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Drought conditioning influences conifer seedling height but not survival three growing seasons after planting

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ABSTRACT

Reforestation success in areas impacted by high-severity wildfire and seasonal moisture limitations require nursery-grown seedlings capable of establishing and surviving in harsh environments. Drought conditioning (i.e. restricted irrigation regimes) has the potential to improve planting outcomes, although assessments of effectiveness based on replicated field trials in operational settings are rare. In 2022, we conducted a drought conditioning experiment on second-year stock of ponderosa pine (*Pinus ponderosa*), western white pine (*Pinus monticola*) and two seed sources of western larch (*Larix occidentalis*) using well-watered (control) and water-limited (drought) treatments. Seedlings were outplanted in the spring of 2023 at two sites (a hot/dry, low elevation site and a cool/moist, higher elevation site) within a high-severity burn scar in western Montana, USA. To test treatment effectiveness, we measured seedling survival and height growth over three growing seasons along with pre-dawn water potential in the first growing season. Survival was not affected by drought conditioning ($p > 0.05$); instead, site and seed source explained seedling survival ($p < 0.001$). While ponderosa pine had high survival at both sites, the hot/dry site resulted in high mortality for western white pine and western larch. Average seedling height by the third growing season revealed interesting treatment effects: shorter drought conditioned ponderosa pine (5.6–6.2 cm difference), taller droughted western white pine (6.8 cm difference), and while initially shorter, droughted western larch height converged with control seedlings. Our results highlight the importance of following greenhouse experiments with field trials and the value of monitoring beyond the first growing season.

1. Introduction

Successful tree seedling establishment and natural regeneration are increasingly threatened by shifts in disturbance regimes, including more severe and frequent droughts and increasing wildfire activity. Climate change coupled with a history of fire suppression in the western U.S. has altered fire regimes (Abatzoglou and Williams, 2016) and increased severity (Kreider et al., 2024), frequency (Higuera et al., 2021), and fire season duration (Balch et al., 2022). High-severity, stand-replacing fire can overwhelm forest recovery (Tepley et al., 2017), leading to conversion of forest to non-forest states (Coop et al., 2020; Crausbay et al., 2017). After such fires, seedling establishment in the first few years strongly influences species composition and stand structure (Martínez-Vilalta and Lloret, 2016), which is impacted by distance to mature seed trees (Vieira et al., 2024). Regardless of the presence or absence of fire, seedling recruitment and establishment success is dictated by temperature averages and extremes, timing and amount of precipitation, and soil moisture availability (Davis et al., 2019; Davis et al., 2023; Kolb and Robberecht, 1996; Petrie et al., 2016; Seidel, 1986) suggesting that dry forest regions are increasingly vulnerable (Dodson and Root, 2013; Donato et al., 2016; Kemp et al., 2019; Rother and Veblen, 2016). To facilitate reforestation success in water-limited landscapes, advanced silvicultural techniques are needed to promote adaptation locally and globally (Nagel et al., 2017).

Reforestation efforts that plant native tree seedlings is a strategy to resist transition from forest to persistent non-forest states following high-severity fires (Larson et al., 2022). In recent analyses of reforestable area on Forest Service land in the contiguous U.S., post-fire

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landscapes accounted for 15% in 2007 but increased to 81% after 2017, highlighting the increased need for post-fire revegetation (Dumroese et al., 2019). While there are many challenges to the reforestation pipeline and an increasing amount of area that meet reforestation requirements (Fargione et al., 2021), successful tree planting requires nursery grown seedlings that match the site conditions into which they will be planted (Dumroese et al., 2016). Cultivating stock types for water-limited sites by influencing plant water relations, and carbon acquisition, use, and storage could ultimately promote planted seedling survival and performance (Puértolas et al., 2024).

Drought conditioning is a nursery culturing technique that restricts irrigation during growth phases and is hypothesized to improve survival and performance of seedlings planted on environmentally stressful sites (Grossnickle, 2012; Kozlowski and Pallardy, 2002; Toca et al., 2025). The imposed drought stress can cause morphological and physiological acclimation (i.e. drought memory) expressed as adaptive traits (Toca et al., 2025) that improve stress resistance and establishment (Landis et al., 2010). Experiments provide evidence that culturing techniques may influence plant functional traits to promote drought resistance, although treatment influence varies by species (Ross et al., 2025). Nursery experiments have found that drought conditioning can influence plants' osmotic adjustment (Deligoz and Gur, 2015; Hennessey and Dougherty, 1984; Kandiko et al., 1980; Royo et al., 2001), nonstructural carbohydrates (Ross et al., 2025), ability to maintain high net photosynthesis (Pinto et al., 2023; Seiler and Johnson, 1988), and induce morphological change (Moler and Nelson, 2021; Ross et al., 2025; Royo et al., 2001; Sloan et al., 2020; Vale et al., 2021). While nursery experiments provide valuable insights of morphological and physiological adjustments due to drought conditioning, assessing treatment effectiveness requires operational field trials.

Following nursery experiments with performance-based field trials is the most robust test of effectiveness (Johnson et al., 1986; Landis et al., 2010). Recent meta-analyses of drought conditioning experiments reveal a shortage of long-term field validation (Puértolas et al., 2024; Villar-Salvador et al., 2026). Of those that include a field trial, studies show increased survival (Cregg, 1994; Valliere et al., 2019; van den Driessche, 1992), no effect or decreased survival (Grossnickle et al., 1991; Kitao et al., 2022; O'Reilly et al., 1994; Royo et al., 2001; Villar-Salvador et al., 2013a), and some report improved performance without survival (Johnson et al., 1986; Rook, 1973). Further, few have outplanted seedlings under operational conditions, with several studies instead planting in pots or sand beds (Cregg, 1994; van den Driessche, 1991; van den Driessche, 1992; Villar-Salvador et al., 2013a). Thus, there remains a need for replicated field trials under conditions representative of operational reforestation practices.

Here, we evaluate the effectiveness of a drought-conditioning treatment (i.e., restricted irrigation nursery regime) applied in a greenhouse by assessing multi-year performance and survival of seedlings planted under operational field conditions. We planted seedlings of three conifer species that had been cultured under two irrigation regimes in their second year (Ross et al., 2025): a well-watered control and a water limited drought treatment. While most experiments use first-year seedlings, we explored the use of second-year stock when seedlings have transitioned from relying on primary xylem (during the first year) to more embolism-resistant secondary xylem (Miller and Johnson, 2017). Seedlings were outplanted at two severely burned sites with contrasting environmental stress (relatively hot and dry vs. relatively cool and moist). We sought to answer three questions. Relative to well-watered controls, is there evidence that drought-conditioned seedlings (i) physiologically acclimate via increased plant water potentials, (ii) increase survival, and (iii) exhibit different height growth patterns? We evaluated these questions with measurements from the first three growing seasons after planting.

2. Methods

2.1. Study species and seed sources

Ponderosa pine (*Pinus ponderosa* Lawson & Lawson var. *ponderosa* C. lawson), western white pine (*Pinus monticola* Douglas ex D. Don) and western larch (*Larix occidentalis* Nutt.) are conifer species native to western North America and important for reforestation. Additionally, these species exemplify a gradient of drought vulnerabilities reflecting their ecological niche and disturbance adaptations. Ponderosa pine is considered an extremely drought tolerant species capable of surviving hot, dry sites where other species might fail to establish (Daubenmire and Daubenmire, 1968). Physiological and morphological traits such as high stomatal control, high sapwood-to-leaf ratio, a deep rooting strategy, and ability to deal with low osmotic potentials are some traits that drive survival under dry conditions (Kolb and Robberecht, 1996; Piñol and Sala, 2000).

Western white pine is considered a keystone species of moist northern Rocky Mountain forests, although it has experienced extreme population decline due to timber harvesting, fire exclusion, and, especially, the introduced fungal pathogen white pine blister rust (*Cronartium ribicola*) (Hann et al., 1998; Fins et al., 2001). Western white pine is a moderately shade tolerant (Jain et al., 2004) early seral species with low drought tolerance (Burns, 1990). Although potentially a vulnerable species, western white pine also has traits associated with drought resistance such as a deep rooting strategy and high stomatal regulation potentially leading to physiological plasticity (Robinson et al., 2023) and morphological adaptation (Haig, 1936).

Western larch is a fast-growing deciduous conifer that grows in relatively cool and moist forests with species like western white pine (Burns, 1990). Western larch is considered drought-intolerant in comparison to ponderosa pine (Arno, 1976; Steed and Goeking, 2020). Though western larch exhibits lower stomatal control relative to co-occurring conifers (Zhang and Marshall,1994), this species has mechanisms allowing for survival in dry areas such as high resistance to xylem cavitation (Steed and Goeking, 2020; Piñol and Sala, 2000).

2.2. Seedling preparation and drought conditioning

In March of 2021, seed and seedlings were sourced from the U.S. Forest Service (USFS) Nursery in Coeur d'Alene, Idaho for all seed sources (Table 1). Ponderosa pine, western white pine and western larch 2 were grown in Styrofoam block containers containing 77 cells, each cell being 164 ml in volume (Styroblock 77/170, Beaver Plastics, Acheson, Alberta, Canada) at the University of Montana Memorial Greenhouse in Missoula, Montana. Due to low germination rates of western larch 2, a complement of one-year old western larch seedlings (western larch 1) was purchased. Western larch 1 grew in an operational regime to meet target specifications in Styrofoam block containers containing 112 cells (Styroblock V112105EXT, Stuewe & Sons, Inc, Tangent, OR, USA) at the nursery in Coeur d'Alene. All seedlings were watered using the "manager technique" described by Dumroese et al. (2015) and watered when racks dried down to 70–80% of their container capacity (CC). In preparation for cold storage, all seedlings were exposed to 400 h below 4 °C, packaged in wax boxes and stored below 0 °C from December 2021 to May of 2022. In May, seedlings were thawed for two weeks at 3 °C before being transplanted in preparation for the greenhouse experiment.

In June of 2022, our second-year seedlings were exposed to a drought conditioning experiment in a greenhouse at the University of Montana Environmental Control for Organismal Research facility (Ross et al., 2025; Fig. 1 A). A single container type (TP49 containers, MT49TI trays, Stuewe & Sons, Inc, Tangent, OR, USA) was used to grow seedlings from May until December 2022 (Fig. 1B). Seedlings were grown in trays (16 containers per tray) organized by seed source × irrigation treatment combination (Fig. 1 A). Seedlings were well-watered (80–90% of

Table 1
Summary of total number of seedlings planted at each site (hot/dry or cool/moist) within each treatment (control or drought) along with seed source geographic information. Non-supplemental mass pollination (NSMP) refers to natural pollination versus supplemental mass pollination (SMP).

