional samples from each seed source were kept at 4 °C instead of freezing as controls. After the freeze treatment, needles were placed in glass test tubes with deionized water and sat for 19 h at room temperature. Next, water conductivity was assessed by placing a conductivity meter (AquaSearcher AB33EC Bench Meter, OHAUS Instruments Co. Ltd.) in each tube for an initial measurement. Tubes were then placed in a water bath with boiling water for 15 min. After boiling, the tubes sat at room temperature for 17 h before conductivity was measured a second time. Electrolyte leakage was calculated using an injury index (I) that accounts for background leakage levels from the unfrozen controls (average of our four controls) by converting the percentage release of electrolytes to a scale where the unfrozen sample is given a value of zero and the heat-killed sample a value of 100 (Flint et al. 1967) as follows:

$$I = 100 * (\frac{L_t}{L_k} - \frac{L_o}{L_d})/(1 - \frac{L_o}{L_d})$$

where:

L_t = specific conductance of leachate from a sample frozen at temperature (t).

L_k = specific conductance of leachate from a sample frozen at temperature (t) and then heat-killed in boiling water.

L_o = specific conductance of leachate from an unfrozen sample.

L_d = specific conductance of leachate from an unfrozen sample, heat killed in boiling water.

Statistical analysis

To address our research questions, we applied a two-step approach. We first used the Kaplan–Meier estimator (a non-parametric approach) to broadly assess overall tree survival probabilities as a function of time since planting across seed source and plot elevation (Kaplan and Meier 1958). Survival probabilities were compared using the log-rank test with the Survival package in R (Therneau and Grambsch 2000; Therneau 2026) and visualized with the survminer package (Kassambara et al. 2017). The Kaplan–Meier estimator accounts for censored observations which in this study represent seedlings that were alive at the end of the study period (Kaplan and Meier 1958; Maringer et al. 2021).

Then, to better understand the influence of abiotic and biotic factors on seedling mortality and growth, we followed an inference-based modeling approach (Tredennick et al. 2021). For seedling mortality, we used discrete-time survival analysis with both time-fixed and time-varying predictors. Generalized linear mixed models (GLMMs) with a binomial error distribution and a cloglog link were fit to the response seedling mortality (0 = alive, 1 = dead) at each survey date as a function of biotic and abiotic predictors (Table S2). Biotic predictors included variables at the tree-level including seed source, initial seedling size, and canopy cover directly over the seedling. Initial seedling size was defined by root collar diameter, height, or height to root collar diameter ratio (HDR) at the time of planting, which can relate to seedling survival and growth (Chen and Nelson 2020). Models with height had more support than other metrics of initial seedling size based on AIC, and height was included in the final model. Days since planting was included as a fixed effect in all models, and its interaction with seed source was tested, as some studies have found outcomes differ between seed sources over time. Abiotic predictors included microclimate variables summarized over the survey interval that we expected to be related to seedling survival: absolute minimum temperature (minimum temperature of the coldest day in the interval), mean minimum temperature, absolute maximum temperature (maximum temperature of the hottest day in the interval), mean maximum temperature, mean soil moisture (volumetric water content; VWC), and minimum soil moisture (lowest VWC in a single day in the interval). The temperature metrics were correlated with each other (r = 0.59–0.93 depending on comparison) but less correlated with mean or minimum soil moisture (r = − 0.34–0.08). To minimize issues with collinearity, we constructed initial models that contained one soil moisture metric and one temperature metric, both with and without an interaction between the climate metrics and seed source. To confirm collinearity was not an issue, we calculated variance inflation factors (VIF) and only proceeded with models where the VIFs were < 5. We also included the plot-level variable aspect, which accounted for additional variability in site conditions and solar radiation not captured by our microclimate variables. All models included an offset to account for the time difference between survey intervals and a random

effect of plot. We used delta AIC to select the model with the most support from among the different combinations of microclimate predictors (Burnham and Anderson 2004). Results were qualitatively similar regardless of which microclimate metric was included in the models. To better understand how drivers of mortality change over time, we also fit a model with the same predictors that were included in the final mortality model described above to mortality data from just the first growing season with two exceptions: this model did not include days since planting or an offset for survey interval because it only included the data from the first growing season.

For these models, and those described below, we examined simulated residuals of the final model using the DHARMa package (Hartig 2026) and calculated marginal (fixed effects only) and conditional (fixed and random effects) R^2 values with the "performance" package (Lüdecke et al. 2021). Marginal effects were calculated and plotted with the "ggeffects" package (Lüdecke 2018). When making marginal effects plots, non-focal predictors were marginalized over all observations, and predicted values were then averaged across all subjects while holding other variables at their median values. For all analyses, we removed eight seedlings that were planted with their roots visible above the soil level, because they would be more susceptible to mortality due to poor planting technique.

We followed a similar modeling process for seedling growth, but, given the distribution of our response, used linear mixed-effect models. The response we modeled was the change in height from the time of planting in spring 2021 to the last measurement in fall 2023. We first created models with the predictors seed source, initial seedling size, canopy cover, fire severity, and one of the following climate predictors with and without an interaction with seed source: summer (June–August) mean maximum temperature, summer mean minimum temperature, spring (March–May) mean soil moisture, and summer mean soil moisture. All models also included a random effect of plot. Initial seedling size was defined by root collar diameter, height, or HDR at the time of planting and, based on AIC comparisons between models, HDR was included in the final model. Fire severity and canopy cover were included in each model because of their potential importance to western larch seedling establishment and growth (Schmidt et al. 1976; Hopkins et al. 2014; Alexander et al. 2018). We expected that mean climate conditions might have a greater impact on growth than extreme events, especially since growth occurred over two and a half years. To account for this, we averaged the climate predictors across the time period that we measured growth. The two models with the lowest AICs (within 0.60 AIC of each other) contained summer mean maximum temperature and spring mean soil moisture. Given the low correlation between these two climate predictors (− 0.07), we included both in the final model. Because we observed some non-linearities in the relationship between growth and certain predictors, we included second-order polynomial terms for the predictors HDR and spring mean soil moisture.

