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RESEARCH ARTICLE

The Importance of Tree Regeneration for Maintaining Mountain Forest Ecosystem Services Under Global Change

Seed source climate and precipitation timing determine dryland tree recruitment in hot and dry range margins

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Abstract

1. Dryland forests face multiple climate change-related threats, including more frequent droughts and shifts in the seasonality of precipitation. While dryland tree species tend to have adaptations for adult persistence during drought, recruitment is often episodic, occurring only in years with favourable conditions. As conditions become more arid, with fewer favourable periods for seedling establishment, variation in the presence of drought-adapted phenotypes among populations may determine recruitment potential and lead to different outcomes.
2. We used a 4-year common garden experiment to evaluate seedling survival and growth in response to varying precipitation timing and amount for 23 populations of *Pinus monophylla*, a tree species occurring in semiarid forests of south-western United States. Previous research on *P. monophylla* showed that intraspecific phenotypic variation in maternal trees persists in seedling offspring, yet fitness implications are unknown. We sowed seeds at the dry edge of the species' climatic distribution and used experimental watering treatments to simulate four seasonal precipitation regimes: ambient control (drought), spring supplemental watering, summer supplemental watering and spring + summer supplemental watering. We used a randomized block design, sowing seeds under the canopy of the native shrub *Artemisia tridentata* to meet known shade requirements for seedling establishment.
3. Seed source climate was associated with differences in recruitment. Seedlings sourced from more arid climates had higher survival and above-ground growth than seedlings from wetter climates under all simulated precipitation regimes. Climate transfer distance relationships were consistent with local adaptations to mean annual temperature and spring water availability, and supplemental summer water increased seedling survival. We found large differences in seedling establishment between sowing years, highlighting the importance of episodic recruitment under favourable conditions. Nurse shrub canopy cover was also a strong predictor of survival in the first 2 years of establishment.

4. *Synthesis*. Our results show that intraspecific phenotypic variation mediates the effect of seasonal drought on dryland tree recruitment, suggesting that different populations may respond uniquely to changes in climate. The effects of precipitation may be contingent on shifts in seasonal timing and amount, and *P. monophylla* seedling survival may decline with increasing temperatures or decreased summer water availability.

KEYWORDS
adaptive capacity, climate change, common garden, drought, intraspecific phenotypic variation, local adaptation, pinyon pine, precipitation seasonality

1 | INTRODUCTION

The velocity of anthropogenic climate change creates unprecedented challenges for long-lived tree species, particularly in water-limited environments (Loarie et al., 2009). Dryland forests worldwide are experiencing widespread mortality events, driven by rising temperatures and increasingly frequent and severe droughts (Allen et al., 2010; Maestre et al., 2021). Seedling recruitment is critical for long-term forest persistence because it enables recovery following overstorey mortality (Brown & Wu, 2005; Petrie et al., 2023). While dryland tree species tend to have adaptations that promote adult persistence during drought (Andivia et al., 2020), recruitment is often episodic, occurring only in years with favourable conditions (Urza et al., 2021; Wiegand et al., 2004). As conditions become more arid and the frequency of favourable recruitment years declines, variation in the presence of drought-adapted phenotypes may determine recruitment potential and lead to different responses among populations (Ramírez-Valiente et al., 2021). Declining recruitment in the driest margins of species' ranges has been observed in response to increasing aridity, suggesting a 'trailing edge' dynamic in which forest range contraction may occur (Freeman et al., 2018). Anticipating ecological responses to ongoing and rapid climate change requires an improved understanding of intraspecific variation in seedling adaptations to drought and the extent to which extant populations may sustain recruitment under novel climate stressors.

A species' adaptive capacity—the ability to cope with, adjust to and persist in changing conditions—is strongly influenced by local environmental conditions (Dawson et al., 2011). Even when genetic connectivity is high, geographically structured phenotypic variation is common in tree species (Savolainen et al., 2007), and species distributed over heterogeneous landscapes often consist of populations with highly differentiated responses to climate change (Bisbing et al., 2021; Martínez-Berdeja et al., 2019). Phenotypic variation among populations may reflect local adaptation to environmental selection pressures or may arise from phenotypic plasticity with or without a heritable genetic basis (Benito Garzón et al., 2011; Kawecki & Ebert, 2004). For species occupying mountainous topography with steep climatic gradients, phenotypic variation may exist among populations that are relatively close geographically (Rixen et al., 2022). As dry forest edges typically experience the most intense drought effects, they may contain phenotypes that are drought-adapted and better equipped to survive in arid environments (Gonzalez de Andrés et al., 2021). Seedling drought adaptations may allow for sustained recruitment in increasingly arid conditions, although under continued climate change, populations may eventually become maladapted to local climate (Aitken et al., 2008). Where strong regional gradients of precipitation seasonality exist, adaptations to local precipitation regimes may prove maladaptive if precipitation timing shifts, potentially constraining a population's ability to adapt to new conditions (Schwinning & Ehleringer, 2001; Schwinning & Sala, 2004).

Past research on intraspecific variation has found that phenotypic differences and resulting variation in adaptive capacity often shift with ontogeny (Andivia et al., 2020; Spasojevic et al., 2014). Long-lived tree species experience profound changes in environmental tolerance and resource needs over their lifetime, and mature trees typically have higher resource requirements but greater drought-buffering capacity than seedlings or juveniles, which are generally more sensitive to abiotic extremes (Niinemets, 2010). Seedling emergence and establishment are often primary demographic bottlenecks for tree species, and these stages are subject to strong environmental selection pressures (Uriarte et al., 2005). Common garden experiments have been widely used to assess climate adaptations and potential responses to climate change in tree species (Johnson et al., 2022). However, most tree common gardens use glasshouse-propagated juveniles that bypass the establishment bottleneck under artificial conditions, potentially obscuring ecologically relevant responses (Gibson et al., 2016).

Pinus monophylla (Torr. & Frem.; single leaf pinyon pine) is one of the most widely distributed tree species in North America, co-dominating with *Juniperus* species in some of the most xeric forests in the world (Miller et al., 2019). Its occurrence across a topographically and climatically heterogeneous landscape makes *P. monophylla* well suited for studying intraspecific variation in drought responses. Its range encompasses gradients of aridity at both regional (north–south) and local (elevational) scales (Cole et al., 2013; Urza et al., 2020). Although its overall distribution is characterized by winter-dominated precipitation, summer precipitation increases along a northwest-to-southeast gradient (Chenoweth et al., 2023). Previous research found substantial intraspecific variation in *P. monophylla* maternal foliar and reproductive traits (Vasey et al., 2022). Trait differences persisted in

glasshouse-grown seedling offspring (Vasey et al., 2023), but because nearly all seedlings survived the study, the implications for seedling survival under field conditions remain unknown.