Seed source	Seed lot origin	Elevation	Seed lot number	Treatment	Hot/Dry (n)	Cool/Moist (n)
Ponderosa pine	Bigfork Timber Improvement Area	1417 m	7741–18-NSMP	Control	84	84
				Drought	86	85
Western white pine	Idaho Panhandle National Forest	655 m	7461–16	Control	88	83
				Drought	87	84
Western larch 1	Kootenai National Forest	1037–1463 m	7663	Control	84	85
				Drought	84	85
Western larch 2	Bigfork Timber Improvement Area	1158 m	7659–14-SMP	Control	44	43
				Drought	44	43

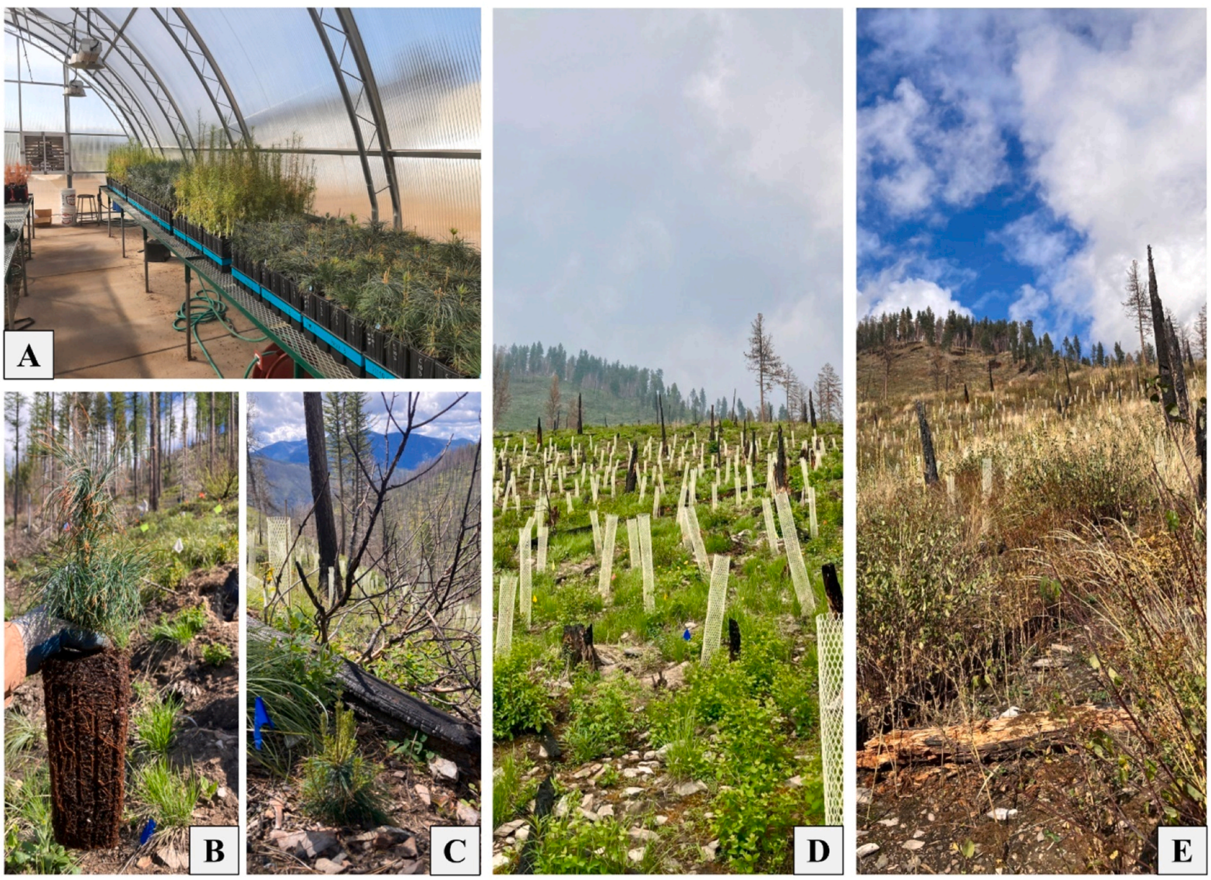

Fig. 1. (A) Seedlings during drought conditioning experiment at the University of Montana Environmental Control for Organismal Research Facility, (B) a ponderosa pine seedling plug about to be planted, (C) a western white pine (control) seedling planted at the cool/moist site, (D) the hot/dry site in May 2023, and (D) the hot/dry at the end of the first growing season in October 2023.

container capacity (CC) using the "scientific technique" described in Dumroese et al., 2015) for the first 2–4 weeks, then successively dried down at increments of 10% to reach their target treatment CC. Racks were randomly assigned an irrigation treatment: a well-watered control (75% CC) or a water-limited drought conditioning treatment (40% CC). Once a target level was reached for half or more of the racks within a treatment group, all racks were irrigated to 100% CC. Fertilizer was applied during irrigation in a manner that resulted in seed sources receiving similar amounts of total nitrogen. A suite of morphological and physiological variables were measured during the greenhouse study (Ross et al., 2025). Summary treatment effects of the greenhouse drought conditioning experiment are reported in Table 2.

In December 2022, all seedlings were irrigated to saturation in preparation for cold storage. Seedlings accumulated 400 h below 4 °C in preparation for storage, given unique identification numbers, removed from containers, and packed in boxes based on treatment. Seedlings were stored below 0 °C from December 2022 until April 2023 at the USFS Coeur d'Alene Nursery.

2.3. Planting site selection

This study was replicated at two sites that burned at high severity in the Thorne Creek Fire on the Lolo National Forest, Montana, USA. Lightning ignited the Thorne Creek Fire on the Plains/Thompson Falls Ranger District on July 7th, 2021. Terrain in the burned area is steep and rocky with elevations ranging from 762 to 2133 m above sea level. The fire burned with varying severity, leaving a mosaic of burn patterns on the landscape that ranged from unburned to areas where the canopy was completely consumed (Fig. 2).

A Reforestation Assessment was conducted by the U.S. Forest Service to evaluate management and post-fire reforestation needs. This assessment was based on overlaying RAVG imagery (Fig. 2) and Regenmapper

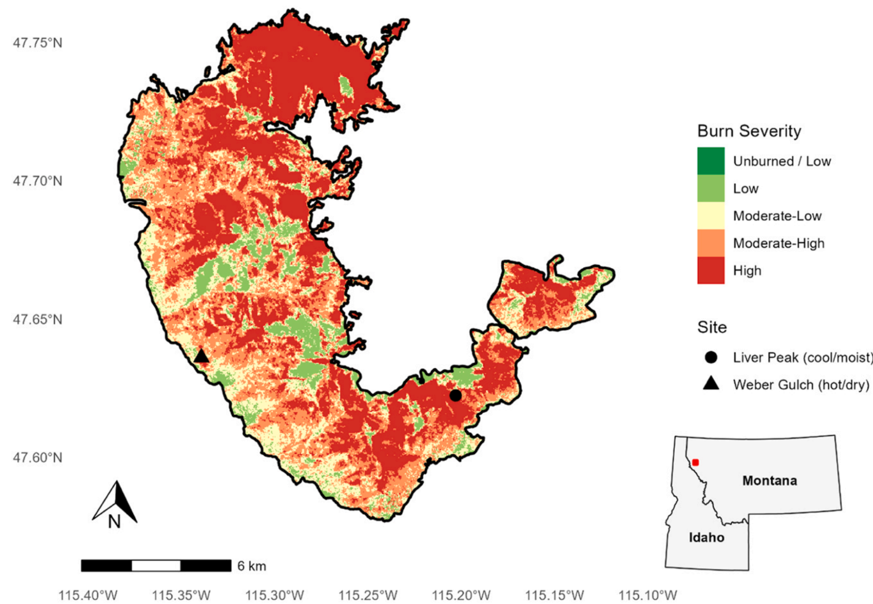

Fig. 2. Rapid initial assessment of post-fire vegetation conditions displayed as burn severity across the 2021 Thorne Creek Fire, Lolo National Forest, Montana, USA. Experimental site locations are indicated (circle = Liver Peak (cool/moist), triangle = Weber Gulch (hot/dry)). Data were provided by the RAVG program and managed by the Geospatial Technology and Applications Center (GTAC, part of the USDA Forest Service Geospatial Office).

(a web-based model used to estimate probability of natural regeneration) to inform post-fire reforestation management (Holden et al., 2022, 2025). Two suitable planting sites were identified based on these analyses with additional consultation from the district silviculturist (P. Collier, personal communication, March 2023). Planting sites were selected at two different elevations within the burned area with differential levels of expected regeneration success. Elevational differences allowed for the inclusion of a hot, dry lower elevation site that was expected to limit regeneration success (Fig. 1D and E) and a cool, moist higher elevation site that typified areas expected to harbor successful reforestation (Fig. 1 C).

2.4. Site descriptions and planting procedure

Weber Gulch, hereafter referred to as the hot/dry site, was identified as a high-severity patch with 100% tree mortality of its mixed-conifer overstory. This site was selected as the low elevation, hot/dry site (47.63855° N, 115.34605° W). It is located on a SW aspect at 1060 m a.s.l. Management history includes a shelterwood harvest with helicopter yarding followed by broadcast burning in 2009. The broadcast burn caused greater than planned overstory tree mortality, resulting in < 1 live tree/ha in the 40-ha area surveyed after the broadcast burn. An assessment conducted 3 years later found less than 10 seedlings had naturally regenerated in the examined area, which was attributed to the harsh SW exposure and competing vegetation. The site burned again in the 2021 Thorne Creek wildfire. Surrounding forest composition was dominated by ponderosa pine and Douglas-fir (*Pseudotsuga menziesii* var. *glauca)* with a small population of western larch within about 150 m of the planting site. Soils at this site were classified as Vision-Lick families complex with stony, colluvial aprons and alluvial fans (Soil Survey Staff, 2026).

Liver Peak, hereafter referred to as the cool/moist site, was identified as a high-severity patch, although some live overstory western larch trees remain adjacent to the planting area. This site occupies a SW aspect (47.63040° N, 115.20821° W) positioned at 1548 m a.s.l. Management history included regeneration harvest followed by broadcast burning and planting of ponderosa pine, western white pine, and western larch in 2006. The site then burned in the 2021 Thorne Creek wildfire. Surrounding forest composition was dominated by western larch and Douglas-fir, with scattered individuals of ponderosa pine, lodgepole pine (*Pinus contorta* ssp. *latifolia*), and western white pine. Soils at this site were classified as Beeskove-Bendahl-Foyslake families complex with moderately steep mountain slopes (Soil Survey Staff, 2026).

Seedlings were outplanted on 24 April 2023 at our hot/dry site and on 16 May 2023 at our cool/moist site due to later snowmelt at upper elevations. Seedlings of a given seed source × treatment combination were planted in a single randomly assigned row per block, resulting in 8 rows per block (4 seed sources × 2 treatments). This planting design was replicated in 4 blocks at each planting site. Seedlings were hand-planted with tree planting shovels at 1.8 m spacing for all seed sources except western larch 2 which had lower seedling-level replication (Table 1) and was therefore planted at 3.7 m spacing to cover the same spatial footprint within blocks as other seed sources. Mesh seedling protectors were installed around each seedling (Rigid Seedling Protector Tubes, 17040/17041, Forestry Suppliers, Inc, Jackson, MI, USA) due to heavy ungulate browsing in the area.