We assessed differences in seedling root to shoot ratio between seed sources, because higher seedling root to shoot ratio can be related to higher planted seedling survival and growth, especially on drier sites (Larsen et al. 1986; Boyer and South 1987; Grossnickle 2012; Grossnickle and MacDonald 2018). Given its link to plant water relations (Parker 1949), root to shoot ratio can be influenced by soil texture and moisture (Gao et al. 2017; Ye et al. 2021). To assess if root to shoot ratio at the end of the first growing season varied by seed source, soil moisture, and/or soil texture, we used linear mixed-effect models to model root to shoot ratio as a function of seed source, minimum soil moisture during the first growing season, percent sand content in the soil, and the interaction between seed source and minimum soil moisture. We also included a fixed effect of diameter at planting to account for initial seedling size and a random effect of plot, because 10 seedlings (5 per seed source) were sampled per plot.

To assess if freeze tolerance, as measured by electrolyte leakage, differed between seed sources, we used a linear model with percent electrolyte leakage as the response and seed source and plot elevation as the predictors. We included plot elevation because the seedlings at the low-elevation and mid-elevation plots leafed out earlier than the high-elevation plot and thus had older needles. Initially, we also tested including plot as a random effect because multiple seedlings per plot were sampled, but the variance of the random effect was zero which caused a singular fit and thus we removed the random plot effect (which resulted in the same coefficient estimates).

Results

Seedling mortality

Overall, seedling mortality was higher and more variable in the low-elevation plots than in the mid- and high-elevation plots. For example, percent seedling mortality between planting in May 2021 and the last survey in May 2024 at low-elevation plots ranged from 15% for seedlings from the high-elevation seed source in plot Low 2 to 94% also for seedlings from the high-elevation seed source but in plot Low 3. The mean 3-year mortality for seedlings planted at low elevation averaged across seed source and plot combinations was 60% (sd: 28%). Mortality in mid- and high-elevation plots 3 years post-planting