In this study, we used a 4-year field common garden to evaluate intraspecific variation in seedling responses to precipitation timing and amount for 23 populations of *P. monophylla*. Our experimental site was located near the hot, dry edge of the species' climatic distribution, and we used experimental watering treatments to simulate four seasonal precipitation regimes: ambient control (drought), spring supplemental watering, summer supplemental watering and spring + summer supplemental watering. We used a randomized block design, sowing seeds in the soil under shrub canopies to provide shade requirements for establishment (Chambers, 2001). We asked: (1) Are there population-level differences in seedling survival under varying seasonal precipitation regimes, and do these differences vary with seedling age or among study years? (2) Is there evidence of local adaptation to temperature and precipitation seasonality? (3) Are there population-level differences in seedling size under varying precipitation regimes, and do these differences predict survival? We expected survival to be highest for seedlings from more arid seed sources, with an interaction between seed source summer precipitation and watering treatment such that summer-wet populations would benefit most from supplemental summer water. Additionally, we predicted that population-level differences would decline with seedling age but would be consistent among study years. We expected our results to be consistent with local adaptation, with survival optimized when seedlings' source climate closely matched the conditions experienced in the experiment (Kawecki & Ebert, 2004). Finally, we expected greater early above-ground growth to facilitate resource acquisition, such that populations with larger seedlings would also have greater survival (Ramírez-Valiente et al., 2021).

2 | MATERIALS AND METHODS

2.1 | Seed source selection and seed collection

Seeds were collected in September 2019 from 23 populations of *P. monophylla* (Figure 1; Table S1). We selected nine mountain ranges from across the species' distribution that spanned regional gradients of mean annual precipitation and proportion of summer precipitation (July, August, September) to annual precipitation using 30-year climate means from PRISM (Daly et al., 1994). At each mountain range, we aimed to locate three seed collection sites along the elevational gradient of *P. monophylla*, ranging from the lowest to highest elevation stands of cone-bearing trees that were accessible from a road. Three mountain ranges had fewer than three sites due to narrow woodland elevation ranges or a lack of available cones.

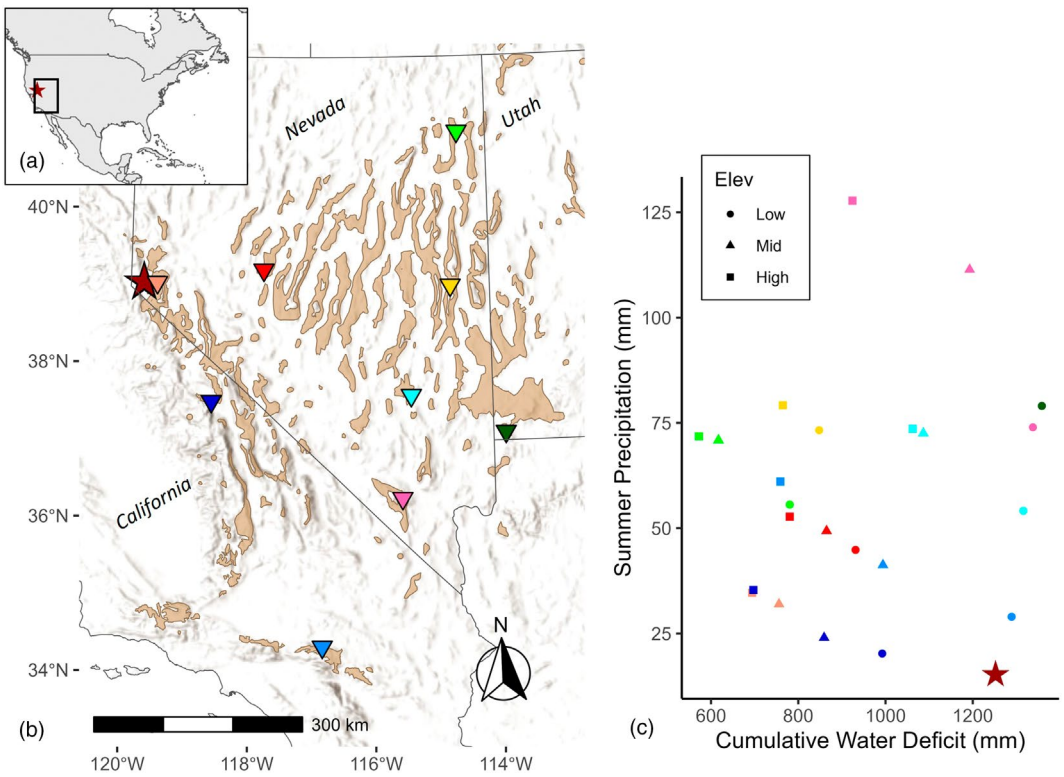

FIGURE 1 Locations of seed sources and the common garden experiment site. In all panels, the common garden site is shown with a dark red star. (a) Location of the study area within North America. (b) General locations for each of the nine mountain ranges where seeds were collected (upside-down triangles); each mountain range contained up to three seed collection sites that were stratified across a gradient of elevation. Beige polygons show the distribution of *Pinus monophylla* (Cole et al., 2013). (c) Climate conditions in the seed source locations (30-year mean). Colours show the mountain ranges; symbols show the relative elevation strata of each site.

At each seed collection site, we harvested cones from six cone-bearing trees that were representative of the stand based on tree size and cone production. Permissions for cone collection were approved by the US Forest Service and the Bureau of Land Management. Cones were placed in trays on a warm greenhouse benchtop until they opened, after which the seeds were removed and tested for seed fill following the acoustic method described in Chambers (2001). Seeds were air-dried for 2 weeks and refrigerated (2°C–4°C) until sown. Twenty filled seeds per tree were weighed to the nearest 0.01 g to calculate mean seed mass for each population (Table S1), with an overall mean seed mass of 0.618 g.

2.2 | Common garden experimental design

Our common garden was located near Carson City, NV, USA (39.0729°, −119.784°), at an elevation of 1448 m. Permission for the field experiment was given by the Humboldt-Toiyabe National Forest. The common garden location receives a mean of 245 mm of annual precipitation and has a mean annual temperature of 10.1°C (30-year mean from 1991 to 2020; Daly et al., 1994). Compared to the seed source locations, the common garden's climate is warm and has low precipitation, especially in the spring and summer (Figure 1c). Relative to the seed collection sites, its mean annual temperature is in the 70th percentile (70% of seed source climates are cooler); its total annual precipitation is in the 20th percentile (20% of sites receive less), with spring and summer precipitation in the 17th and <1st percentiles, respectively.

We used a randomized block design, sowing filled seeds in the soil under the canopy of the native shrub *Artemisia tridentata* (Nutt. ssp. *wyomingensis* Beetle & Young) to meet known nurse plant requirements for seedling establishment (Chambers, 2001; Chambers et al., 1999; Urza et al., 2019). Under the north side of each shrub canopy, we sowed one seed from each of the 23 populations in a randomized 5 × 5 grid (45 cm × 45 cm; 0.2 m^2). Seeds were sown at a depth of 3 cm, and each grid was caged with wire mesh to protect from seed predators (Chambers, 2001). We sowed seeds in two successive years to test whether population differences in recruitment were contingent on weather conditions in the study year. We sowed 288 blocks (6624 seeds) in November 2019 ('cohort one') and 128 blocks (2667 seeds) in November 2020 ('cohort two'). In cohort two, only 22 of our 23 populations were included due to limited seed availability for one seed source. Seedling blocks were weeded after spring green-up each year to remove potentially confounding effects of species interactions.