2.5. Edaphic and atmospheric monitoring

Air temperature, precipitation, and soil moisture were monitored from planting (April or May 2023) until October 2025 (Fig. 3). Both sites were equipped with weather stations and sensors connected to data loggers. Soil sensors (TEROS 11, METER Group Inc., Pullman, WA, USA) were placed at two depths of −15 and −25 cm to measure soil temperature and volumetric water content. Additionally, soil matric potential was collected (TEROS 21, METER Group Inc., Pullman, WA, USA) at a depth of −20 cm. Data was recorded hourly with data loggers (ZL6, METER Group Inc., Pullman, WA, USA). Atmospheric data was also collected hourly using a weather station (ATMOS 41, METER Group Inc., Pullman, WA, USA) that measured temperature and precipitation 50 cm above ground level.

2.6. Field measurements

Pre-dawn water potential was measured using a pressure chamber (Scholander PMS Instrument, Corvallis, OR, USA) on a branch of one seedling in each species × treatment combination per block (n = 4 seedlings per treatment × site × seed source combination) in June 2023

Table 2
Summary of treatment effects for variables measured during the greenhouse experiment for all seed sources (Ross et al., 2025). Arrows (↓↑) indicate direction of significant change ($p < 0.05$) for the drought treatment compared to control. A dash (–) indicates no data collected while 'n.s.' indicates no significant difference. Peak summer (August/September 2022) measurements included pre-dawn and mid-day water potentials (MPa), photosynthesis (A) (μmol/m^{2}s), transpiration (E) (mol/m^{2}s), and stomatal conductance (gsw) (mol/m^{2}s) measured at saturated (100%) container capacity or at target (40% or 70%) container capacity. Post-treatment (December 2022) measurements included height (cm), root-collar diameter (mm), root:shoot ratio, root mass (g), shoot mass (g), and nonstructural carbohydrates (NSCs) (mg·g^{-1}).

Ponderosa pine	Western white pine	Western larch 1	Western larch 2	Response variable	Collection period
n.s.	↓	↓	↓	Height	Post-treatment
n.s.	↓	↓	↓	Root-collar diameter	
n.s.	n.s.	n.s.	n.s.	Root:shoot	
n.s.	n.s.	↓	n.s.	Root mass	
n.s.	n.s.	↓	↓	Shoot mass	
↓	n.s.	n.s.	–	Pre-dawn water potential (target)	Peak summer
n.s.	n.s.	n.s.	–	Mid-day water potential (target)	
n.s.	↑	n.s.	n.s.	A (saturated)	
↓	↓	↓	↓	A (target)	
n.s.	n.s.	n.s.	n.s.	E (saturated)	
↓	↓	↓	↓	E (target)	
n.s.	n.s.	n.s.	n.s.	gsw (saturated)	
↓	↓	↓	↓	gsw (target)	
n.s.	↑	–	–	Total needle NSCs	Post-treatment
n.s.	↑	–	–	Needle soluble sugars	
n.s.	↑	n.s.	n.s.	Stem soluble sugars	
↓	n.s.	n.s.	n.s.	Total root NSCs	
n.s.	n.s.	↓	n.s.	Root soluble sugars	

and August 2023. Sample sizes in the August measurement decreased due to mortality at the hot/dry site for some seed sources.

Survival assessments were conducted in June 2023, August 2023, October 2023, October 2024, and October 2025 where seedlings were assessed and recorded as live or dead. All live seedling heights were measured (measured from root-collar to terminal bud) in August 2023, October 2024, and October 2025.

2.7. Statistical analysis

All statistical analyses were conducted using R statistical software (R Core Team, 2025; version 4.1.2). Seedling performance responses (pre-dawn water potentials and height) were modeled with linear mixed effect models (LMMs) using the 'lme4' package while seedling survival analyses used generalized linear mixed models (GLMMs) with the 'glmmTMB' package. Model significance of fixed effects was assessed using a Type III ANOVA via the 'car' package, which tests fixed effects based on Wald Chi-square statistics. We inspected all models – residuals, collinearity, and dispersion– using the 'performance' and 'DHARMa' packages in R. If significant effects or interactions were detected, estimated marginal means and pairwise comparisons were examined using the 'emmeans' package.

Pre-dawn water potentials were analyzed to compare and quantify plant moisture stress between treatments and to capture site differences. Treatment (control or drought), site (hot/dry or cool/moist), and initial height (height at planting) along with the interaction between treatment and seed source were included as fixed effects. Height of surviving seedlings were included in the height analysis at each survey date (August 2023, October 2024, October 2025). Fixed effects included treatment, site, and initial height as well as interaction terms between treatment and site, and seed source and site. A random effect term to account for rows nested within blocks was included along with block in our height LMMs, whereas solely block was included as a random effect in pre-dawn water potential LMMs.

To analyze if drought conditioning affected seedling survival, GLMMs were fit for each end of season survey (October 2023, October 2024, October 2025) including all seed sources. Models explored how treatment, site, initial height, and the interaction of seed source with treatment influenced cumulative (i.e., planting to assessment date) survival. A random effect term to account for rows nested within blocks was included along with block. Further, the binary nature (live or dead) of this data allowed for the quantification of proportion surviving of each row and the use of a binomial logit-link function.

3. Results

3.1. Edaphic and atmospheric conditions

Environmental conditions differed strongly and in the expected direction between our two planting sites (Fig. 3). In 2023, the hot/dry site accumulated 224 mm of precipitation during the growing season (April-October 2023). Over this growing season, the hot/dry site had average temperatures of 16 °C (min = −9 °C, max = 40 °C). In comparison, the cool/moist site accumulated 280 mm of precipitation in 2023 and had average temperatures of 15 °C (min = −12 °C, max = 34 °C). Conditions led to minimum soil matric potentials of −5.7 MPa at the hot/dry site and −0.8 MPa at the cool/moist. In 2024, the hot/dry site accumulated 241 mm of precipitation during the second growing season (April-October 2024). This site had average temperatures of 14 °C (min = −4 °C, max = 40 °C). The wet/moist site accumulated 264 mm of precipitation with average temperatures of 7 °C (min = −34 °C, max = 34 °C). Conditions led to minimum soil matric potentials of −3.5 MPa at the hot/dry site and −1.2 MPa at the cool/moist. The final growing season of 2025 experienced some sensor issues resulting in data gaps at the cool/moist site. Please see Fig. 3 for general 2025 environmental conditions.

3.2. Pre-dawn water potentials (MPa)

Pre-dawn water potentials of seedlings were primarily influenced by site, with seedlings planted at the cool/moist site exhibiting higher water potential than the hot/dry site in both June and in August 2023 (Table S1; $p < 0.001$). June pre-dawn water potentials at both sites for all seed sources exhibited high values of around −0.5 MPa (Fig. 4). Results from the model in August for the cool/moist site indicated no significant treatment effect (Table S1; $p = 0.319$), but drought conditioned seedlings maintained apparently higher median pre-dawn water potentials than control seedlings (Fig. 4). Examining August 2023 pre-dawn water potentials at the hot/dry site proved difficult due to the high mortality rates leading to an unbalanced sampling design.

3.3. Survival

The drought conditioning treatment did not affect survival at any survey date for any seed source (Table S2; $p = 0.608$, 0.313, 0.376). Seedling survival was strongly dependent on seed source (Table S2; $p < 0.001$) and site (Table S2; $p < 0.001$) at each date whereby survival odds were significantly higher for a seedling planted at the cool/moist site. Ponderosa pine had the highest survival rates for both treatments

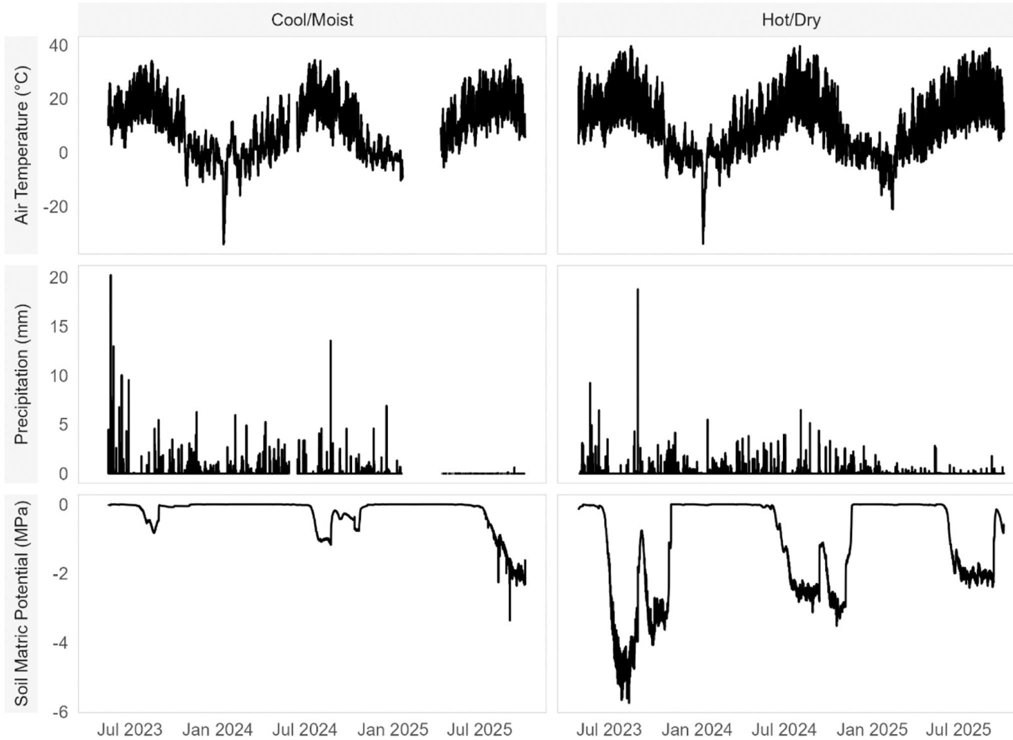

Fig. 3. Air temperature (°C), precipitation (mm) and soil matric potentials (MPa) over three growing seasons (April 2023-October 2025). Values for soil matric potential represent averages from three soil sensors at the cool/moist site and two at the hot/dry. Technical issues at the cool/moist site resulted in data gaps between January 2025 and July 2025.