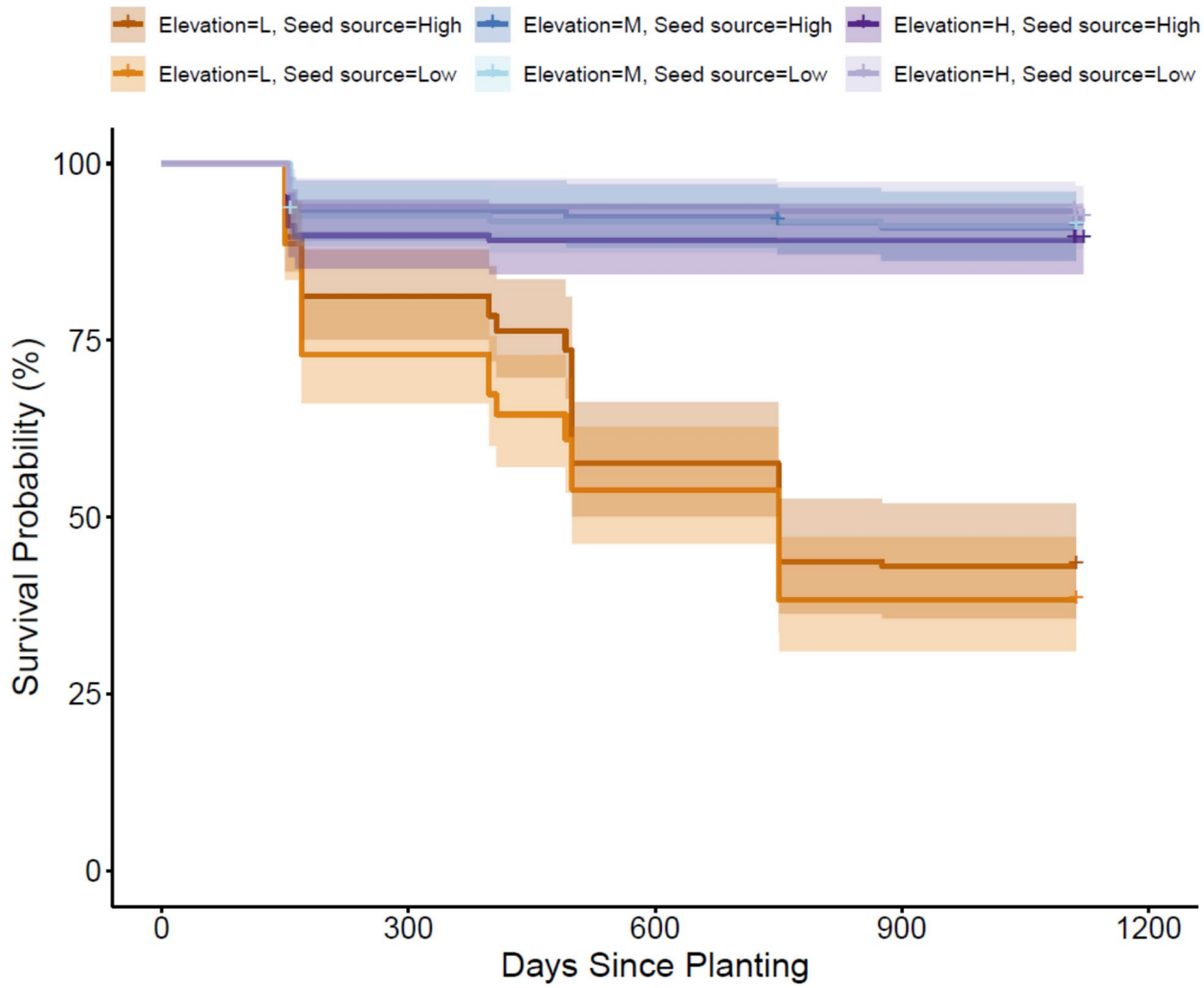

Fig. 1 Kaplan–Meier survivorship curves grouped by elevation and seed source. Data from the three plots in each elevation band were combined. "L" is low-elevation plots, "M" is mid-elevation plots and "H" is high-elevation plots. Shaded bands are 95% confidence intervals

averaged 9% with a standard deviation of 5.6% and a range of 2–19% across different combinations of seed source and plot.

In agreement with the raw mortality numbers, survivorship probabilities were far lower at the low-elevation plots compared to mid-and high-elevation plots. The log-rank test revealed strong evidence for a difference in survival probability between elevations ($X^2 = 255$, $p < 0.0001$), but there was little evidence for a difference in survival probability between seed sources ($X^2 = 0$, $p = 1$; Fig. 1). The low-elevation plots experienced the largest temperature fluctuations, consistently experiencing some of the highest maximum temperatures but also coldest minimum temperatures, especially over the winter and early spring when snow had presumably melted at the low-elevation plots but not mid-elevation or high-elevation plots (Figs. S7 and S8). Mortality was largely driven by abiotic factors, with limited evidence of herbivory or fungal pathogens.

There were also fluctuations in mortality over time, with most mortality occurring in the first 2 years (Fig. 2). Examining seasonal mortality patterns shows small differences between seed sources at the low-elevation plots, where most mortality occurred (Fig. 2). The low-elevation seed source had higher mortality during time periods which included low minimum temperatures and spring frost events: Summer 2021 (which included May), Winter 2021–2022 (which included May), and Winter 2022–2023 (which included 3 weeks of May). The high-elevation seed source had higher mortality than the low-elevation seed source over summer 2022, which had the highest maximum temperature of the three sample years.

The final model for seedling mortality included fixed predictors of initial seedling size (height at planting),