We used experimental watering treatments to simulate four seasonal precipitation regimes, which were designed based on the observed extremes of precipitation seasonality from the seed sources (Figure 2a). The 'control' treatment had no added water and thus experienced ambient, dry conditions of the common garden site. The 'spring' watering treatment received additional water weekly from April to June. The 'summer' watering treatment received additional water weekly from July to September. The spring + summer ('both') watering treatment received additional water biweekly from April to September. Each watering addition simulated a rainfall event of approximately 10 mm. A couple of deviations from this design occurred. In 2020, we were concerned about high mortality in the first year of a multi-year study, so in addition to the watering schedule described above, the 'spring' and 'summer' watering treatments received three additional watering inputs (once/month) over the 3 months outside their treatment window (spring: July–September; summer: April–June). Additionally, watering treatments were not implemented during September 2021 due to health concerns caused by heavy smoke from a nearby wildfire. Treatment precipitation amounts used in analyses reflect the actual amount of water received, including these changes.

2.3 | Data collection

2.3.1 | Environmental data

Environmental conditions were obtained for the seed source locations and the common garden experiment site. We used 30-year means (1980–2009) for water balance variables (annual cumulative climate deficit and vapour pressure deficit), which were extracted from AdaptWest (Dobrowski et al., 2013). Available water capacity, which represents the amount of water the soil can make available for plant use, was extracted from POLARIS (Chaney et al., 2019). Temperature and precipitation data were extracted from PRISM (Daly et al., 1994) and summarized into the following variables: mean and minimum annual temperature, annual precipitation and spring (April–June) and summer (July–September) precipitation. We used 30-year means (1991–2020) to characterize climate regimes in each location and monthly data for seasonal conditions during the study period (2020–2023).

2.3.2 | Common garden environmental measurements

We installed environmental measuring equipment to monitor local conditions at the common garden site. A weather station (ATMOS 41; METER Group, Inc.) was mounted at a height of 2 m, collecting hourly data on air temperature, precipitation, solar radiation and relative humidity from March 2020 to July 2023. 'Precipitation' for the supplemental watering treatments was calculated as the observed ambient precipitation plus the water addition. We measured volumetric soil water content (VWC) using sensors (TEROS 12; METER Group, Inc.) that were installed vertically 3 cm under the soil surface. The soil sensors have a measurement volume of 1010 mL and, as installed, integrated soil moisture from the top 10–15 cm of the mineral soil. We installed seven sensors in each of the four watering treatments ($N = 28$). Data were collected hourly and summarized to daily means.

We estimated canopy cover for each nurse shrub using hemispherical photographs (Olympus Tough TG-6 digital camera equipped with an FCON-T01 Fisheye Converter with a 130° angle of view). Two photos were taken near midday from perpendicular angles from the

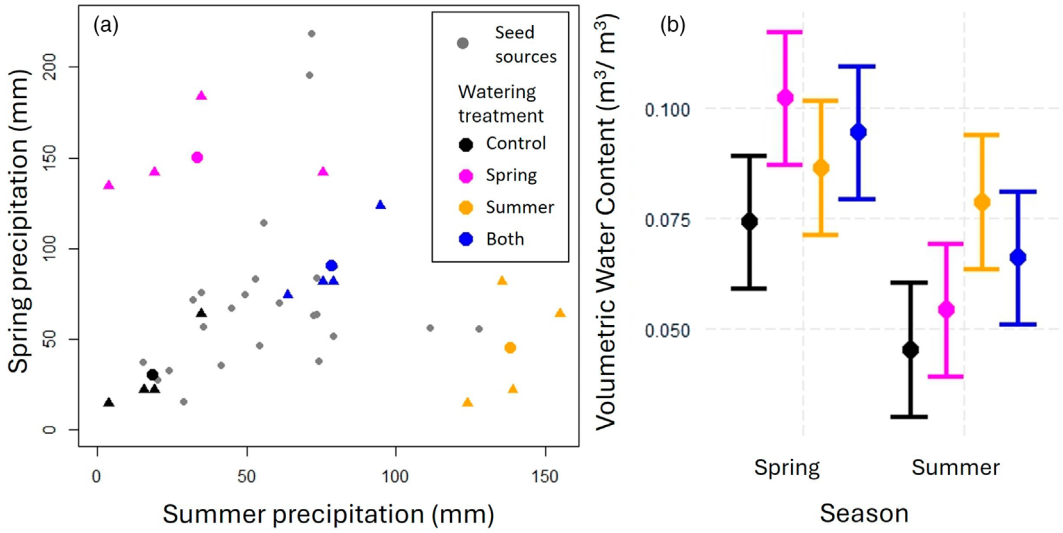

FIGURE 2 Experimental watering treatment effects on simulated precipitation amount and soil moisture during the spring (April–June) and summer (July–September) treatment seasons. (a) Seed source precipitation values (grey points) are 30-year means. To calculate 'precipitation' in the watering treatments, the amount of supplementary water input in each season was added to observed ambient precipitation from the common garden location. Black and coloured circles: Mean for the 4-year study period; triangles: Annual values. (b) Volumetric soil water content (VWC) in each watering treatment during the spring and summer seasons (predicted means ±95% confidence interval [CI]).

centre of each seedling block. Percent cover was calculated using the ForestCrowns program (Winn et al., 2016), and the average value from the two images was used for each seedling block.

2.3.3 | Seedling measurements

We tracked seedling emergence and survival biweekly from April to October during the first year after sowing. In October of each year, we recorded year-end survival for all seedlings that emerged and measured above-ground dimensions for all live seedlings. We measured seedling height (0.1 cm precision) and canopy diameter of the longest axis and perpendicular-to-longest axis (0.1 cm precision). Seedling canopy area was calculated based on the two canopy diameters using the formula for the area of an ellipse:

$$\text{area} = \pi \times (\text{diameter1}) / 2 \times (\text{diameter2}) / 2.$$

2.4 | Data analysis

All analyses were done in R version 4.5.0 (R Core Team, 2025) in R Studio (Posit Team, 2025). All continuous predictor variables were scaled and centred during analyses.

To quantify treatment effects on soil moisture, we used a mixed-effects model to compare mean daily VWC during the spring (April–June) and summer (July–September) treatment seasons. Sensor data were only included for a season-year combination if the sensor had at least 60 consecutive days of data during the 3-month treatment season. We modelled mean daily VWC (Gaussian distribution) as a function of treatment, measurement season (spring or summer) and their interaction, using the lme4 package (Bates et al., 2015). We included a random intercept for each sensor to account for repeated sensor measurements.

For seedling survival analyses, we included only seedlings that emerged and were not affected by herbivory or sheet flow from flooding. We used specific seed source location as the unit of replication for seed source climate conditions, because climate varied among elevational strata more than among mountain ranges (Figure 1c). This is consistent with previous work that showed much higher *P. monophylla* trait variation among elevational strata than among mountain ranges (Vasey et al., 2022).

To evaluate the effect of seed source climate on seedling survival, we used logistic regression with the glm function (binomial distribution, logit link). Many candidate seed source climate variables were highly correlated (Figure S1). We explored using a principal component analysis to decompose seed source climate into fewer axes, but we found that the first two principal component axes were nearly identical to gradients of water deficit and summer precipitation (Figure S2). For this reason, we chose to use water deficit and summer precipitation to represent seed source climate in our models. Final predictor variables included seed source water deficit, seed source summer precipitation, treatment, shrub cover and interactions between treatment and each seed source climate variable. To evaluate whether differences in survival varied with seedling age, we built separate models predicting annual survival in each of the 4 years of the study as well as cumulative survival over the entire 4-year period (*N* for each model shown in Table 2).