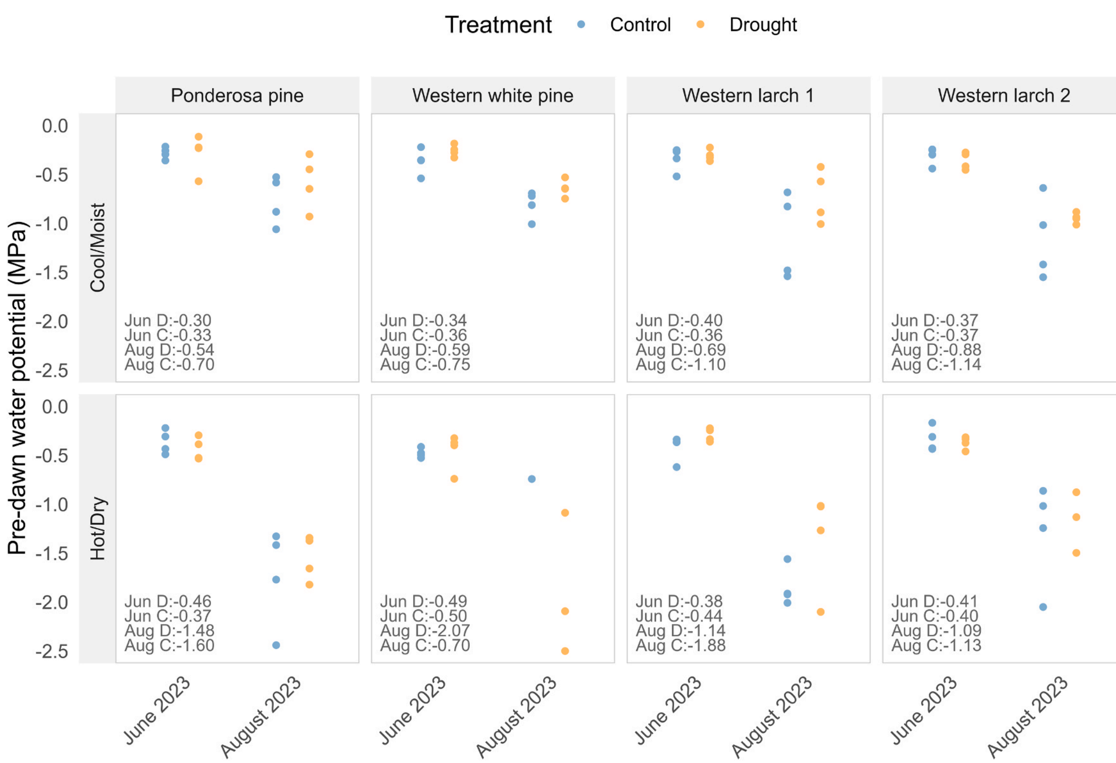

Fig. 4. Pre-dawn water potentials (MPa) of branch tissue measured at establishment (June 2023) and during peak summer drought conditions (August 2023) for both treatments and all seed sources. Text indicates median pre-dawn water potential values for each survey date and treatment.

and both sites (Fig. 5) maintaining 100% survival at the cool/moist and above 75% at the hot/dry site. Western white pine also maintained nearly 100% survival for both treatments at the cool/moist site but experienced high mortality rates at the hot/dry site. This site-specific trend also applied to both seed sources of western larch, although these seed sources experienced more mortality at the cool/moist site than either *Pinus* species (Fig. 5).

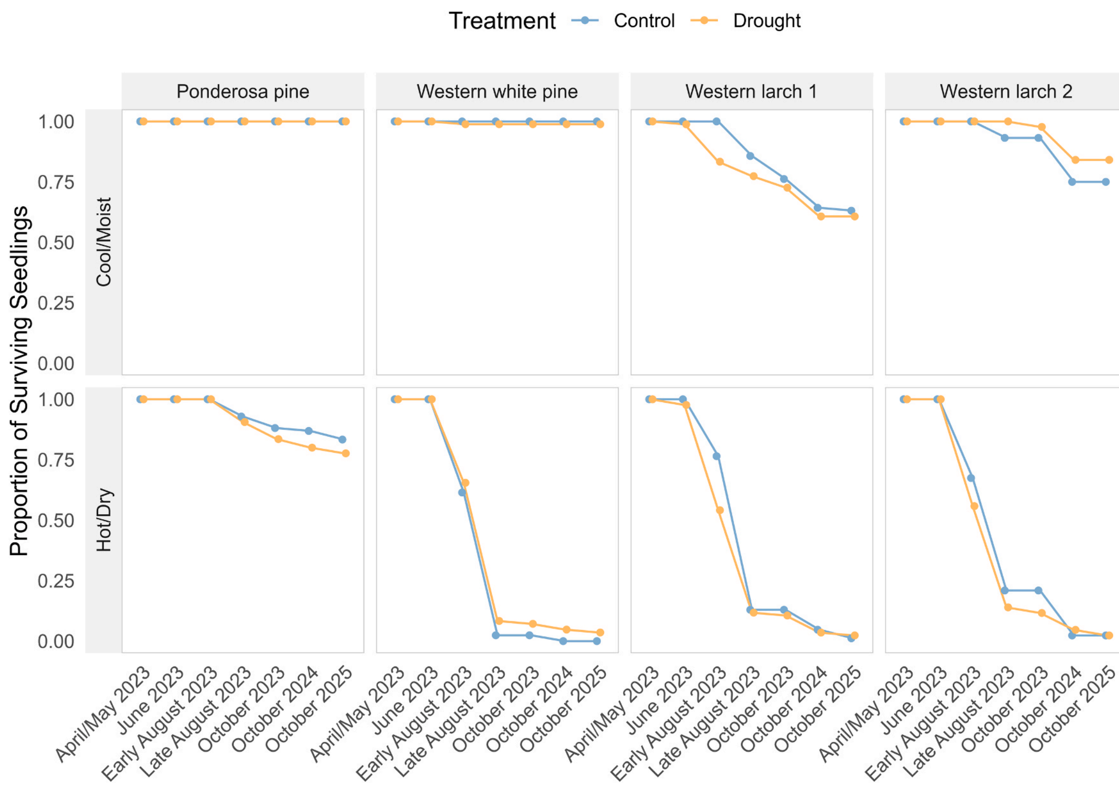

Fig. 5. Proportion of surviving seedlings at both sites (cool/moist and hot/dry) for all four seed sources. Survey dates span from planting date (April/May 2023) until October 2025. Note that x-axis spacing does not scale with measurement intervals.

3.4. Height

The drought conditioning treatment influenced height of surviving seedlings in August 2023 (Table 3; $p < 0.001$) and marginally in October 2025 (Table 3; $p = 0.070$). These effects also varied significantly by seed source at each survey date (Table 3; $p = <0.001, 0.002, 0.007$) along with the interaction between treatment and seed source (Table 3; $p = 0.001, <0.001, 0.031$). While treatment responses differed between seed sources, treatment responses did not differ between sites (Table 3; $p = 0.196, 0.419, 0.905$). Results from the ANOVA revealed that along with site, initial height at planting was also highly significant (Table 3; $p < 0.001$).

Although drought conditioned ponderosa pine seedlings had similar heights at planting (Table 2), height trends show that droughted seedlings were generally shorter than control seedlings throughout time (Fig. 6). Pairwise comparisons of estimated marginal means found that droughted ponderosa pine at both the hot/dry and cool/moist site were significantly shorter than controls in August 2023 (Table S3; $p = 0.002$, $p = 0.050$) and remained shorter in October 2025 (Table S3; $p = 0.084$, $p = 0.098$).

Drought conditioned western white pine seedlings were statistically similar in August of 2023 at both the hot/dry and cool/moist site, respectively (Table S3; $p = 0.890$, $p = 0.180$). However, at the cool/moist site droughted western white pine seedlings were 5.5 cm taller than controls in October 2024 (Table S3; $p = 0.055$) and 6.8 cm taller than controls in October 2025 (Table S3; $p = 0.055$).

Drought conditioned western larch 1 seedlings were significantly shorter than controls at both sites in August 2023 (Table S3; $p < 0.001$, $p = 0.010$) and in October 2024 at the cool/moist site (Table S3; $p = 0.002$). Mortality overrode these differences at the hot/dry site in October 2024 for western larch 1 (Table S3; $p = 0.130$). By October 2025, western larch 1 seedlings at the cool/moist site were not statistically different in height (Table S3; $p = 0.240$). Western larch 2 treatment comparisons proved statistically insignificant throughout survey dates (Table S3).

Table 3
Seedling height type III ANOVA (Wald chi-square test) for each LMM at each survey date (August 2023, October 2024, October 2025). Bolded p-values indicate significance ($p < 0.05$).

	August 2023			October 2024			October 2025		
Fixed effects	Chi-sq	Df	p-value	Chi-sq	Df	p-value	Chi-sq	Df	p-value
Treatment (Drought)	10.84	1	**< 0.001**	0.52	1	0.472	3.27	1	0.070
Seed source	126.65	3	**< 0.001**	14.62	3	**0.002**	11.96	3	**0.007**
Site	8.23	1	**< 0.001**	11.53	1	**< 0.001**	**7.01**	**1**	**0.008**
Initial height	1256.96	1	**< 0.001**	177.97	1	**< 0.001**	87.33	1	**< 0.001**
Treatment:Seed source	14.79	3	**< 0.001**	18.19	3	**< 0.001**	8.88	3	**0.031**
Treatment:Site	1.67	1	0.196	0.65	1	0.419	0.01	1	0.904
Seed source:Site	34.31	3	**< 0.001**	3.17	3	0.366	5.77	3	0.124

4. Discussion

4.1. Effect of drought conditioning on seedling survival

Our drought conditioning treatment did not affect seedling survival, in agreement with recent meta-analyses (Villar-Salvador et al., 2026). Instead, site and seed source (species) had significant impacts on seedling survival. The influence of site on seedling survival has long been recognized (Del Campo et al., 2007; Hobbs, 1992). We saw a clear divergence in outcomes for western white pine and western larch: high survival rates at our cool/moist site contrasted sharply with low survival rates at the hot/dry site. While both sites had access to adequate soil moisture during establishment (June 2023), August 2023 soil matric potentials (Fig. 3) and pre-dawn water potentials (Fig. 6) exceeded lethal thresholds and caused mass mortality of these two species at the hot/dry site. On this environmentally stressful site, high surface temperatures and summer drought exceeded the hydraulic safety margins of western white pine and western larch (Burns, 1990; Zhang et al., 2021). The association between south facing slopes and soil temperatures resulting in mortality is widely recognized, especially for western larch (Chen et al., 2025; Schmidt et al., 1976). While our research study design led to high mortality for western larch and western white pine, it is worth noting that operationally, these species would not have been planted at the hot/dry site due to the harsh, SW aspect (though there is a native, regenerating larch population within about 150 m of the planting site on locally flat terrain). The inclusion of a third site of intermediate environmental stress may have helped reveal treatment effects in western white pine and western larch.

