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RESEARCH ARTICLE

What common-garden experiments tell us about climate adaptation in plants

Local climate adaptations in two ubiquitous Mojave Desert shrub species, *Ambrosia dumosa* and *Larrea tridentata*

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Abstract

1. Widely distributed species are often locally adapted to climate gradients across their ranges. But little is known about the patterns of intraspecific adaptation in desert shrubs.
2. We examined the questions of local adaptation in multiple populations of two common shrub species of the winter-wet Mojave Desert in North America in a multiple common garden experiment. Plants were raised in the greenhouse and transplanted at the age of 1 year. *Ambrosia dumosa* is a drought-deciduous low shrub and *Larrea tridentata* is an exceptionally long-lived evergreen. Over 4 years, we monitored growth, survivorship, leaf and reproductive cover and once measured leaf N content, $\delta^{13}C$ and SLA. We hypothesized that populations of both species would be differentiated along a growth–survivorship trade-off according to homesite aridity.
3. Both species exhibited previously undocumented population differences along gradients of winter precipitation and temperature. In general, populations from more winter-mesic regions had faster growth in more mesic gardens and lower survivorship in the most arid garden. Homesites with more variable summer precipitation had greater growth for *A. dumosa* populations, but lower growth for *L. tridentata*. Among *L. tridentata* populations, leaf cover correlated positively with growth and negatively with survival time. For *A. dumosa* populations, growth and survival could not be attributed to specific traits across gardens. However, larger transplants had generally lower growth rates and higher survival rates across gardens, except in the driest garden, where the population averages of intrinsic water use efficiency (iWUE) and stem growth rate were positively correlated.
4. *Synthesis*. Two dominant species of the Mojave Desert adapted locally to variation in winter and summer precipitation and temperature. They did so in different ways, suggesting that *L. tridentata* mitigated the risk of hydraulic failure, while *A. dumosa* optimized carbon assimilation for growth.

KEYWORDS

climate adaptation, ecological restoration, fast–slow spectrum, phenological plasticity, reciprocal transplant experiment, reproductive trade-off, winter precipitation gradient

1 | INTRODUCTION

Much of plant trait variation can be attributed to adaptations to the physical environment, including soil properties and climate (Caruso et al., 2020; Li et al., 2018; Oliveira et al., 2019; Shipley et al., 2012; Wright et al., 2000). The direction of quantitative trait change along ubiquitous environmental gradients such as elevation (Halbritter et al., 2018), aridity (Ivanova et al., 2019) or seasonality (Pearse & Hipp, 2012) is often repeated within and across species, providing fertile ground for the development of general principles of environmental adaptation to inform theories of species coexistence (Chesson et al., 2004), the role of 'environmental filtering' in community assembly (Ackerly & Cornwell, 2007; Adler et al., 2010; Kraft et al., 2015) and climate niche evolution (Martinez-Cabrera & Peres-Neto, 2013). These perspectives are also important for the management of ecosystems increasingly disrupted by anthropogenic forces, including the selection of ecotypes for revegetation (Corlett, 2016; Laughlin, 2014).

An essential part of this effort is the reduction of multiple trait spectra down to a few dimensions of a strategic continuum. A simple but universal framework is the fast–slow plant economics spectrum (Chave et al., 2009; Reich, 2014; Westoby et al., 2002; Wright et al., 2005), which is rooted in the assumption of an optimal allocation of internal plant resources to maximize carbon assimilation and biomass accumulation under the constraints of a given environment (Bloom et al., 1985). 'Fast' plants have traits that permit rapid resource acquisition and processing when or where resources are readily available. This requires leaves with a high capacity for gas exchange and support by a whole-plant hydraulic architecture built for high transport rates. 'Slow' plants have traits that permit resource extraction and a positive carbon balance even when resource levels are low or temperature is extreme. This usually requires leaves with lower carbon and energy demands and a hydraulic architecture with greater structural resistance to embolism (Reich, 2014). While the mechanistic basis of the fast–slow economics spectrum is well-fleshed out, its integration with demographic trade-offs such as between growth and survivorship has been incomplete, especially in non-forest biomes, where resource limitations other than light are more dominant (Russo et al., 2008).