To test whether there was evidence of seedling adaptation to local climate conditions, we calculated climate transfer distances. Climate transfer distances represent the degree of difference between the weather a seedling experiences in the common garden and the climate of its seed source (Mátyás, 1994). The weather experienced by a

seedling was represented by observed temperature and precipitation means during the 4 years of the study (2020–2023), with precipitation calculated as ambient precipitation plus treatment-related water additions. Seed source temperature and precipitation were represented as the 30-year mean from the period preceding the study (1991–2020). We modelled cumulative 4-year seedling survival using logistic regression with the glm function (binomial distribution, logit link; $N = 3378$). Predictor variables included linear and quadratic terms for spring precipitation distance, summer precipitation distance and mean annual temperature distance, as well as shrub cover.

To evaluate differences in seedling size, we used linear regressions (Gaussian distribution) to predict seedling height and canopy area for all seedlings alive at the end of the first growing season ($N = 1697$). Predictor variables included seed source water deficit, seed source summer precipitation, treatment, shrub cover and interactions between treatment and both seed source climate variables. To explore the relationship between early seedling size and survival, we modelled cumulative 4-year seedling survival as a function of first-year seedling height or canopy area for seedlings that were alive to be measured at the end of the first year ($N = 1697$). Separate models were built for height and canopy area due to their collinearity.

3 | RESULTS

3.1 | Weather conditions during study period

Weather conditions differed greatly over the 4 years of our study (Figure S3). In the first growing season that followed the sowing of cohort one (2020), temperatures were generally lower, and relative humidity was higher than in the growing season that followed the sowing of cohort two (2021). The third year of the study (2022) was intermediate in conditions, falling within the range of the other years in the study during spring and early summer. A large precipitation pulse occurred in August 2022, and a period of very high precipitation began in November 2022 and continued into the summer of the following year. The final year (2023) was unusually wet, with high relative humidity coinciding with heavy precipitation periods through the winter and spring.

3.2 | Watering treatment effects

The 'control' treatment experienced ambient conditions of the common garden site, which were characterized by spring and summer precipitation at or near the low end of the range of the seed source locations (black symbols in Figure 2a). The 'spring' watering treatment (pink symbols in Figure 2a) received spring precipitation at or near the upper end of the range of the seed source locations, with low summer precipitation. The 'summer' watering treatment (orange symbols in Figure 2a) experienced the opposite: summer precipitation at or near the upper end of the range of the seed source locations, with low spring precipitation. The spring + summer watering treatment ('both'; blue symbols in Figure 2a) experienced intermediate levels of precipitation in both spring and summer.

The watering treatments had the expected effect on soil water content during the treatment periods (Figure 2b). During the spring season, VWC was highest in the 'spring' watering treatment, lowest in the 'control' and intermediate in the other treatments. During the summer season, VWC was highest in the 'summer' watering treatment. VWC differences among treatments and seasons were statistically strong ($p < 0.001$), yet mean differences were small in magnitude (Figure 2b), reflecting overall low soil moisture at the site, ephemeral effects of watering additions and temporal variation across the growing season.

3.3 | Overall seedling survival

There were large differences in emergence and survival between the two cohorts (Table 1). In cohort one (sown in fall 2019), 3378 seedlings emerged. Annual seedling mortality was approximately 50% in the first and second years, and then mortality declined in the third and fourth years, resulting in 18% that were alive at the end of 4 years. Cohort two (sown in fall 2020) had much lower emergence than cohort one and very low survival; only 3.6% of seedlings survived the first year, and 1.2% were alive after 3 years.

3.4 | Population-level differences in seedling survival under varying precipitation regimes

We found strong effects of seed source climate, watering treatment and nurse shrub cover on the survival of cohort one seedlings, especially in the first 2–3 years after emergence. Seedlings from seed sources with high cumulative water deficit (more arid conditions) had higher survival in all watering treatments than seedlings from cooler/wetter seed sources. This effect declined with seedling age but was strong in the first 3 years (Figure 3a,d,g). After 4 years, seedlings whose seed sources had a water deficit in the 5th percentile of our

TABLE 1 Seedling survival in each year.

Cohort	# seeds sown	# emerged	First year (% alive)	Second year (% alive)	Third year (% alive)	Fourth year (% alive)
Cohort one	6624	3378	50.2%	24.6%	18.4%	18.0%
Cohort two	2667	647	3.6%	1.4%	1.2%	–

Note: Survival percentages represent the % of seedlings that were alive at the end of each year, relative to the number of seedlings that emerged after sowing. Cohort two was sown 1 year into the study and thus does not have fourth-year survival data.

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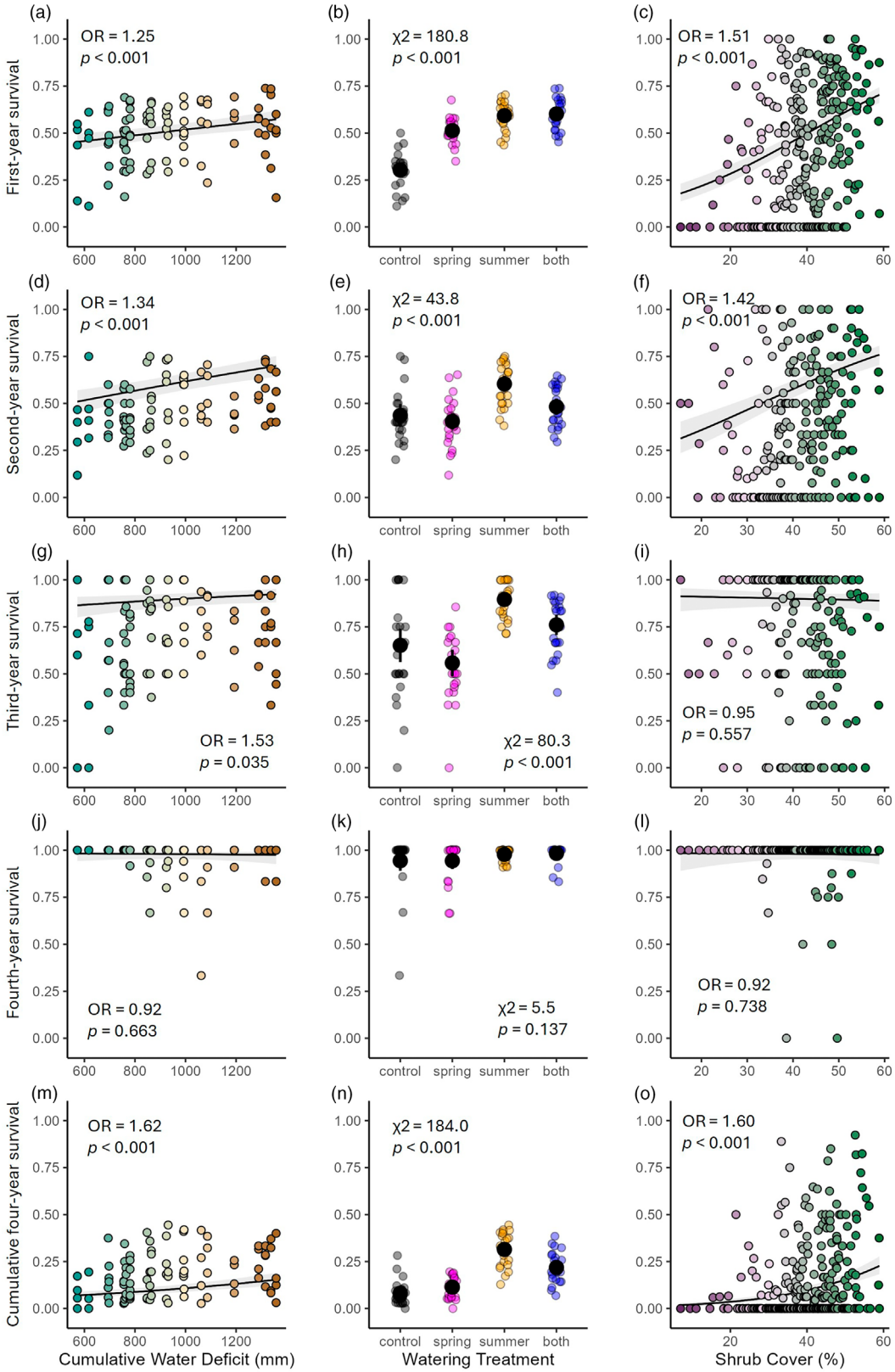