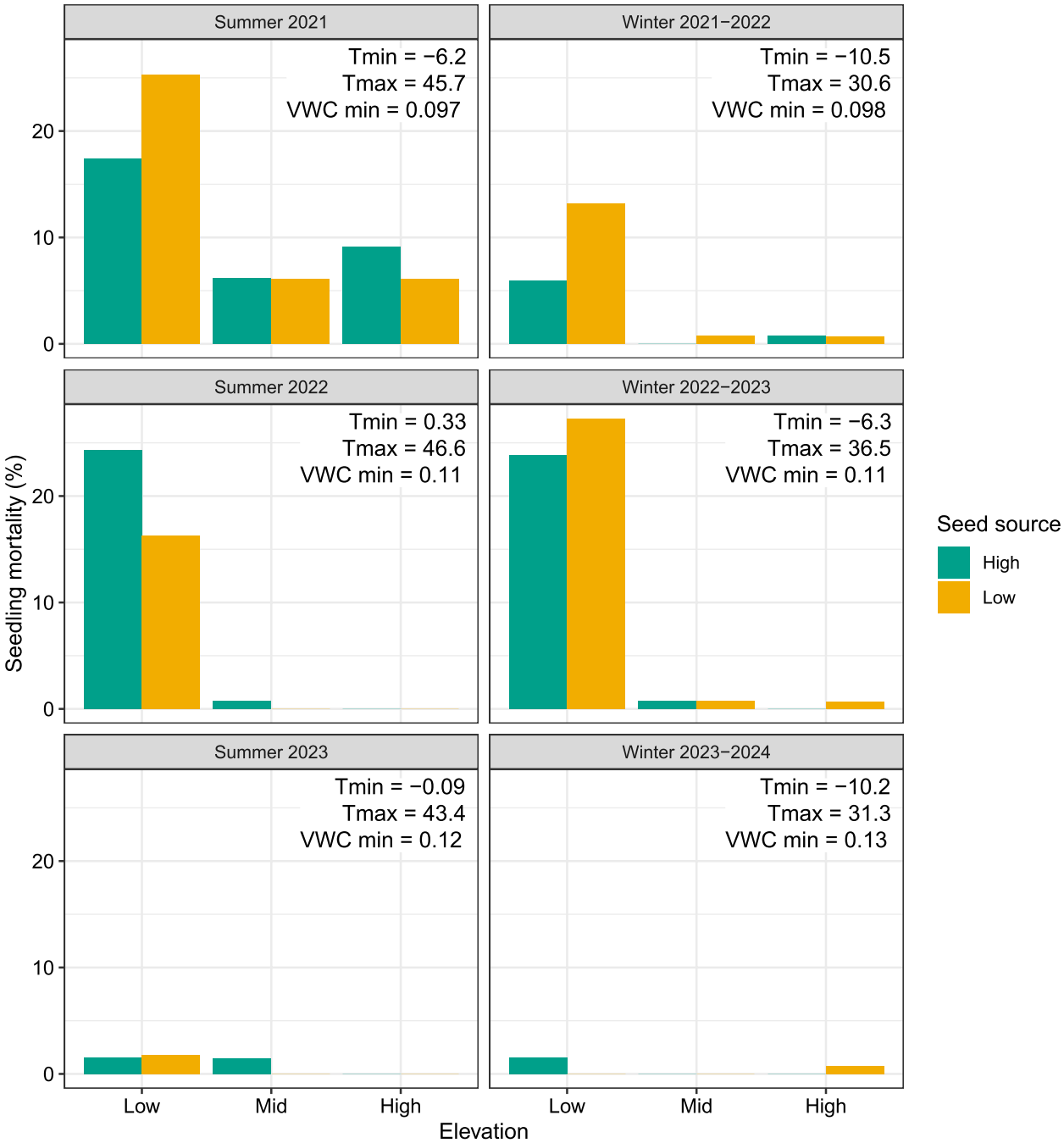

Fig. 2 Percent seedling mortality over each seasonal sampling interval for seedlings from the high-elevation and low-elevation seed source. Data from all plots at each elevation are combined. Average minimum and maximum temperatures (°C; "Tmin" and "Tmax", respectively) and minimum soil moisture (volumetric water content; "VWC") in each survey interval are shown. Note that the summer 2021 interval included the month of May which had low minimum temperatures, while most of May was included in the winter survey periods for the following years

canopy cover, aspect, days since planting, absolute maximum temperature, absolute minimum VWC, seed source and the interaction between seed source and absolute maximum temperature, absolute minimum VWC, and days since planting (Fig. 3; Table S3). The marginal R^2 was 0.57 (conditional $R^2 = 0.81$). The strongest predictor of mortality was aspect ($p = 0.005$, $\chi^2 = 10.67$, df = 2), with even small differences in aspect moving from SW-facing to W-facing slopes reducing mortality (Fig. 3C). The probability of mortality

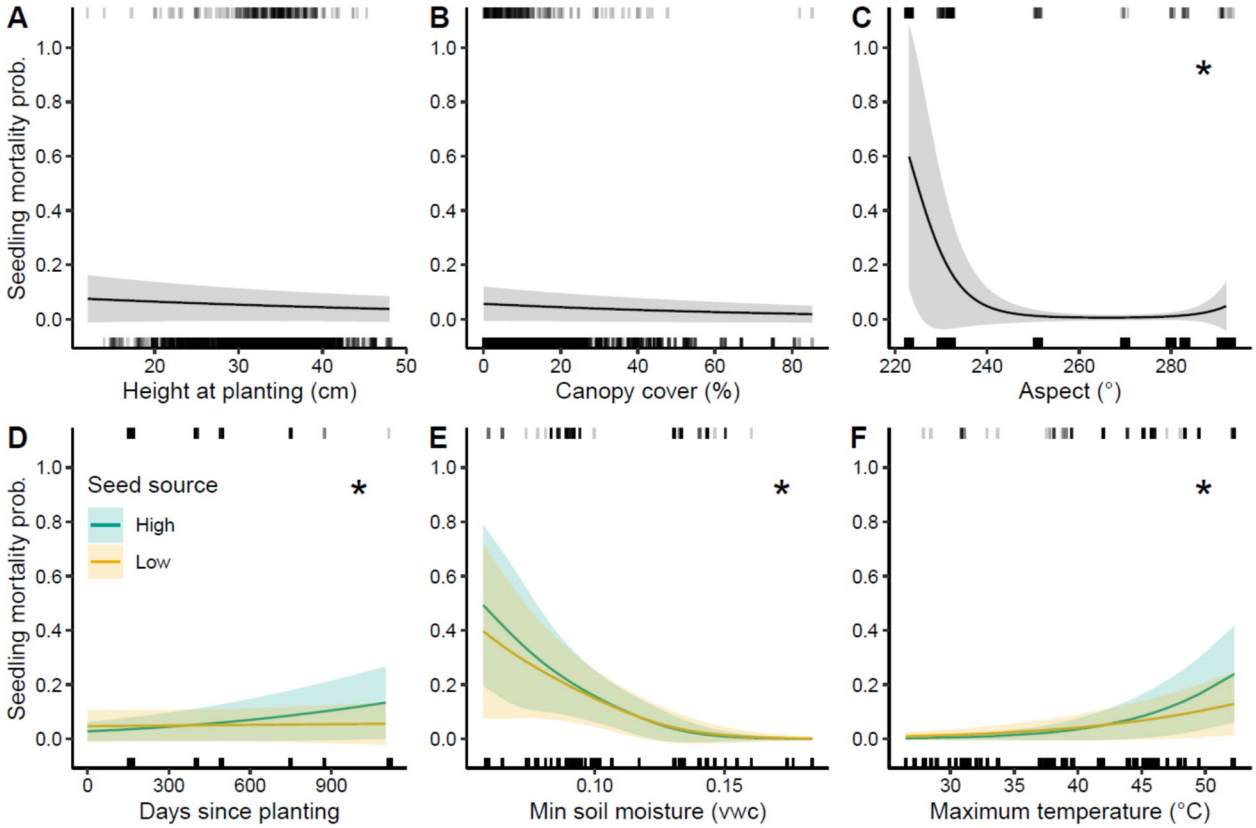

Fig. 3 Biophysical drivers of planted western larch seedling mortality. Marginal effects plots for the seedling mortality model showing the relationship between model predictors and seedling mortality probability ("prob."). Predictors that had a statistically significant ($p < 0.05$) relationship with mortality are indicated with an "*". Significant interactions between seed source and other predictors are shown with a green line for seedlings from the high-elevation seed source and an orange line for seedlings from the low-elevation seed source. The rug plots show the distribution of observations with (top) or without (bottom) mortality events across each predictor. Bands are 95% CIs