Although drought conditioning did not affect seedling survival, the ability for ponderosa pine to maintain high survival at the hot/dry site with soil matric potentials of −5 MPa is extraordinary. While some reports have argued that older 2 + 0 stock like we use are likely to encourage an imbalanced shoot-to-root ratio and thereby increase vulnerability to drought (Villar-Salvador et al., 2026), our 2 + 0 ponderosa pine stock and container selection seemed to have allowed for an optimal ratio (1.33; Ross et al., 2025) for both the hot/dry and cool/moist sites. While balancing shoot-root attributes have long been identified (Burdett et al., 1983), a recent paper proposed optimal values for shoot-root ratios for hot, dry sites of western North America along with the recommendation of deep growing containers (Grossnickle and MacDonald, 2026). These researchers recommend shoot-root ratios of 1–2 for hot, dry sites along with deep root plugs of 20–25 cm. All our seedlings fall within this drought-avoiding stocktype recommendation (24.1 cm container depth; TP49 containers, Stuewe & Sons, Inc, Tangent, OR, USA).

The lack of treatment effect for ponderosa pine survival is not surprising due to morphologically equivalent seedlings at planting with regards to height, root-collar diameter, shoot-to-root ratio, root mass and shoot mass (Table 2). Drought conditioning has been reported to increase survival with planting site aridity, but that effect depends on the species' inherent drought tolerance (Puértolas et al., 2024; Toca et al., 2025; Villar-Salvador et al., 2026) as well as the duration and intensity of the drought treatment (Toca et al., 2022). Ponderosa pine seems to have achieved hydraulic equilibrium with a low shoot-to-root ratio, opportunistic use of moisture availability at establishment, and highly responsive stomata (Piñol and Sala, 2000) resulting in biomass accumulation and survival (Pinto et al., 2023; Zhang et al., 1996, 1997) at both sites.

The traits measured and influenced by our greenhouse experiment did not confer a survival benefit for western white pine. Our greenhouse experiment resulted in significant morphological and physiological differences although effectively similar shoot-to-root ratios (Table 2). In addition, western white pine accrued measurable traits by the end of the greenhouse drought conditioning treatment that could hypothetically improve survival and establishment (increased root mass and enriched needle NSC's; Table 2). Instead, we saw nearly 100% survival of both treatments of western white pine at our cool/moist site and no significant treatment effect. The climatic environment of this cool/moist site seems to match well with our nursery grown stocktype with regards to shoot-to-root ratios along with the seed source used (Table 1). A

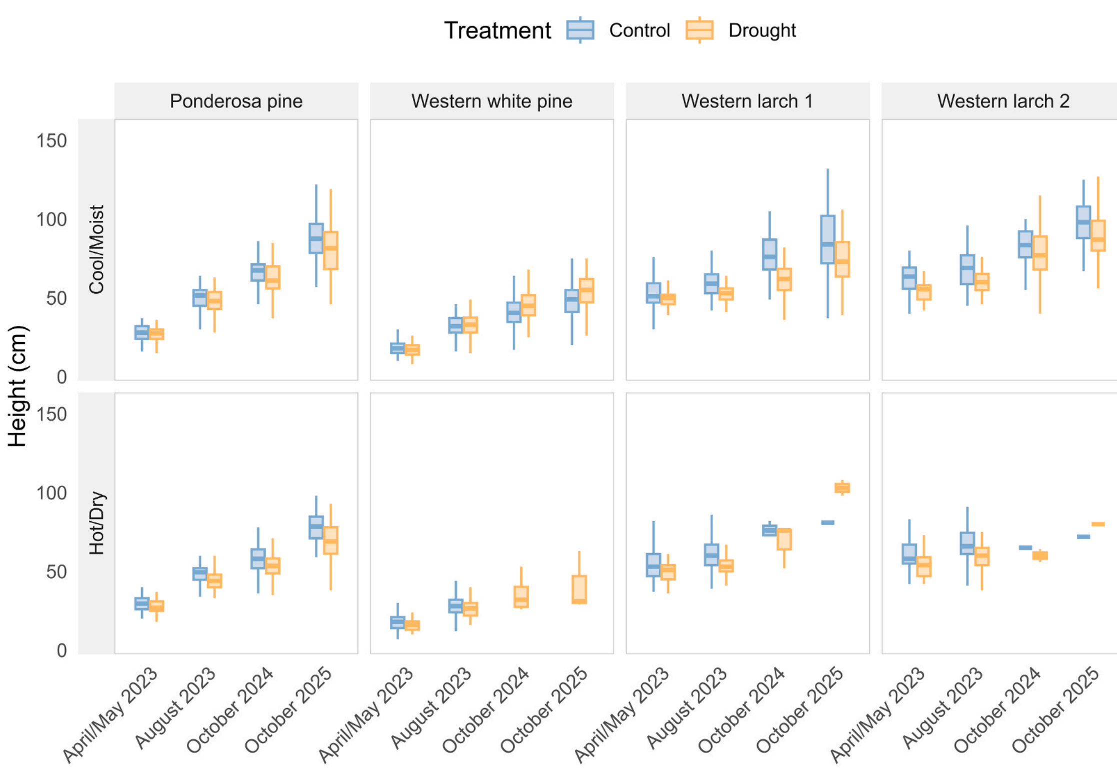

Fig. 6. Height (cm) of all surviving seedlings at each survey date. Boxplots display treatment distributions with horizontal lines as median values, boxes extend from 25th percentile to the 75th percentile while vertical lines denote the most extreme values within 1.5 interquartile range of the 25th and 75th percentile.

noteworthy legacy of our experimental study design is that we effectively moved our western white pine seed source from its original seed zone of 655 m (Table 1) to 1548 m, a 893 m transfer. Evaluating the effects of nursery growing regimes and resulting stocktype while matching seed source to future climates (Bower et al., 2024; McKenney et al., 2009) will be important when engaging in reforestation adaptation strategies.

Similar to western white pine, drought conditioning western larch did not improve or reduce survival. Growth patterns (slow or fast) reflect trade-offs between survival and growth (Reich, 2014) whereby plants with rapid growth often have higher rates of mortality than slow growing species (Rose et al., 2009). Western larch is a fast-growing conifer that was particularly sensitive to our drought treatment and resulted in seedlings that were significantly shorter, smaller in root-collar, and with generally less root mass and shoot mass (Table 2). The resulting drought conditioned western larch seedlings, while morphologically different, had similar shoot-to-root ratios at planting. Results from our study imply that adequate soil moisture was accessed in each treatment, prompting evaluation of the significance of deep pots. Recent analyses concluded that large seedlings within the same species and age increase outplanting survival globally (Andivia et al., 2021; Puértolas et al., 2024). Establishing roots and adequate root architecture is critical for seedling survival (Grossnickle, 2005a; Grossnickle, 2012; Padilla and Pugnaire, 2007), a process potentially aided by our container type.

4.2. *Effect of drought conditioning on seedling height*

Initial seedling height (height at planting) can forecast growth (Grossnickle 2005b; Pinto et al., 2011). Rapid and sustained height growth following planting is crucial for seedlings due to competing vegetation and need for light (Hobbs, 1992; Grossnickle and MacDonald, 2018; Rose and Ketchum, 2003). Drought conditioning generally reduces seedling size (Puértolas et al., 2024; Toca et al., 2022; Villar-Salvador et al., 2026) while also shifting biomass allocation (Toca et al., 2025). Reductions specifically regarding height and root-collar diameter have been reported in response to drought conditioning (Deligoz and Gur, 2015; Pinto et al., 2023; Royo et al., 2001; Ross et al., 2025), with increases in root development (Moler and Nelson, 2021; Vale et al., 2021) in conifer species. The long-term nature of our dataset provides interesting insights with regards to the direction and magnitude of height growth increments after drought conditioning. While ponderosa pine and western white pine experienced persistent treatment effects on height growth due to the drought treatment, western larch treatment groups converged over time indicating more rapid growth in drought treated seedlings.

Drought conditioned ponderosa pine seedlings experienced a reduction in height increment once outplanted. Interestingly, our greenhouse experiment resulted in ponderosa pine seedlings with similar shoot heights (Table 2; Ross et al., 2025). This shoot-growth conserving strategy displayed by drought conditioned ponderosa pine seedlings points to potential drought-memory (Toca et al., 2025) and a trade-off between growth and resistance to drought and high temperatures (Kerr et al., 2015). While our drought conditioned ponderosa pine seedlings experienced a 11.9% (hot/dry) and 5.6% (cool/moist) reduction to height growth compared to control seedlings by the end of the third growing season, whether this reduction will impact long-term seedling survival or competitive interactions remains to be seen. In general, seedlings of shorter or intermediate heights (10–25 cm) are recommended for hot, dry reforestation sites as they have less photosynthetic surface area vulnerable to transpiration water loss (Grossnickle and MacDonald, 2026). Additionally, on the slow-fast continuum, slower growing seed sources of *Pinus sylvestris* were found to be more drought tolerant (Cregg and Zhang, 2001). If drought conditioned seedlings can partition growth to roots while minimizing leaf mass area, long-term performance could be improved with drought conditioning.

Drought conditioned western white pine seedlings displayed an impressive height growth increment that surpassed controls by the end of the second season, widening even further to 11.9% difference by October 2025. Western white pine has been observed to possess the potential for high levels of physiological (Robinson et al., 2023) and phenological plasticity (Chuine et al., 2006). Chuine et al. (2006) found that shoot elongation in western white pine was determined by the number of internodes set from the previous growing season. Drought conditioned Douglas-fir seedlings expressed drought memory through earlier bud break and higher biomass allocation to new foliage (Toca et al., 2025). It is possible the treatment primed seedlings with enriched needle nonstructural carbohydrates (Ross et al., 2025), enabling a sustained carbon assimilation feedback loop. Potential increases of internodes, prompt use of available water during establishment, and high rates of photosynthesis could lead to early bud break (longer growing window) and energy for greater shoot elongation. While we did not assess metrics related to phenology, the demonstrated increased height growth could improve performance with relation to competition (Robinson et al., 2022). While there is a possibility that rapid growth reduces cold tolerance (Rehfeldt, 1980; Rehfeldt et al., 1984), these seedlings survived temperatures as low as −34°C at the cool/moist site. This surprising result highlights the importance of long-term field trials.

By the third growing season, western larch seedling height differences converged across treatments. Yet at planting, drought conditioned western larch seedlings were shorter than control seedlings (Table 2). This convergence in heights indicates increased growth rates in drought treated western larch seedlings. As the fastest growing conifer in the Inland Northwest (Parent and Mahoney, 2008), and a seral species significantly impacted by competition (Pinto et al., 2018), shoot growth is crucial for survival. In milder areas, like the cool/moist site, higher growth rates could increase performance by enhancing competitive ability (Onofrio et al., 2021). In provenance and common garden trials on height growth in western larch, researchers have found low population differences, suggesting a reliance on phenotypic plasticity over local adaptation (Roskilly and Aitken, 2024). Simultaneously, tree breeding programs selecting for enhanced growth in western larch have not been found to reduce drought resistance (Roskilly et al., 2025). Studies have found that the most influential predictors of height growth for planted western larch seedlings are initial seedling height (Chen and Nelson, 2020), soil temperature, and aspect (Chen et al., 2025). These findings call into question the ideal target stocktype for western larch, which traits are most important for seedling survival and performance, all while highlighting the importance of site selection for this species.