FIGURE 3 Seedling survival during the 4-year study period (cohort one). Predicted partial effects (mean ± 95% CI) of seed source cumulative climatic water deficit (a, d, g, j, m), watering treatment (b, e, h, k, n) and shrub cover (c, f, i, l, o). Points show mean survival for each level of the predictor variable. OR, standardized odds ratios.

study sites (617 mm) had a 15% probability of survival, compared to a 29% probability of survival for seedlings from the 95th percentile (1338 mm; Figure 3m). Contrary to our hypothesis, differences in survival were not explained by variation in summer precipitation in the seed source locations ($p=0.739$, 0.553, 0.279 and 0.168 across the 4 years of the study). We found no interactions between seed source climate and watering treatment (Table 2), which indicates that seed source differences in water deficit or summer precipitation did not influence the effects of watering treatments.

The effect of treatment varied somewhat among the years of the study (Figure 3, middle column), although survival was consistently highest for seedlings in the summer watering treatment. After 4 years, seedlings in the summer watering treatment had a 29% predicted probability of survival, compared to 8% in the control, 10% in the spring treatment and 21% in the spring + summer treatment.

Nurse shrub cover was the strongest predictor of seedling survival in the first 2 years after emergence (Figure 3c,f), but this effect declined with seedling age and there was no effect in the third or fourth years (Figure 3i,l). Seedlings under 40% canopy cover had a 10% probability of being alive after 4 years, whereas seedlings under 55% canopy cover had a 36% survival probability (Figure 3o).

Only 3.6% of cohort two seedlings survived to the end of their first year (1.2% in the control treatment), compared to more than 50% of cohort one seedlings (30.3% in control; Table 1; Table S2). We found weak positive effects of seed source water deficit ($p=0.24$), summer precipitation ($p=0.39$) and nurse shrub cover ($p=0.16$) on the first-year survival of cohort two seedlings (Table S3; Figure S4). Survival was highest for seedlings in the spring + summer watering treatment ($p=0.02$). Consistent with our results for cohort one, we found no interactions between seed source climate and watering treatment (Table S3).

3.5 | Effect of climate transfer distances on seedling survival

We found a quadratic relationship between survival and the climate transfer distance of mean annual temperature (Table 3; Figure 4a), which represents the degree of difference between the temperature experienced by a seedling in the common garden and the temperature at its seed source. Seedling survival was estimated to be high across a broad range of temperature transfer distances near or below 0, meaning that the highest survival was in seedlings from seed sources that were as warm or warmer than the common garden. Seedling survival declined substantially as temperature transfer distances increased, with the lowest survival among seedlings from the coolest seed sources.

We also found a quadratic relationship between survival and spring precipitation transfer distance (Table 3). Survival was highest for seedlings whose seed source locations received similar amounts of spring precipitation to the common garden, with the estimated optimum at a distance of −9.1 mm, a very small difference compared to the range included in the study (Figure 4b). Seedling survival declined if seedlings received much more or much less spring precipitation in the common garden than experienced in their seed source (Figure 4b).

Finally, the relationship between summer precipitation distance and survival was monotonically positive (Table 3; Figure 4c). This indicates that, within the range included in our study, additional summer precipitation had a consistently positive effect on survival, even

TABLE 3 Results of logistic regression model predicting cumulative 4-year survival for cohort one seedlings, as a function of climate transfer distances.

Predictor variables	Odds ratio	95% CI	*p*-value
Mean annual temp. distance	**0.82**	**0.74–0.91**	**<0.001**
(Mean annual temp. distance)^2	**0.88**	**0.79–0.99**	**0.025**
Summer precipitation distance	**1.78**	**1.56–2.02**	**<0.001**
(Summer precipitation distance)^2	0.92	0.82–1.04	0.175
Spring precipitation distance	0.98	0.86–1.11	0.707
(Spring precipitation distance)^2	**0.88**	**0.78–0.99**	**0.028**
Shrub cover	**1.62**	**1.46–1.80**	**<0.001**

Note: Bolded where $p<0.05$ to emphasize important effects.

TABLE 2 Results of logistic regression models predicting cohort one seedling survival in each year of the study.

Predictor variables	First year survival ($N=3378$) χ^2-value (*p*-value)	Second year survival ($N=1697$)	Third year survival ($N=830$)	Fourth year survival ($N=622$)	4-year cumulative survival ($N=3378$)
Seed source water deficit	**14.3 (<0.001)**	**20.7 (<0.001)**	**4.4 (0.035)**	0.19 (0.663)	**29.6 (<0.001)**
Seed source summer precipitation	0.11 (0.739)	0.35 (0.553)	1.2 (0.279)	1.9 (0.168)	2.1 (0.146)
Treatment (factor, 4)	**180.8 (<0.001)**	**43.8 (<0.001)**	**80.3 (<0.001)**	5.5 (0.137)	**184.0 (<0.001)**
Water deficit × treatment	1.7 (0.631)	0.30 (0.961)	2.7 (0.519)	0.05 (0.997)	4.2 (0.242)
Summer precipitation × treatment	3.5 (0.315)	1.4 (0.698)	4.2 (0.246)	3.0 (0.388)	7.6 (0.055)
Shrub cover	**121.4 (<0.001)**	**47.9 (<0.001)**	0.35 (0.557)	0.11 (0.738)	**86.8 (<0.001)**

Note: Bolded where $p<0.05$ to emphasize important effects. Effect sizes (odds ratios) are shown for continuous variables in Figure 3.

when the amount of water the seedlings received in summer far surpassed the climate of their seed source.

3.6 | Population-level differences in early seedling growth and effects on survival

At the end of the first growing season, seedlings from more arid locations (higher water deficit) were taller and had a larger canopy area than seedlings from cooler/wetter locations (Table 4; Figure 5a,d). Seedlings from seed sources with higher summer precipitation were slightly smaller than those from seed sources with low summer precipitation, though this relationship was weak for both height and canopy area (Table 4; Figure 5b,e). Treatment had a weak effect on seedling height, with seedlings grown in the summer watering treatment finishing their first growing season approximately 0.1–0.3 cm taller than seedlings in the other treatments—a difference that barely exceeded the precision of our measurements (Figure 5c). There was no effect of treatment on canopy area (Figure 5f). We found no interactions between seed source climate and treatment. We also found no effect of nurse shrub canopy cover on seedling size.