increased over time for the high seed source but not the low seed source (Fig. 3D; $p = 0.008$, $\chi^2 = 7.09$, df = 1). The relationship between mortality and microclimate also depended on seed source. The probability of mortality increased more for the high than low seed source with higher temperatures ($p = 0.003$, $\chi^2 = 8.89$, df = 1; Fig. 3F) and lower soil moisture ($p = 0.002$, $\chi^2 = 9.23$, df = 1; Fig. 3E), although the effect size for soil moisture was small despite statistical significance. Finally, there were minimal effects of canopy cover ($p = 0.054$, $\chi^2 = 3.71$, df = 1; Fig. 3B) and initial seedling height ($p = 0.16$, $\chi^2 = 2.01$, df = 1; Fig. 3A) on mortality.

Mortality probability over the first growing season increased with decreasing canopy cover ($p = 0.019$, $\chi^2 = 5.46$, df = 1) and on more south-facing slopes ($p < 0.0001$, $\chi^2 = 47.17$, df = 2; Fig. S14). There was weak statistical support for an effect of initial seedling height ($p = 0.069$, $\chi^2 = 3.31$, df = 1), with shorter seedlings exhibiting slightly higher likelihood of mortality (Fig. S14). None of the other predictors had a significant relationship to mortality (Table S5).

Seedling growth and root to shoot ratio

The final model for seedling height growth included the fixed predictors of height to diameter ratio at planting, canopy cover, fire severity, and both spring mean soil moisture and summer mean maximum temperature interacted with seed source (Table S4). The marginal R^2 was 0.20 (conditional $R^2 = 0.30$). Height growth declined with increasing height to diameter ratio ($p < 0.0001$, $\chi^2 = 33.6$, df = 2) and higher canopy cover ($p = 0.0006$, $\chi^2 = 11.9$, df = 1) and increased at plots with higher fire severity ($p = 0.01$, $\chi^2 = 6.56$, df = 1; Fig. 4). There was a significant interaction between seed source and spring mean VWC ($p < 0.0001$, $\chi^2 = 23.2$, df = 2) whereby height growth for seedlings from the high seed source did not vary with spring mean soil moisture, while growth for seedlings from the low seed source peaked at intermediate levels of spring mean soil moisture (Fig. 4). There was also a significant interaction between seed source and summer mean maximum temperature ($p = 0.001$, $\chi^2 = 10.4$, df = 1), with decreasing growth as temperature increased for seedlings from the high-elevation seed