4.3. *Effect of drought conditioning on plant water status*

Our study was designed to include two sites with strongly contrasting environmental stress, to ensure planted seedlings were challenged by drought. Our sites proved to significantly affect plant water status with higher values (i.e., less moisture-stress) at our cool/moist site compared to the hot/dry site. Though mortality resulted in smaller sample sizes for some species, there is some evidence of physiological acclimation in drought conditioned seedlings provided by our pre-dawn water potential data (Fig. 4). Johnson et al., (1986) postulated that an osmotic adjustment greater than −0.3 MPa is probably significant enough to affect seedling performance. Drought conditioned seedlings at the cool/moist site appeared to have higher pre-dawn water potential than controls (Fig. 4), although not statistically significant. Plants are capable of osmotically adjusting in many ways including through the accumulation of osmo-protectant solutes (Kozlowski and Pallardy, 2002) and soluble sugars (Martínez-Vilalta and Garcia-Forner, 2017), or by developing roots deeper in the soil profile (Cregg and Zhang, 2001). Future assessments on planted seedling water status under field conditions should be a priority to further inform the effect of drought conditioning.

4.4. Implications for future research and adaptive management

Our experimental evidence is not compelling enough to advocate for widespread adoption of drought conditioning as an operational nursery practice. However, our results are promising enough that we encourage continued basic ecophysiology research as well as practical applied research to evaluate drought conditioning effectiveness relative to a wider range of reforestation techniques, such as seedlings of varying ages and container sizes.

Common nursery practice is to outplant seedlings at the end of the first cultivation season, but there have been confounding perspectives on whether an older/larger seedling would increase (Cuesta et al., 2010; Pinto et al., 2011; Pinto et al., 2012) or reduce survival (Rose et al., 1993; Trubat et al., 2011) on dry sites. Grossnickle and MacDonald (2026) have concluded that shoot-to-root ratios of 1–2 along with deep pots are best for harsh sites. While studies have shown strong correlation between seedling size and increasing seedling container volume (Carlson and Endean, 1976; Dominguez-Lerena et al., 2006; Sutherland and Day, 1988), our ability to disentangle the effect of using older, second-year stock and the use of large growing containers, is impossible to parse apart due to the study design. To disentangle this effect, we recommend field trials that compare drought treatments with both 1 + 0 and 2 + 0 seedlings grown in the same container. Such a design would provide important information about the relative effect size (and cost effectiveness) of nursery conditioning experiments while refining stocktypes for environmentally constrained outplanting sites.

Planting trials under field conditions are the ultimate assessment of treatment effectiveness and we have demonstrated the importance of monitoring beyond the first growing season. Operational field trials are an important opportunity for partnerships between researchers and forest managers using active adaptive management (Larson et al., 2013). Long-term (decadal scale) field trials are needed to evaluate if our observed treatment effects on height persist, and if they are ecologically and operationally meaningful over time scales relevant to forest structural development, and to management objectives like habitat development and wood fiber production. Modeling studies may help explore these questions over the short term while empirical data accumulate.

5. Conclusion

Post-fire landscapes under future and current climates face a gradient of recovery trajectories, especially for large-high severity fires that burn topographically diverse terrain like the Throne Creek wildfire. Our field study revealed intriguing effects of drought conditioning on three ecologically and economically important conifer species native to western North America. Drought conditioning did not significantly affect planted seedling survival, in agreement with current reviews and meta-analyses of global literature (Toca et al., 2022; Villar-Salvador et al., 2026). However, we found effects on seedling height growth over three growing seasons, and those effects differed across species. Results from our study indicate that land managers can use planting to resist ecosystem change and meet management objectives in areas vulnerable to regeneration failure, and that drought conditioning can influence seedling performance over multiple growing seasons after planting.

CRediT authorship contribution statement

Jeremiah R. Pinto: Writing – review & editing, Resources, Methodology, Funding acquisition, Conceptualization. **Andrew J. Larson:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization. **David L.R. Affleck:** Writing – review & editing, Formal analysis, Data curation. **Justin S. Crotteau:** Writing – review & editing, Resources, Methodology, Conceptualization. **Anna C. Ross:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization.

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Declaration of Competing Interest

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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.2026.123825.

Data availability

Data will be made available on request.

References

Abatzoglou, John T., Williams, A.Park, 2016. Impact of anthropogenic climate change on Wildfire across Western US Forests. Proc. Natl. Acad. Sci. 113 (42), 11770–11775. https://doi.org/10.1073/pnas.1607171113.

Andivia, Enrique, Villar-Salvador, Pedro, Oliet, Juan A., et al., 2021. Climate and species stress resistance modulate the higher survival of large seedlings in forest restorations worldwide. Ecol. Appl. 31 (6), e02394. https://doi.org/10.1002/eap.2394.

Arno, Stephen F. 1976. *The Historical Role of Fire on the Bitterroot National Forest*. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.

Balch, Jennifer K., John T. Abatzoglou, Maxwell B. Joseph, et al. “Warming Weakens the Night-Time Barrier to Global Fire.” *Nature* 602, no. 7897 (2022): 442–48.

Bower, Andrew D., Katie L. Frerker, Carolyn C. Pike, et al. 2024. “A Practical Framework for Applied Forestry Assisted Migration.” *Frontiers in Forests and Global Change* 7 (October). https://doi.org/10.3389/ffgc.2024.1454329.

Burdett, A.N., Simpson, D.G., Thompson, C.F., 1983. Root development and plantation establishment success. Plant Soil 71 (1), 103–110. https://doi.org/10.1007/BF02182645.

Burns, R.M., United States Forest Service, 1990. Silvics of North America. U.S. Department of Agriculture, Forest Service.

Carlson, L.W., Endean, F., 1976. The effect of rooting volume and container configuration on the early growth of white spruce seedlings. Can. J. For. Res. 6 (2), 221–224.

Chen, Cen, Nelson, Andrew S., 2020. Growth and mortality of planted interior douglas-fir and western larch seedlings during the establishment phase in Idaho, USA. For. Ecol. Manag. 474 (October), 118386. https://doi.org/10.1016/j.foreco.2020.118386.

Chen, Cen, Reely, Jacob A., Nelson, Andrew S., 2025. Early field performance of three planted inland northwest conifer species: effects of root growth potential, morphology, and environmental conditions. For. Ecosyst. 12 (April), 100280. https://doi.org/10.1016/j.fecs.2024.100280.

Chuine, Isabelle, Rehfeldt, Gerald E., Aitken, Sally N., 2006. Height growth determinants and adaptation to temperature in pines: a case study of *Pinus contorta* and *Pinus monticola*. Can. J. For. Res. 36 (5), 1059–1066. https://doi.org/10.1139/x06-005.

Coop, Jonathan D., Parks, Sean A., Stevens-Rumann, Camille S., Crausbay, Shelley D., Higuera, Philip E., Hurteau, Matthew D., Tepley, Alan, et al., 2020. Wildfire-driven forest conversion in western North American landscapes. BioScience 70 (8), 659–673.

Crausbay, Shelley D., Higuera, Philip E., Sprugel, Douglas G., Brubaker, Linda B., 2017. Fire Catalyzed rapid ecological change in lowland coniferous forests of the Pacific

Northwest over the past 14,000 years. Ecology 98 (9), 2356–2369. https://doi.org/10.1002/ecy.1897.

Cregg, B.M., 1994. Carbon allocation, gas exchange, and needle morphology of pinus ponderosa genotypes known to differ in growth and survival under imposed drought. Tree Physiol. 14 (7), 883–898.

Cregg, B.M., Zhang, J.W., 2001. Physiology and morphology of *Pinus sylvestris* seedlings from diverse sources under cyclic drought stress. For. Ecol. Manag. 154 (1), 131–139. https://doi.org/10.1016/S0378-1127(00)00626-5.

Cuesta, Bárbara, Villar-Salvador, Pedro, Puértolas, Jaime, Jacobs, Douglass F., Rey Benayas, José M., 2010. Why do large, nitrogen rich seedlings better resist stressful transplanting conditions? A physiological analysis in two functionally contrasting mediterranean forest species. For. Ecol. Manag. 260 (1), 71–78. https://doi.org/10.1016/j.foreco.2010.04.002.

Daubenmire, R., Daubenmire, J.B., 1968. Forest vegetation of eastern Washington and northern Idaho. Tech. Bull. 60, 104. WA: Washington State University, College of Agriculture, Washington Agricultural Experiment Station.

Davis, Kimberley T., Dobrowski, Solomon Z., Higuera, Philip E., et al., 2019. Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. Proc. Natl. Acad. Sci. 116 (13), 6193–6198. https://doi.org/10.1073/pnas.1815107116.

Davis, Kimberley T., Robles, Marcos D., Kemp, Kerry B., et al., 2023. Reduced fire severity offers near-term buffer to climate-driven declines in conifer resilience across the Western United States. Proc. Natl. Acad. Sci. 120 (11), e2208120120. https://doi.org/10.1073/pnas.2208120120.

Del Campo, Antonio D., Navarro Cerrillo, Rafael M., Hermoso, Javier, Ibáñez, Antonio J., 2007. Relationships between Site and Stock Quality in Pinus halepensis Mill. Reforestation on Semiarid Landscapes in Eastern Spain. Ann. For. Sci. 64 (7), 719–731. https://doi.org/10.1051/forest:2007052.

Deligoz, Ayse, Gur, Merve, 2015. Morphological, physiological and biochemical responses to drought stress of stone pine (Pinus pinea L.) seedlings. Acta Physiol. Plant. 37 (ember). https://doi.org/10.1007/s11738-015-1998-1.

Dodson, Erich K., Root, Heather T., 2013. Conifer regeneration following stand-replacing wildfire varies along an elevation gradient in a Ponderosa Pine Forest, Oregon, USA. For. Ecol. Manag. 302 (August), 163–170. https://doi.org/10.1016/j.foreco.2013.03.050.

Dominguez-Lerena, S., Herrero Sierra, N., Carrasco Manzano, I., Ocaña Bueno, L., Peñuelas Rubira, J.L., Mexal, J.G., 2006. Container characteristics influence *Pinus pinea* seedling development in the nursery and field. For. Ecol. Manag. 221 (1), 63–71. https://doi.org/10.1016/j.foreco.2005.08.031.

Donato, Daniel C., Harvey, Brian J., Turner, Monica G., 2016. Regeneration of montane forests 24 years after the 1988 yellowstone fires: a fire-catalyzed shift in lower treelines? Ecosphere 7 (8), e01410. https://doi.org/10.1002/ecs2.1410.

Dumroese, R.Kasten, Balloffet, Nicole, Crockett, John W., Stanturf, John A., Nave, Lucas E., 2019. A national approach to leverage the benefits of tree planting on public lands. N. For. 50 (1), 1–9. https://doi.org/10.1007/s11056-019-09703-2.