Seedling size was positively related to seedling survival, and the seedlings that were greater than 4 cm tall at the end of their first year were twice as likely to survive to the end of the fourth year than seedlings less than 2 cm tall (Figure 5g,h).

4 | DISCUSSION

Seedling establishment is a demographic bottleneck for many tree species (Andivia et al., 2020; Padilla & Pugnaire, 2007), yet recruitment may be a critical determinant of forest composition in future climate conditions (Clark et al., 2016). Using a 4-year common garden experiment, we found that seed source climate was associated with meaningful differences in *P. monophylla* recruitment, indicating the presence of drought-adapted phenotypes at the arid edge of the species' range. However, evidence of local adaptation to temperature and sensitivity to levels of spring precipitation suggests that future recruitment may be constrained by changing climate, such as increasing temperatures, shifts in precipitation seasonality and declining soil moisture (Schlaepfer et al., 2025; Snyder et al., 2019). Collectively, our findings indicate that reduced seedling survival under hotter and drier conditions may reduce the frequency of episodic recruitment events and make some populations of *P. monophylla* vulnerable to maladaptation and extirpation.

4.1 | Trailing edge or stress-adapted?

Species distribution models often predict that species' suitable habitat will shift to track changes in climate, based on the assumption that

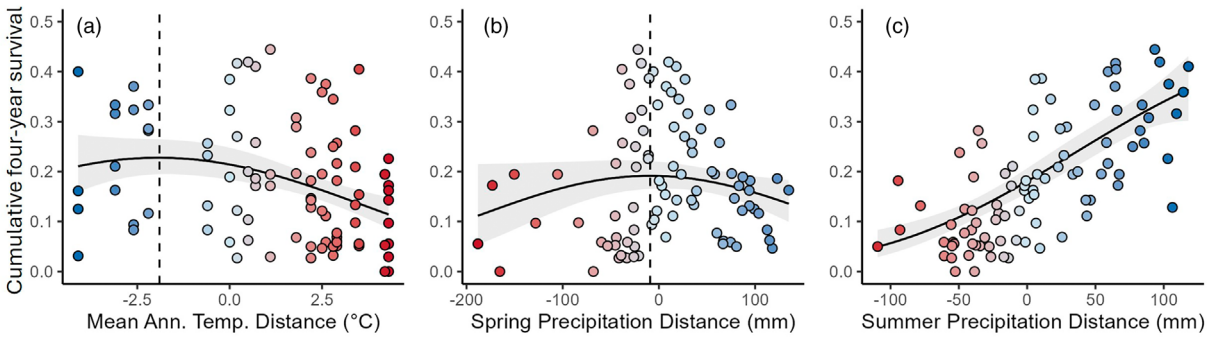

FIGURE 4 Cumulative seedling survival after the 4-year study, as a function of climate transfer distances (cohort one). Predicted partial effects (mean ± 95% CI) of climate transfer distances for (a) mean annual temperature, (b) spring precipitation and (c) summer precipitation. Vertical dashed lines in (a) and (b) show the estimated optima for the quadratic relationships. In all panels, blue points show where the common garden site is cooler or wetter than the seed source location, and red points show where the site is warmer or drier than the seed source.

TABLE 4 Results of models predicting cohort one seedling size metrics at the end of their first year.

	First year height ($N = 1697$)	First year canopy area ($N = 1697$)
Predictor variables	χ^2-value (p-value)	
Seed source water deficit	**223.2 (<0.001)**	**226.0 (<0.001)**
Seed source summer precipitation	**8.6 (0.003)**	2.8 (0.094)
Treatment (factor, 4)	**37.4 (<0.001)**	2.1 (0.542)
Water deficit × treatment	1.3 (0.720)	1.5 (0.691)
Summer precipitation × treatment	2.8 (0.424)	4.7 (0.193)
Shrub cover	2.8 (0.096)	0.63 (0.427)

Note: Bolded where $p < 0.05$ to emphasize important effects. Effect sizes (β-coefficients) are shown for continuous variables in Figure 5a–f.

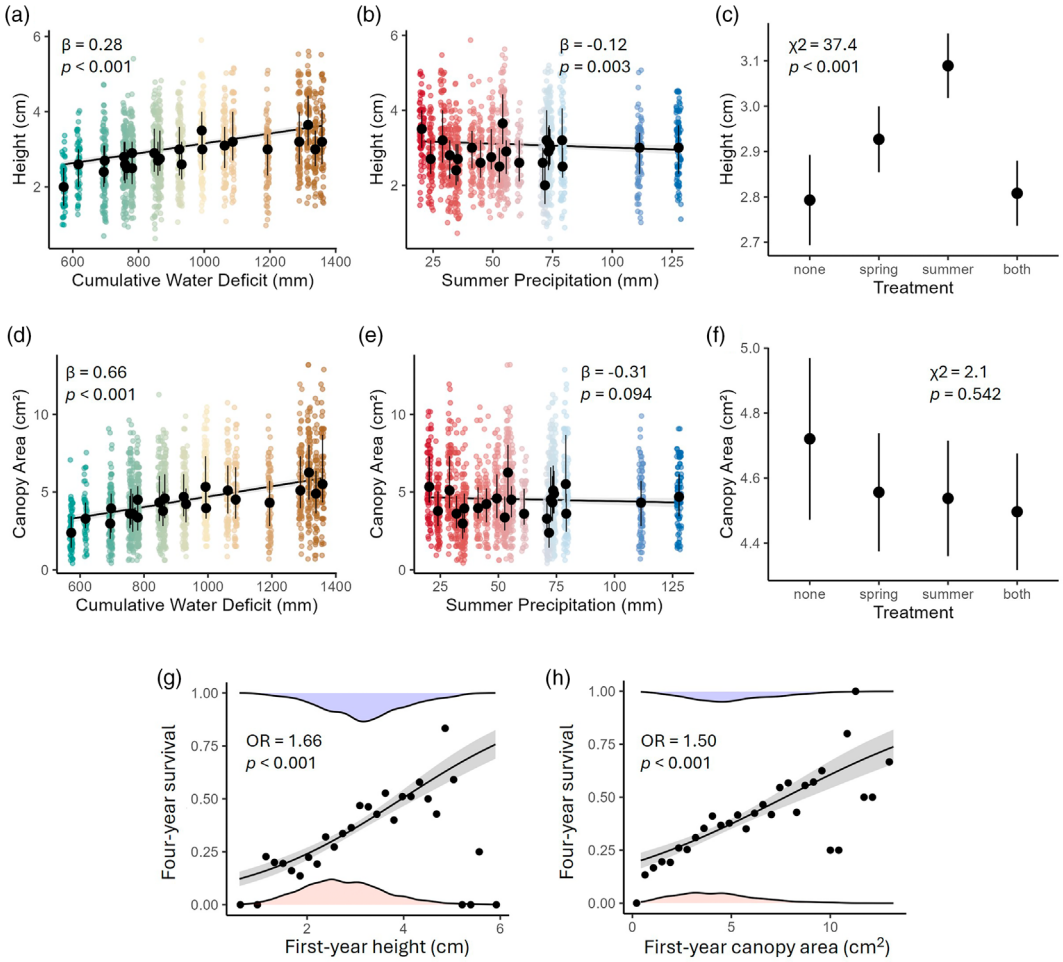

FIGURE 5 Seedling size at the end of the first year and relationship with survival (cohort one). Predicted partial effects (mean ± 95% CI) of seed source climate and watering treatment on seedling height (a–c) and canopy area (d–f). In (a), (b), (d) and (e), the black dots show the median ± IQR for each level of the predictor, with raw data shown in the background. Predicted effect (mean ± 95% CI) of first-year height (g) and canopy area (h) on 4-year seedling survival. In (g) and (h), the density plots show the distribution of the data (pink = dead; blue = live), and black points show mean survival for discrete bins of each predictor variable. OR, standardized odds ratios.