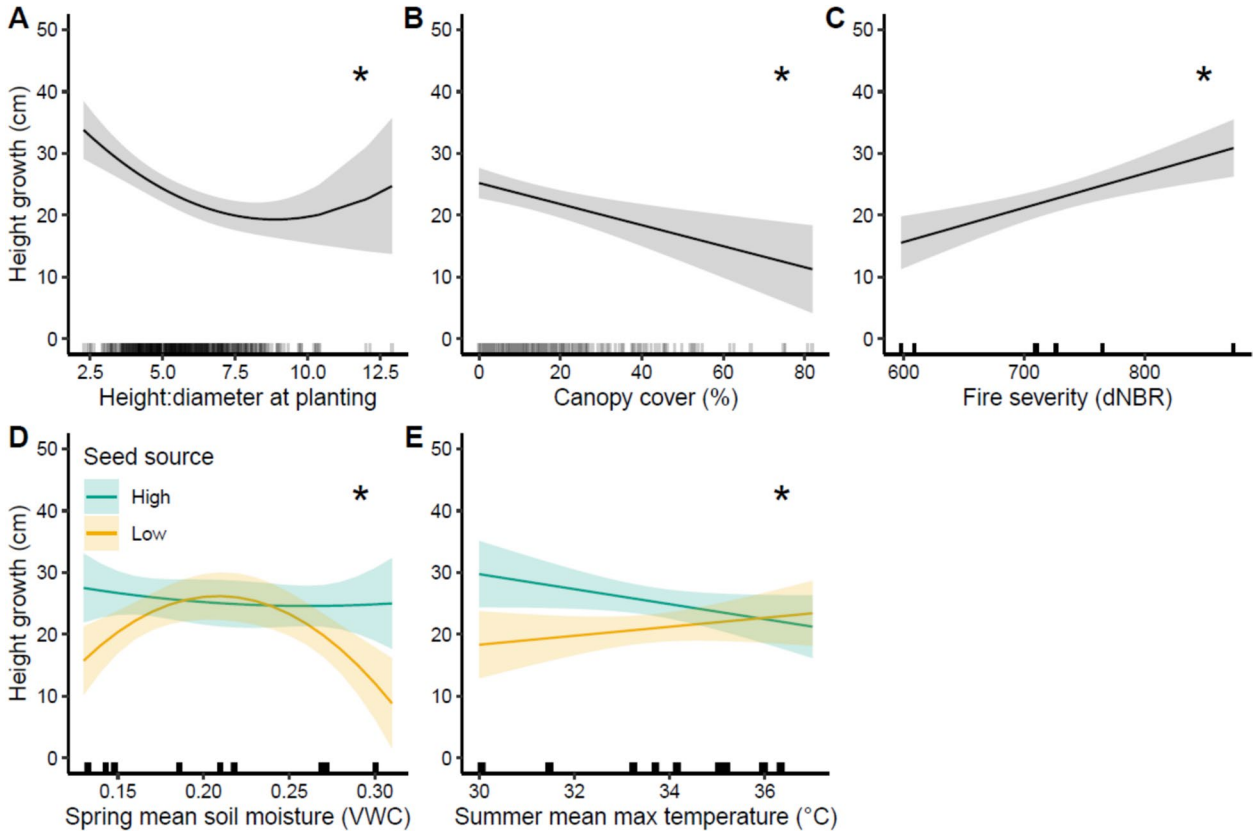

Fig. 4 Biophysical drivers of planted western larch seedling height growth. Marginal effects plots for the seedling height growth model showing the relationship between model predictors and seedling height growth from spring 2021 through fall 2023. Predictors that had a statistically significant ($p < 0.05$) relationship with mortality are indicated with an "*". Significant interactions between seed source and other predictors are shown with a green line for seedlings from the high-elevation seed source and an orange line for seedlings from the low-elevation seed source. Bands are 95% CIs

source but marginally increasing growth for seedlings from the low-elevation seed source with increasing summer mean maximum temperature (Fig. 4).

Seedling root to shoot ratio after one growing season increased with increasing percent sand in the soil ($p = 0.025$, $\chi^2 = 4.99$, df = 1; Fig. S9). While there was a trend that the root to shoot ratio increased with lower soil moisture for seedlings from the low-elevation seed source but not the high-elevation seed source (Fig. S9), the interaction between seed source and minimum soil moisture was not statistically significant ($p = 0.13$, $\chi^2 = 2.31$, df = 1). There was a lot of individual variability in root to shoot ratio and the model marginal R^2 was only 0.14.

Seedling frost tolerance

Cold damage as measured by electrolyte leakage did not vary with seed source ($p = 0.85$, $F_{1,41} = 0.04$) but did vary with elevation ($p < 0.001$, $F_{2,41=9.12}$). Seedlings planted at high elevations, which had more recently leafed out, had significantly higher electrolyte leakage than the seedlings planted at mid or low elevations (Fig. S10).

Discussion

The increasing demand and insufficient resources for post-fire reforestation (Dobrowski et al. 2024) underscore the need to identify factors most likely to lead to successful reforestation despite increasingly stressful climatic conditions (North et al. 2019). Our results highlight the importance of microsite conditions for post-fire-planted western larch seedling mortality and growth, which is consistent with prior work on other conifer species (e.g., Hill and Ex 2020; Hankin et al. 2023; Marshall et al. 2023, 2024). Cooler and moister sites experienced low mortality of seedlings from both seed sources, despite these sites exceeding the elevation recommended for planting the seedlings from the low-elevation seed source. These findings are important in the context of projected climate change-driven shifts to the geographic area with high

climate suitability for western larch (Rehfeldt and Jaquish 2010).

Planted tree seedling survival in dry mixed conifer forests is frequently limited by high temperatures and/or low soil moisture (Schmidt et al. 1976; Hill and Ex 2020; Chen and Nelson 2020; Dixit et al. 2021; Marsh et al. 2022; Marshall et al. 2023, 2024). Here, seedlings from both seed sources had the highest mortality in the low-elevation plots due to increased mortality probability associated with the higher maximum temperatures and lower soil moisture that occurred on these plots, which were both at a lower elevation and a more southwestern aspect than the mid-elevation and high-elevation plots which were more directly west-facing (Table S1).

Higher mortality with low soil moisture can occur due to reduced seedling hydrologic function and linked changes to carbon relations and photosynthesis (Reinhardt et al. 2015; Pinto et al. 2016). Although drought strongly influences seedling survival, a recent drought experiment of western larch seedlings from different populations found limited genetic variation in drought resistance traits (Roskilly et al. 2025). Consistent with these findings, although we found a statistically significant interaction between seed source and minimum soil moisture in our mortality model, large overlap between the confidence bands suggests high uncertainty and potentially limited difference in response to soil moisture between seedlings from the two seed sources (Fig. 3). The trend toward higher root to shoot ratios with lower soil moisture for seedlings from the low-elevation but not high-elevation seed source (Fig. S9), although not statistically significant ($p=0.13$), could partially explain the slightly lower mortality for seedlings from the low-elevation seed source at the driest sites. Higher root to shoot ratio allows seedlings to increase water uptake capacity relative to transpiration, which helps overcome planting stress and can decrease mortality, especially for bare-root seedlings on dry sites (Lopushinsky and Beebe 1976; Grossnickle 2012; Villar-Salvador et al. 2026). The lack of strong statistical significance for this trend may be due to our relatively small sample size and high individual variability in root to shoot ratio.