Dumroese, R.Kasten, Jeremiah, Pinto, Montville, M., 2015. Using container weights to determine irrigation needs: a simple method. Nativ. Plants J. 16 (March), 67–71. https://doi.org/10.3368/npj.16.1.67.

Dumroese, R.Kasten, Landis, Thomas D., Pinto, Jeremiah R., Haase, Diane L., Wilkinson, Kim W., Davis, Anthony S., 2016. Meeting forest restoration challenges: using the target plant concept. Reforesta (1), 37–52. https://doi.org/10.21750/REFOR.1.03.3.

Fargione, Joseph, Haase, Diane L., Burney, Owen T., et al., 2021. Challenges to the reforestation pipeline in the United States. Front. For. Glob. Change 4 (February). https://doi.org/10.3389/ffgc.2021.629198.

Fins, L., Byler, J., Ferguson, D., Harvey, A., Mahalovich, M. F., McDonald, G. I., ... & Zack, A. (2001). Return of the giants: Restoring white pine ecosystems by breeding and aggressive planting of blister rust-resistant white pines. *Station Bulletin 72. Moscow, ID: University of Idaho, Wildlife and Range Experiment Station. 21 p.*

Grossnickle, S.C., 2005a. Importance of root growth in overcoming planting stress. New 30, 273–294.

Grossnickle, S.C., 2005b. Seedling size and reforestation success. How big is big enough? In: Colombo SJ (Compiler) The thin green line: a symposium on the state-of-the-art in reforestation. Ont. For. Res. Inst. Ont. Minist. Nat. Resour. For. Res. Info Pap. 160, 138–144.

Grossnickle, S.C., 2012. Why seedlings survive: influence of plant attributes. N. For. 43 (5), 711–738. https://doi.org/10.1007/s11056-012-9336-6.

Grossnickle, S.C., Arnott, J.T., Major, J.E., 1991. Influence of dormancy induction treatments on western hemlock seedlings. II. Physiological and morphological response during the first growing season on a reforestation site. Can. J. For. Res. 21 (2), 175–185. https://doi.org/10.1139/x91-021.

Grossnickle, S.C., MacDonald, J.E., 2018. Why seedlings grow: influence of plant attributes. N. For. 49 (1), 1–34.

Grossnickle, S.C., MacDonald, J.E., 2026. Seedling field performance on hot, dry forest restoration sites: influence of plant attributes. N. For. 57 (2), 16. https://doi.org/10.1007/s11056-025-10140-7.

Haig, Irvine, 1936. Factors controlling initial establishment of western white pine and associated species. Yale Sch. Environ. Bull. Ser. 41 (January). ⟨https://elischolar.library.yale.edu/yale_fes_bulletin/20⟩.

Hann, Wendel J., Jeffrey L. Jones, Robert E. Keane, Paul F. Hessburg, and Rebecca A. Gravenmier. "ICBEMP: Landscape Dynamics." *Journal of Forestry* 96, no. 10 (1998): 10–15. https://doi.org/10.1093/jof/96.10.10.

Hennessey, T.C., and P.M. Dougherty. 1984. Characterization of the Internal Water Relations of Loblolly Pine Seedlings in Response to Nursery Cultural Treatments: Implications for Reforestation Success." In Seedling Physiology and Reforestation Success, edited by Mary L. Duryea and Gregory N. Brown, vol. 14. Forestry Sciences. Springer Netherlands. https://doi.org/10.1007/978-94-009-6137-1_10.

Higuera, Philip E., Shuman, Bryan N., Wolf, Kyra D., 2021. Rocky mountain subalpine forests now burning more than any time in recent millennia. Proc. Natl. Acad. Sci. 118 (25), e2103135118. https://doi.org/10.1073/pnas.2103135118.

Hobbs, S.D., 1992. Seedl. site Interact.

Holden, Zachary A., Jungck, Ellen, Davis, Kimberley T., et al., 2025. A post-fire reforestation assessment and prioritization tool for the western United States. Fire Ecol. 21 (1), 83. https://doi.org/10.1186/s42408-025-00405-z.

Holden, Z.A., Warren, D., Davis, K., Jungck, E., Maneta, M., Dobrowski, S., Archer, V., 2022. REGEN MAPPER: A web-based tool for predicting postfire conifer regeneration and prioritizing reforestation efforts in the western United States. Jain, Theresa B.; Schuler, Thomas M. [Comp.]. Foundational Concepts in Silviculture with Emphasis on Reforestation and Early Stand Improvement - 2022 National Silviculture Workshop. Proc. RMRS-P-80. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, *Fort Collins, CO*, p. *80*. ⟨https://www.fs.usda.gov/research/treesearch/64703⟩. *2 p.*.

Jain, Theresa B., Russell T. Graham, and Penelope Morgan. "Western White Pine Growth Relative to Forest Openings." *Canadian Journal of Forest Research* 34, no. 11 (2004): 2187–98. https://doi.org/10.1139/x04-094.

Johnson, J.D., Seiler, J.R., McNabb, K.L., 1986. Manipulation of pine seedling physiology by water stress conditioning. In: South, D.B. (Ed.), International symposium on nursery management practices for the southern pines. Alabama Agricultural Experiment Station, AuburnUniv., Auburn, A.L., pp. 290–302.

Kandiko, R.A., Timmis, R., 1980. Pressure–Volume Curves of Shoots and Roots of Normal and Drought Conditioned Western Hemlock Seedlings. Canadian Journal of Forest Research 10 (1), 10–16. https://doi.org/10.1139/x80-003.

Kemp, Kerry B., Higuera, Philip E., Morgan, Penelope, Abatzoglou, John T., 2019. Climate will increasingly determine post-fire tree regeneration success in low-elevation forests, Northern Rockies, USA. Ecosphere 10 (1), e02568. https://doi.org/10.1002/ecs2.2568.

Kerr, Kelly L., Meinzer, Frederick C., McCulloh, Katherine A., Woodruff, David R., Marias, Danielle E., 2015. Expression of functional traits during seedling establishment in two populations of pinus ponderosa from contrasting climates. Tree Physiol. 35 (5), 535–548. https://doi.org/10.1093/treephys/tpv034.

Kitao, Mitsutoshi, Agathokleous, Evgenios, Harayama, Hisanori, et al., 2022. Tolerance of Japanese Larch to Drought Is Modified by Nitrogen and Water Regimes during Cultivation of Container Seedlings. European Journal of Forest Research 141 (4), 699–712. https://doi.org/10.1007/s10342-022-01470-8.

Kolb, P.F., Robberecht, R., 1996. High temperature and drought stress effects on survival of Pinus ponderosa seedlings. Tree Physiol. 16 (8), 665–672. https://doi.org/10.1093/treephys/16.8.665.

Kozlowski, T.T., Pallardy, S.G., 2002. Acclimation and adaptive responses of woody plants to environmental stresses. Bot. Rev. 68 (2), 270–334. https://doi.org/10.1663/0006-8101(2002)068[0270:AAAROW]2.0.CO;2.

Kreider, Mark R., Higuera, Philip E., Parks, Sean A., Rice, William L., White, Nadia, Larson, Andrew J., 2024. Fire suppression makes wildfires more severe and accentuates impacts of climate change and fuel accumulation. Nat. Commun. 15 (1), 2412. https://doi.org/10.1038/s41467-024-46702-0.

Landis, Thomas D., Kasten Dumroese, R., Haase, Diane L., 2010. The container tree nursery manual: volume 7, seedling processing, storage, and outplanting. Agric. Handbook No. 674. Washington, DC. U.S. Department of Agriculture, *For*est Service, p. 674. ⟨https://research.fs.usda.gov/treesearch/35195⟩. *199 p.*

Larson, Andrew J., Belote, R.Travis, Williamson, Matthew A., Aplet, Gregory H., 2013. Making monitoring count: project design for active adaptive management. J. For. 111 (5), 348–356. https://doi.org/10.5849/jof.13-021.

Larson, Andrew J., Jeronimo, Sean M.A., Hessburg, Paul F., et al., 2022. Tamm review: ecological principles to guide post-fire forest landscape management in the Inland Pacific and Northern Rocky Mountain Regions. For. Ecol. Manag. 504 (January), 119680. https://doi.org/10.1016/j.foreco.2021.119680.

Martínez-Vilalta, Jordi, Garcia-Forner, Núria, 2017. Water potential regulation, stomatal behaviour and hydraulic transport under drought: deconstructing the iso/anisohydric concept. Plant Cell Environ. 40 (6), 962–976. https://doi.org/10.1111/pce.12846.

Martínez-Vilalta, J., Lloret, F., 2016. Drought-induced vegetation shifts in terrestrial ecosystems: The key role of regeneration dynamics. Glob. Planet. Change 144, 94–108. https://doi.org/10.1016/j.gloplacha.2016.07.009.

McKenney, Dan, Pedlar, John, O'Neill, Greg, 2009. Climate change and forest seed zones: past trends, future prospects and challenges to ponder. For. Chron. 85 (2), 258–266. https://doi.org/10.5558/tfc85258-2.

Miller, M.L., Johnson, D.M., 2017. Vascular development in very young conifer seedlings: Theoretical hydraulic capacities and potential resistance to embolism. American Journal of Botany 104, 979–992. https://doi.org/10.3732/ajb.1700161.

Moler, Ehren Reid Von, Nelson, Andrew Steven, 2021. Perspectives on drought preconditioning treatments with a case study using Western Larch. Front. Plant Sci. 12 (September). https://doi.org/10.3389/fpls.2021.741027.

Nagel, Linda M., Palik, Brian J., Battaglia, Michael A., et al., 2017. Adaptive silviculture for climate change: a national experiment in manager-scientist partnerships to apply an adaptation framework. J. For. 115 (3), 167–178. https://doi.org/10.5849/jof.16-039.

O'Reilly, Conor, Owens, J.N., Arnott, J.T., Dunsworth, B.G., 1994. Effect of nursery culture on morphological development of western hemlock seedlings during field establishment. I. Flushing, shoot elongation, and bud development. Can. J. For. Res. 24 (1), 53–60. https://doi.org/10.1139/x94-009.

Onofrio, Lauren, Hawley, Gary, Leites, Laura P., 2021. Ecological genetics of juglans nigra: differences in early growth patterns of natural populations. Ecol. Evol. 11 (12), 7399–7410. https://doi.org/10.1002/ece3.7571.

Padilla, F.M., Pugnaire, F.I., 2007. Rooting depth and soil moisture control mediterranean woody seedling survival during drought. Funct. Ecol. 21 (3), 489–495. https://doi.org/10.1111/j.1365-2435.2007.01267.x.

Parent, Dennis, and Ronald Mahoney. Western Larch*: A Deciduous Conifer in an Evergreen World*. Station Bulletin no. 90, Idaho Forest, Wildlife and Range Experiment Station, College of Natural Resources, 2008, https://jdforestmanagement.com/wp-content/uploads/2022/11/Larch-Species-Overview.pdf.