current distributions reflect an equilibrium with historical climate (Elith & Leathwick, 2009). Species distribution models for *P. monophylla* predict declines in suitability as a result of climate change for the hottest and driest margins of its range, which are projected to become climatically unsuitable by the end of the 21st century (Noel et al., 2025; Urza et al., 2020). This suggests that populations at the arid edge of the species' distribution may be 'trailing edge' populations, where range contraction may occur in newly unsuitable habitat as climate becomes hotter and drier (Freeman et al., 2018). However, this expectation ignores potential functional trait differences among populations that result in differential capacity for tolerating abiotic stress such as drought (Gonzalez de Andrés et al., 2021). In this study, we found that *P. monophylla* seedlings sourced from hotter, drier locations had higher survival than seedlings from milder climates under all simulated precipitation regimes, especially in the first 2–3 years after emergence. These results suggest that populations that historically experienced arid conditions may have drought-adapted phenotypes that allow for successful recruitment despite abiotic stress. This finding is consistent with several studies in other tree species, which have found higher survival of tree seedlings from populations with dry origins when grown under hot and dry conditions (Matías & Jump, 2014; Ramírez-Valiente et al., 2009). Importantly, our experimental study site was located near the hot, dry edge of the species' range, so our results do not provide insight into likely responses of populations experiencing more mesic conditions.

Recruitment differences among seed sources are likely related to clinal variation in functional traits that determine seedling emergence, survival and growth. Several studies have found that tree populations from more arid environments produce heavier seeds (Ramírez-Valiente et al., 2009; Salazar-Tortosa et al., 2019), potentially as a strategy to improve individual reproductive success in stressful conditions (Muller-Landau, 2010; Westoby et al., 2002). Seed mass can enhance germination, and the reserves associated with a larger seed can increase early seedling growth and survival in water-limited environments (Murray et al., 2004; Ramírez-Valiente et al., 2021). Previous studies on the same populations of *P. monophylla* found that trees in more arid environments produced heavier seeds than trees in wetter locations (Vasey et al., 2022), and their seedling offspring had consistently faster growth of both above-ground and below-ground biomass when grown

in a common garden (Vasey et al., 2023). In our study, we found that seedlings sourced from more arid locations were larger above-ground than seedlings from mesic locations after their first growing season and that seedling size and survival were positively related. However, as we did not include root measurements in our study, the role of root trait differences among treatments or populations is unknown. Rapid development of root biomass is critical for seedling survival, facilitating resource acquisition and providing an opportunity for a seedling to overcome the establishment bottleneck in harsh abiotic conditions (Larson & Funk, 2016). Biomass allocation patterns have been found to be sensitive to irrigation conditions for many species, and drier conditions are often associated with an increased root biomass fraction (Bachofen et al., 2019; Taeger et al., 2015; Vasey et al., 2023). Whereas other studies have found that increased above-ground biomass can increase the risk of mortality in water-limited conditions (Augustine & Reinhardt, 2019), potentially because higher above-ground growth comes at the expense of root growth, we did not see evidence of a growth-survival trade-off, instead finding that seedling size and survival were positively related. Although it is unknown whether the observed variation in *P. monophylla* seed and seedling traits is genetically determined or representative of plastic responses via maternal effects, the association between increased seed size, seedling growth and seedling survival suggests that populations in arid locations are likely to produce seedlings that can withstand drought.

Despite the presence of drought-adapted phenotypes, increasingly hot, water-limited conditions may eventually overwhelm the capacity for extant populations to persist in situ (Davis & Shaw, 2001). Adaptive responses such as selection, demography and dispersal are expected to be much slower than the velocity of anthropogenic climate change (Lambers, 2015), resulting in adaptation 'lags' that manifest as observed mismatches between current and optimal climate conditions (Mátyás, 1994). Our results were consistent with patterns of local adaptation to mean annual temperature, shown by a quadratic relationship between seedling survival and climate distance. However, survival was highest for seedlings for whom the common garden location was cooler than their seed source, shown by an estimated optimum at climate distances at or below zero. This suggests that the warmest populations in our study may be adapted to optimize seedling survival in temperatures that are cooler than they currently experience. Similar mismatches have been observed in other *Pinus* species of North America (Bisbing et al., 2021; Martínez-Berdeja et al., 2019), with local genotypes being outperformed in their home environments by genotypes which evolved under historically warmer climates.

4.2 | Local adaptation to seasonal precipitation regimes?

Precipitation regimes dictate the timing of soil water that is available for plant use, and differences in seasonal precipitation patterns may result in distinct selection pressures (Schwinning & Ehleringer, 2001; Schwinning & Sala, 2004). While adaptations to local precipitation regimes may optimize seedling success in a constant environment, strong local adaptation may become maladaptive as climate changes (Mátyás, 1994). We found mixed evidence for local adaptation to seasonal precipitation regimes, as patterns of survival were consistent with adaptation to levels of spring, but not summer, precipitation. Adaptation to specific precipitation regimes is challenging to examine because the timing of precipitation is often confounded with overall differences in annual precipitation or temperature. While reciprocal transplants are considered the gold standard for uncovering evidence of local adaptation (Johnson et al., 2022), experimental manipulations such as ours benefit from the ability to alter the seasonal timing of water while holding other conditions constant.

Even though all supplemental watering treatments in our study received the same total amount of annual water, strong treatment differences illustrate the critical importance of the timing of water availability. Specifically, additional water during the summer months resulted in much greater seedling survival than water in spring, and this effect was not mediated by the amount of summer precipitation experienced in the seed source locations. Watering treatment effects were slightly less pronounced in the first year of the study, when the spring and summer watering regimes were more similar than in subsequent years, suggesting that the effect of precipitation timing may depend on the magnitude of seasonal shifts. Treatment differences mirrored the results of the climate distance analysis, which showed a monotonically positive relationship between summer precipitation and survival, even if the amount of water received far exceeded summer precipitation in the seed source location. Annual precipitation across the range of *P. monophylla* predominantly falls as winter and spring snow and rain, and available soil moisture tends to be especially low during the hot summer months (Chenoweth et al., 2023), a pattern seen in our measurements of soil water content. Thus, summer water inputs that alleviate this period of summer drought may allow seedlings to survive until the arrival of the next cool season (Chambers, 2001). In contrast to the consistently positive effects of summer water, we found that survival was greatest when the spring precipitation received in the experiment matched mean spring precipitation from the seed sources, and receiving more or less spring water than what is experienced in the seed source decreased survival. In other words, seedling survival was optimized under spring precipitation levels similar to those of the population's home environment, consistent with patterns of local adaptation (Kawecki & Ebert, 2004).