Higher seedling mortality with higher maximum temperatures can occur both due to increased soil drying with high maximum temperatures and direct heat damage to seedlings (Kolb and Robberecht 1996; Simeone et al. 2019; Holden et al. 2024). High maximum temperatures have been associated with lower natural post-fire western larch regeneration densities (Clark-Wolf et al. 2022) and lower planted western larch seedling survival (Chen and Nelson 2020). In our study, seedlings from the two seed sources exhibited different responses to maximum temperature for both mortality and growth (Figs. 3 and 4). At the maximum temperatures observed in our plots, seedlings from the high-elevation seed source were more likely to die (0.11 higher mortality probability per survey interval). While small, this difference may compound over time, especially as sites continue to get warmer (Figs. S11–12). We would expect seedlings from the high-elevation seed source, which was genetically improved for growth potential, to grow faster than those from the low-elevation seed source (Chen and Nelson 2020; Roskilly and Aitken 2024), which we did observe except at the highest maximum temperatures. As such our results suggest that seedlings from the low-elevation seed source may perform better at sites with high maximum temperatures; however, whether this pattern would hold across a broader range of seed sources remains to be tested.

Despite concerns of maladaptation to cold conditions when seedlings from lower-elevation seed sources are planted at higher elevations (Benito-Garzón et al. 2013; Montwé et al. 2018; Martínez-Berdeja et al. 2019), several assisted population migration or planting studies have demonstrated that trees from seed sources from lower elevations or farther south tend to perform the same or better than those from local seed sources in the short term (Schreiber et al. 2013; Kueppers et al. 2017; Martínez-Berdeja et al. 2019; Etterson et al. 2020; Young et al. 2020; Moran et al. 2024; Palik et al. 2024; Marshall et al. 2024). Likewise, we observed high survival of both seed sources at the mid-elevation and high-elevation sites, demonstrating the potential to plant western larch seedlings beyond current seed zones. However, inference from our results is limited by the inclusion of only two seed sources in our study. Our results and those of other studies may partially reflect the fact that current climate conditions are already warmer than the conditions that trees from a given elevation are adapted to and seed zones may not be reflective of changes in climate that have occurred in recent decades (Table 1; McKenney et al. 2009; Palik et al. 2022). At our sites, mean coldest and warmest month temperatures tended to be higher at our high-elevation plots during the study years (2021–2024) than the 30-year average conditions from 1961–1990 at the location where the low-elevation seed source was collected (Fig. S11–12). Between the 1961–1990 period and the 1991–2020 period, mean coldest month temperature increased by over 1 °C and mean warmest month temperature increased by about 0.5 °C in our study sites (Fig. S11–12; Wang et al. 2016).

Western larch is particularly susceptible to spring frost damage because of earlier bud flush than co-occurring evergreen conifers (Schmidt et al. 1976; Roskilly and Aitken 2024). In our study, an important consideration related to cold damage is that when measured just above

the soil surface, the low-elevation plots experienced some of the coldest spring minimum temperatures (Figs. S8 and S13), potentially due to cold-air drainage (Dobrowski 2011), and also the coldest winter minimum temperatures during brief periods when snowpack was lost (Fig. S8). Overwinter mortality tended to be marginally higher for seedlings from the low-elevation seed source than from the high-elevation seed source at the low-elevation plots (Fig. 2), and field observations suggest at least some of the mortality was due to spring frost events. Microclimate sensors confirmed that temperatures as cold as − 5 °C occurred in multiple years in April and May, with temperatures as cold as − 10 °C in some plots in April 2022 (Figs. S8 and S13). However, our electrolyte leakage test did not indicate differences in cold injury between the needles of seedlings from the two seed sources. Although we only tested one freezing temperature regime and cold hardiness varies over time (Timmis et al. 1994; Schreiber et al. 2013; Man et al. 2016), our results agree with those of prior studies. Cold injury in seedlings from many different western larch populations had very weak differentiation between populations and no relation to geographic or climatic variables (Rehfeldt 1995; Roskilly and Aitken 2024), contrary to other temperate conifer species in which cold hardiness exhibits strong population differentiation and climatic clines (Howe et al. 2003; Rehfeldt et al. 2014; Bansal et al. 2015). These findings suggest that while spring frosts may present a risk to western larch seedlings planted outside the current western larch distribution (Sang et al. 2021) or if climate change alters spring frost frequency (Augspurger 2013; Liu et al. 2018), the extent of cold injury between seedlings from different populations may be similar. It is possible that longer-term differences in survival and/or growth may arise in the future, especially with more opportunities for extreme events that could differentially impact trees from the two seed sources (Johnson et al. 2004; Benito-Garzón et al. 2013; St. Clair et al. 2020).

Site conditions beyond microclimate also influenced seedling mortality and growth. Consistent with other studies of shade-intolerant conifer seedlings (Vance and Running 1985; Owen et al. 2020; Hill et al. 2024), canopy cover (including cover from dead branches and snags) had a negative relationship with seedling growth. While we did not detect a strong relationship between canopy cover and seedling mortality over the duration of the study, we found that higher mortality was associated with lower canopy cover in the summer after planting. This suggests that immediately after planting canopy cover can help reduce mortality but the effect declines over time. Generally, low canopy cover is required for western larch seedling recruitment given its shade intolerance (Schmidt et al. 1976; Chen and Klinka 1998), contributing to high rates of western larch recruitment immediately post-fire (Steed and Goeking 2020; Hoecker and Turner 2022; Vieira et al. 2024). However, canopy cover, even from standing snags, can reduce maximum surface temperatures in areas burned by wildfire (Wolf et al. 2021), which may benefit seedlings in hot sites as higher canopy cover has been linked to higher post-fire seedling survival (Clark-Wolf et al. 2022). Importantly, all seedlings in our study were planted on the north side of nurse objects, mostly stumps, logs, and standing snags. Findings for other conifer species suggest that planting near nurse objects increases planted seedling survival due to increased moisture retention and temperature moderation (Hill and Ex 2020; Crockett and Hurteau 2022; Marshall et al. 2023; Marsh et al. 2023). Our results suggest that when a nurse object is present, further shading by standing snags has some benefit in the first growing season, but has limited benefit after that, and may even negatively impact growth. Additionally, around 2% of the planted seedlings were either killed or damaged when the snag they were planted next to fell over, suggesting that logs or stumps may be better nurse objects than standing snags where available.