Petrie, M.D., Wildeman, A.M., Bradford, J.B., Hubbard, R.M., Lauenroth, W.K., 2016. A review of precipitation and temperature control on seedling emergence and establishment for ponderosa and lodgepole pine forest regeneration. For. Ecol. Manag. 361, 328–338. https://doi.org/10.1016/j.foreco.2015.11.028.

Piñol, J., Sala, A., 2000. Ecological implications of xylem cavitation for several pinaceae in the Pacific northern USA. Funct. Ecol. 14 (5), 538–545. https://doi.org/10.1046/j.1365-2435.2000.t01-1-00451.x.

Pinto, Jeremiah R., John, D.Marshall, Kasten Dumroese, R., Anthony, S.Davis, Douglas, R.Cobos, 2012. Photosynthetic response, survival, and growth of three ponderosa pine stocktypes under water stress enhanced by vegetative competition. Can. J. For. Res. 42 (333-344), 333–344.

Pinto, Jeremiah R., Marshall, John D., Dumroese, R.Kasten, Davis, Anthony S., Cobos, Douglas R., 2011. Establishment and growth of container seedlings for reforestation: a function of stocktype and edaphic conditions. For. Ecol. Manag. 261 (11), 1876–1884.

Pinto, Jeremiah R., McNassar, Bridget A., Kildisheva, Olga A., Davis, Anthony S., 2018. Stocktype and vegetative competition influences on Pseudotsuga menziesii and Larix occidentalis seedling establishment. Forests 9 (5), 228. https://doi.org/10.3390/f9050228.

Pinto, Jeremiah R., Sloan, Joshua L., Ervan, Gokhan, Burney, Owen T., 2023. Physiological and morphological responses of pinus ponderosa seedlings to moisture limitations in the nursery and their implications for restoration. Front. Plant Sci. 14 (May). https://doi.org/10.3389/fpls.2023.1127656.

Puértolas, Jaime, Villar-Salvador, Pedro, Andivia, Enrique, et al., 2024. Die-hard seedlings. a global meta-analysis on the factors determining the effectiveness of drought hardening on growth and survival of forest plantations. For. Ecol. Manag. 572 (ember), 122300. https://doi.org/10.1016/j.foreco.2024.122300.

R Core Team. 2025. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ⟨https://www.R-project.org/⟩.

Rehfeldt, Gerald E., 1980. Cold acclimation in populations of Pinus contorta from the Northern Rocky Mountains. Bot. Gaz. 141 (4), 458–463. https://doi.org/10.1086/337183.

Rehfeldt, G.E., Hoff, R.J., Steinhoff, R.J., 1984. Geographic patterns of genetic variation in Pinus monticola. Bot. Gaz. 145 (2), 229–239. https://doi.org/10.1086/337451.

Reich, P.B., 2014. The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. J. Ecol. 102, 275–301. https://doi.org/10.1111/1365-2745.12211.

Robinson, Wallis, Kerhoulas, Lucy P., Sherriff, Rosemary L., Roletti, Gabriel, van Mantgem, Phillip J., 2023. Drought survival strategies differ between coastal and Montane Conifers in Northern California. Ecosphere 14 (3), e4480. https://doi.org/10.1002/ecs2.4480.

Rook, D.A., 1973. Conditioning radiata pine seedlings to transplanting, by restricted watering.

Rose, Karen E., Atkinson, Rebecca L., Turnbull, Lindsay A., Rees, Mark, 2009. The costs and benefits of fast living. Ecol. Lett. 12 (12), 1379–1384. https://doi.org/10.1111/j.1461-0248.2009.01394.x.

Rose, R., Gleason, J.F., Atkinson, M., 1993. Morphological and Water-Stress characteristics of three douglas-fir stocktypes in relation to seedling performance under different soil moisture conditions. N. For. 7 (1), 1–17. https://doi.org/10.1007/BF00037468.

Rose, R., Ketchum, J.S., 2003. Interaction of initial seedling diameter, fertilization and weed control on Douglas-fir growth over the first four years after planting. Ann. For. Sci. 60 (7), 625–635.

Roskilly, Beth, Aitken, Sally, 2024. Weak local adaptation to climate in seedlings of a deciduous conifer suggests limited benefits and risks of assisted gene flow. Evolut. Appl. 17 (9), e70001. https://doi.org/10.1111/eva.70001.

Roskilly, Beth A., Henry, Martin R., Aitken, Sally N., 2025. Selective breeding for growth does not compromise drought resistance in western larch seedlings. For. Ecol. Manag. 596 (ember), 123064. https://doi.org/10.1016/j.foreco.2025.123064.

Ross, Anna C., Pinto, Jeremiah R., Crotteau, Justin S., et al., 2025. Morphological and physiological response of conifer seedlings to drought conditioning. N. For. 56 (6), 54. https://doi.org/10.1007/s11056-025-10121-w.

Rother, Monica T., Veblen, Thomas T., 2016. Limited conifer regeneration following wildfires in dry ponderosa pine forests of the colorado front range. Ecosphere 7 (12), e01594. https://doi.org/10.1002/ecs2.1594.

Royo, Antonio, Gil, Luis, Pardos, José A., 2001. Effect of water stress conditioning on morphology, physiology and field performance of Pinus halepensis Mill. Seedlings. N. For. 21 (2), 127–140. https://doi.org/10.1023/A:1011892732084.

Schmidt, Wyman C., Raymond, C., Shearer, Arthur L.Roe, Arthur, Lawrence Roe, 1976. *Ecology and silviculture of western larch forests*. Vol. 1516. US Department of Agriculture, Forest Service.

Seidel, K.W., 1986. Tolerance of seedlings of ponderosa pine, Douglas-fir, grand fir, and Engelmann spruce for high temperatures. Northwest Sci. 60 (1), 1–7.

Seiler, John R., Johnson, Jon D., 1988. Physiological and morphological responses of three half-sib families of loblolly pine to water-stress conditioning. For. Sci. 34 (2), 487–495. https://doi.org/10.1093/forestscience/34.2.487.

Sloan, Joshua, Burney, Owen, Pinto, Jeremiah, 2020. Drought-conditioning of Quaking Aspen (Populus tremuloides Michx.) seedlings during nursery production modifies seedling anatomy and physiology. Front. Plant Sci. 11 (September), 557894. https://doi.org/10.3389/fpls.2020.557894.

Soil Survey Staff, 2026. Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. http://websoilsurvey.sc.egov.usda.gov. http://websoilsurvey.sc.egov.usda.gov.

Steed, James E., Goeking, Sara A., 2020. Western larch regeneration responds more strongly to site and indirect climate factors than to direct climate Factors. Forests 11 (4), 482. https://doi.org/10.3390/f11040482.

Sutherland, D.C., Day, R.J., 1988. Container volume affects survival and growth of white spruce, black spruce, and jack pine seedlings: a literature review. North. J. Appl. For. 5 (3), 185–189. https://doi.org/10.1093/njaf/5.3.185.

Tepley, Alan J., Thompson, Jonathan R., Epstein, Howard E., Anderson-Teixeira, Kristina J., 2017. Vulnerability to forest loss through altered postfire recovery dynamics in a warming climate in the Klamath Mountains. Glob. Change Biol. 23 (10), 4117–4132. https://doi.org/10.1111/gcb.13704.

Toca, Andrei, Gonzalez-Benecke, Carlos A., Nelson, Andrew S., Jacobs, Douglass F., 2025. Drought memory expression varies across ecologically contrasting forest tree species. Environ. Exp. Bot. 231 (March), 106094. https://doi.org/10.1016/j.envexpbot.2025.106094.

Toca, Andrei, Moler, Ehren, Nelson, Andrew, Jacobs, Douglass F., 2022. Environmental conditions in the nursery regulate root system development and architecture of forest tree seedlings: a systematic review. N. For. 53 (6), 1113–1143. https://doi.org/10.1007/s11056-022-09944-8.

Trubat, Roman, Cortina, Jordi, Vilagrosa, Alberto, 2011. Nutrient deprivation improves field performance of woody seedlings in a degraded semi-arid Shrubland. Ecol. Eng. 37 (8), 1164–1173. https://doi.org/10.1016/j.ecoleng.2011.02.015.

Vale, Ashleigh, Moler, Ehren, Nelson, Andrew, 2021. Two studies of the potential of drought preconditioning to enhance deep root production in seedlings of Western Larch (Larix occidentalis). REFORESTA 12 (December), 3–12. https://doi.org/10.21750/REFOR.12.02.94.

Valliere, Justin M., Jacqueline Zhang, M. Rasoul Sharifi, and Phillip W. Rundel. "Can We Condition Native Plants to Increase Drought Tolerance and Improve Restoration Success?" *Ecological Applications* 29, no. 3 (2019): e01863. https://doi.org/10.1002/eap.1863.

van den Driessche, R., 1991. Influence of container nursery regimes on drought resistance of seedlings following planting. I. Survival and growth. Can. J. For. Res. 21 (5), 555–565. https://doi.org/10.1139/x91-077.

van den Driessche, R., 1992. Changes in drought resistance and root growth capacity of container seedlings in response to nursery drought, nitrogen, and potassium treatments. Can. J. For. Res. 22 (5), 740–749. https://doi.org/10.1139/x92-100.

Vieira, Spencer T., Davis, Kimberley T., Holden, Zachary A., Larson, Andrew J., Higuera, Philip E., 2024. Western larch regeneration more sensitive to wildfire-related factors than seasonal climate variability. For. Ecol. Manag. 565 (August), 122011. https://doi.org/10.1016/j.foreco.2024.122011.

Villar-Salvador, Pedro, Enrique Andivia, Barbara Mariotti, et al., 2026. Quality matters. a quantitative review on the effect of seedling morphology and nursery practices on the outplanting performance of forest plantings. Guidelines for Climate Adaptive Forest Restoration and Reforestation Projects, pp. 131–191.

Villar-Salvador, Pedro, Juan, L.Peñuelas, Douglass, F.Jacobs, 2013a. Nitrogen nutrition and drought hardening exert opposite effects on the stress tolerance of Pinus pinea L. Seedlings. Tree Physiol. 33 (2), 221–232.

Zhang, J.W., Feng, Z., Cregg, B.M., Schumann, C.M., 1997. Carbon isotopic composition, gas exchange, and growth of three populations of ponderosa pine differing in drought tolerance. Tree Physiol. 17 (7), 461–466.

Zhang, Xianliang, Li, Xue, Manzanedo, Rubén D., et al., 2021. High risk of growth cessation of planted larch under extreme drought. Environ. Res. Lett. 16 (1), 014040. https://doi.org/10.1088/1748-9326/abd214.

Zhang, Jianwei, Marshall, John D., Fins, Lauren, 1996. Correlated population differences in dry matter accumulation, allocation, and water-use efficiency in three sympatric conifer species. For. Sci. 42 (2), 242–249.

Zhang, Jianwei, Marshall, John D., 1994. Population differences in water-use efficiency of well-watered and water-stressed western larch seedlings. Canadian Journal of Forest Research 24 (1), 92–99. https://doi.org/10.1139/x94-014.