Many observational studies have inferred the importance of precipitation timing on seedling recruitment (e.g. Larson et al., 2021; Shriver et al., 2018), yet few studies have evaluated seedling survival in response to experimentally manipulated precipitation seasonality in a field setting. One such study found that oak seedling survival was not impacted by shifts in precipitation from summer to winter, although reduced carbon accumulation suggested potential long-term effects of summer drought (Weltzin et al., 2001). Other experimental studies have evaluated the effects of changing precipitation seasonality on plant growth, community composition and ecosystem productivity. Several

experimental studies have found plant communities to be relatively insensitive to shifts in precipitation seasonality (reviewed in Miranda et al., 2011), while others have found that biomass and species diversity responded primarily to watering in the fall (Densmore-McCulloch et al., 2016) or in spring (Bates et al., 2006), although these effects were not seen until 2–4 years of treatment.

4.3 | Importance of interannual and microsite variability in abiotic conditions

We found that temporal and spatial variability in climate affected seedling establishment, beyond the effects of the watering treatments. Arid and semiarid regions of the western United States experience very high interannual variability in weather conditions, with fluctuations in the magnitude and seasonality of both temperature and precipitation (Chenoweth et al., 2023). Recruitment is thus often episodic in dryland ecosystems, with long-term population growth reliant on the occurrence of favourable weather conditions (Brown & Wu, 2005; Shriver et al., 2018; Urza et al., 2021). Many previous seedling studies have found that outcomes were affected by weather conditions in the study year (e.g. Chambers, 2001; Ramírez-Valiente et al., 2021). In our study, we saw large differences in first-year survival between the two cohorts that were sown in successive years. While more than 30% of the control treatment seedlings in the first cohort survived to the end of their first year, just over 1% of the second cohort did so, and surprisingly, the supplemental soil moisture provided by the watering treatments did little to offset these effects. Low survival in the second cohort may have been related to overall low winter precipitation and high summer temperatures experienced during their first growing season, although punctuated events such as springtime freezes or extreme heat may have played an important role (Chamberlain & Wolkovich, 2021; Hankin et al., 2025). Additionally, seed viability declined after a year in cold storage, as indicated by the reduced rate of seedling emergence in the second cohort, and the resulting decreases in seed quality may have negatively impacted seedling survival.

We also found a strongly positive effect of nurse shrub canopy cover on seedling survival, illustrating the importance of facilitation for mediating, and in this case buffering, climate effects on demographic processes. Many dryland plants have increased establishment, growth and reproduction in shaded microsites (Maestre et al., 2021). Nurse shrubs alter the microclimatic conditions that are experienced by plants growing under their canopies, thus influencing the range of broad-scale climate conditions in which a dependent species can persist and potentially expanding the species' realized niche (Bulleri et al., 2016). The shrub *A. tridentata* has been shown to buffer elevational differences in climate, ameliorating harsh abiotic conditions and allowing *P. monophylla* seedlings growing under its canopy to overcome an early establishment bottleneck (Chambers, 2001; Urza et al., 2019). We found that *P. monophylla* seedlings were highly sensitive to the amount of shade provided by their nurse shrub, and higher levels of shrub canopy cover greatly improved seedling survival during the first 2 years of establishment. Survival of seedlings older than 2 years was not improved by increasing shrub cover, supporting previous findings that nurse shrub facilitation of *P. monophylla* seedlings is important primarily for the earliest stages of seedling development (Urza et al., 2019).

4.4 | Implications for population persistence in a future climate

Our experimental study site was located near the hot, dry edge of the species' range, and our results provide insight into possible responses of populations experiencing increasingly arid conditions. Climate projections for the range of *P. monophylla* predict continuing temperature increases, with increases in both summer maximum temperatures and winter minimums (Snyder et al., 2019). Projections for precipitation are less certain, with potential increases in annual and seasonal precipitation across some portions of *P. monophylla*'s range (Bradford et al., 2020; Snyder et al., 2019). However, increases in atmospheric water demand associated with higher temperatures may offset the benefits of additional precipitation on soil moisture, resulting in robust projections of reduced summer soil water availability (Palmquist et al., 2016). Rising temperatures are also expected to directly influence soil water dynamics in regions with winter-dominated precipitation regimes, increasing the proportion of precipitation falling as rain, reducing the persistence of winter snowpack and advancing the timing of spring snowmelt (Fyfe et al., 2017; Klos et al., 2014; Petersky & Harpold, 2018). These climate changes may result in shifts in the distribution of *P. monophylla*. At upper elevation forest edges currently limited by low temperatures, continued warming may lead to increased recruitment and expansion into newly suitable habitats, while increasing aridity may result in forest contraction at arid, lower elevation range margins (Noel et al., 2025; Shriver et al., 2022). Recent increases in drought duration and severity have resulted in widespread regeneration failures for other dryland conifer species (Petrie et al., 2023), and range-wide demographic models have found that 10%–20% of *P. monophylla* populations are declining in the warmest and driest locations within the species' range (Shriver et al., 2022).

Nonetheless, our study suggests that populations at the climatic trailing edge may contain valuable drought-adapted seedling phenotypes that can establish in harsh abiotic conditions. Determining thresholds beyond which adaptive capacity is overwhelmed will be critical for anticipating demographic responses to changing climate conditions. Migration may be facilitated by the mountainous basin-and-range topography that characterizes *P. monophylla*'s distribution, because steep climatic gradients enable the upslope dispersal needed to track climate change (Loarie et al., 2009). Assisted population migration may also be used to move drought-adapted seedling phenotypes into warming locations, although there are many related uncertainties (Twardek et al., 2023), and more work is needed to determine the extent to which phenotypic variation is adaptive in later life stages. The strong effect of nurse shrub canopy cover suggests that climate change effects on recruitment may be

partially buffered by local biotic interactions for species such as *P. monophylla*. Importantly, the effects of precipitation shifts may be contingent on seasonal timing, and our results suggest that *P. monophylla* seedling survival in hot and dry locations could depend on the direction of change in summer precipitation. Climate is a multivariate and complex agent of natural selection, and it will be important to disentangle the climate drivers of adaptive variation in *P. monophylla* and associated impacts on recruitment.

AUTHOR CONTRIBUTIONS

Alexandra K. Urza and Peter J. Weisberg conceived the ideas; Alexandra K. Urza, Peter J. Weisberg, David I. Board, Jeanne C. Chambers and Georgia L. Vasey designed the experiment; David I. Board, Alexandra K. Urza and Jeremy S. Adkins analysed the data; Alexandra K. Urza wrote the initial draft of the manuscript; all authors collected data, contributed to the interpretation and edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data are available on the Dryad data repository (Urza et al., 2026; https://doi.org/10.5061/dryad.h18932025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Seed source information.

Table S2. Observed seedling survival for cohort two in each year, for each watering treatment.

Table S3. Results of logistic regression models predicting cohort two seedling survival during the first year after emergence.

Figure S1. Correlation matrix of climate variables from the seed source locations.

Figure S2. Principal component analysis for climate characteristics of the seed source locations.

Figure S3. Monthly climate data for the 4 years of the study.

Figure S4. First-year seedling survival for cohort two.

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