Fire effects also influenced seedling growth. Seedlings had greater height growth in sites that burned at higher fire severity, as measured by dNBR. While all sites had 100% overstory tree mortality, higher values of dNBR could indicate more severe effects to soils (Moody et al. 2015; Fernández et al. 2021). Faster growth has been observed for up to 13 years for western larch seedlings planted on burned seedbeds compared to unburned seedbeds (Haig et al. 1941; Schmidt et al. 1976). Differences in growth due to fire severity could be related to differences in soil nutrients (Certini 2005), microbiology (Taudiére et al. 2017), water infiltration (Certini 2005), or competing vegetation. For example, severe fires can result in a short-term increase in plant available nitrogen (Smithwick et al. 2005; Dove et al. 2020; Clark-Wolf et al. 2022) which could contribute to higher growth rates. Competition with other vegetation or densely planted seedlings has been shown to reduce planted western larch seedling survival and growth (Rehfeldt 1995; Pinto et al. 2018). However, impacts of fire severity on understory cover are variable and cover can reach pre-fire levels within 2 years post-fire (Fornwalt and Kaufmann 2014). We did not measure plant cover around every seedling in this study, which could contribute to unexplained variability in seedling mortality or growth as vegetation gradually reestablished near seedlings following the initial scalp treatment, which anecdotally reduced cover around the seedling for around 2 years.

While site conditions were the dominant drivers of mortality and growth, individual seedling characteristics

were also influential. For example, seedlings that had lower height to root collar diameter ratios when planted tended to grow faster, consistent with effects of initial seedling size on growth observed in other studies (South et al. 2005; Chen and Nelson 2020). In contrast to other work (Grossnickle 2012; Chen and Nelson 2020; Moran et al. 2024; Villar-Salvador et al. 2026), we did not detect a strong effect of initial seedling size on seedling mortality. Generally, larger seedling diameters are associated with more root mass (Grossnickle 2012; Villar-Salvador et al. 2026), which increases access to soil water and can lead to higher seedling survival when outplanted (e.g., Lopushinsky and Beebe 1976; Burdett 1990; Rose et al. 1997; Grossnickle 2005). However, a recent meta-analysis suggested that the positive effect of seedling size on survival was less significant for bareroot seedlings at dry sites (Villar-Salvador et al. 2026), which describes the conditions of this study. Another possible reason for the limited influence of initial seedling size is that the effect of initial seedling morphology on seedling performance can decline over time as seedlings become more limited by environmental and genetic factors (Pinto et al. 2011). Consistent with these findings, when we modeled mortality during just the first growing season, we saw a stronger, although still only marginally statistically significant, relationship with seedling size, with shorter seedlings associated with higher mortality.

As a small study focused on one species and two seed sources, our project inherently has limitations. First, western larch has less steep geographic or climatic clines than some other widespread conifer species in western North America (Rehfeldt 1995; Roskilly and Aitken 2024) and thus results will likely vary for species with steeper clines. Second, by necessity, we compared seedlings from improved and wild seed, which complicates the interpretation of growth patterns. Further, experiments with wild seed from multiple elevations will be necessary to better compare growth rates of seedlings from seed sources of different elevations. Leveraging existing reforestation projects to ask questions about assisted population migration can help overcome barriers for researchers related to the significant amount of time and resources needed to plant hundreds to thousands of tree seedlings; however, it may also limit the number of seed sources or other factors that are practical to assess compared to more traditional outplanting trials.

Conclusions

Our results contribute a few important findings to the growing literature documenting outcomes of assisted population migration experiments and post-fire reforestation projects. First, we found seedling mortality increased with lower soil moisture and higher maximum temperatures, highlighting the importance of site selection for reforestation projects. Further, for our two seed sources, our results suggest that there may be some benefit of planting lower-elevation seed sources as conditions continue to warm, with limited negative impacts in the short-term of planting seedlings at higher elevations than the seed source location. However, more experiments with more seed sources are necessary to understand if this pattern holds more broadly. Second, our findings are consistent with the fact that the climate in many locations may have changed enough in the past few decades that seed sources from a lower-elevation seed zone may now be better matched to contemporary climate conditions. Third, our study highlights the potential and value of collaborations between researchers and those conducting operational plantings, despite the limitations. These partnerships may help facilitate more realistic experimental designs (e.g., matching real planting operations) and better support longer-term monitoring that together improve our ability to understand the role that assisted population migration can play in preparing our forests for ongoing climate change.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-026-00485-5.

Supplementary Material 1: Supplemental methods and results.

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Authors' contributions

KT Davis: Conceptualization; Investigation; Formal Analysis; Writing – Original Draft Preparation; Writing – review and editing. **JD Gay:** Formal Analysis; Writing – original draft; Writing – review and editing.

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Data availability

Data will be made publicly available in the Forest Service Research Data Archive upon publication: https://doi.org/10.2737/RDS-2026-0025.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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