At the heart of the matter are the mechanisms that link mortality risk to plant carbon economy. Originally, growth–survivorship trade-offs were thought of as whole-plant allocation trade-offs between growth, reproduction and survivorship (Stearns, 1999). The assumption was that allocation patterns supporting rapid growth are distinct from patterns supporting survival. For example, in desert biomes, species often vary in allocation to root and shoot biomass (Chapin et al., 1993). Root allocation may be interpreted as a form of allocation to (drought) tolerance or avoidance favouring survival, while shoot allocation increases the potential for rapid growth.

Another way in which high growth potential might increase mortality risk is through carbon starvation (Russo et al., 2008). Slow plants typically have leaves that cost less in production and maintenance, and can therefore maintain positive carbon balance for longer under-resource scarcity. This favours survival but limits growth capacity when resources are abundant (Sartori et al., 2019). Yet another model links growth and mortality to vascular system architecture, suggesting that fast plants with higher water transport efficiency are more prone to dying by hydraulic failure, that is irreparable damage to the vascular system by temperature extremes or drought, compared to slow plants with more resilient xylem structure but limited transport capacity (Anderegg et al., 2013; McDowell et al., 2008; Sperry & Love, 2015).

While species with divergent strategies almost always coexist in the same environment (Aguilar-Romero et al., 2017; Negreiros et al., 2016), the fitness consequences of divergent strategies are best observed by comparison across contrasting environmental conditions. Under more stressful conditions, slower plants are expected to survive longer; and under more productive conditions, faster plants are expected to grow faster. A further corollary of these interactions between growth and survival is that populations should adapt to local climate predictably with shifts towards strengthening survival function under harsher conditions and shifts towards growth potential under more productive conditions (Reich et al., 2003).

Nevertheless, growth–survivorship trade-offs have proven difficult to observe in nature (Adler et al., 2014; Merila & Hendry, 2014). One reason might be that many plants have substantial phenotypic plasticity (Bloom et al., 1985; Perrin, 1992) that may mitigate risks associated with a particular life-history strategy. For example, species susceptible to dying by hydraulic failure may increase hydraulic safety by rapidly reducing leaf area during drought (Arndt et al., 2015; Challis et al., 2021). A species more susceptible to death by carbon starvation may conversely optimize leaf structure, chemistry and life span to maximize the lifetime net productivity (Aronson et al., 1993; Vilela et al., 2008). A second important reason for failing to observe trade-offs between growth and mortality is that the fate of individual plants often depends on their sizes (Esque et al., 2015; Russo et al., 2021). For any given cohort, faster growth early in life can potentially prepare plants better for future stress than chemical, physiological or structural fortification (Van Noordwijk & Dejong, 1986). *On average*, that is, over multiple generations, fortification may be the better strategy in a more stressful environment, but representative averages are rarely observed.

Questions addressing the relationships between climate, mechanisms of selection and adaptive evolution are timely not just for conceptual ecology, but also for addressing applied problems such as ecological restoration (Baughman et al., 2019) and potential responses to climate change. World-wide, numerous common garden experiments are underway to determine the extent of population variation within species' ranges to better understand how plastic and genetically fixed traits affect growth and survivorship. With such knowledge, it may become possible to design more refined revegetation strategies beyond the blanket 'local is best' approach (Bucharova et al., 2017).

Here, we present results from a multiple common garden study conducted in the bioregion of the Mojave Desert, where local

climate is influenced by elevational differences in the basin–range topography (Beatley, 1975) and the spatially and temporally variable influence of the North American monsoon system (Truettner et al., 2019). It is the first multiple common garden study with a focus on the two most common perennial plant species of the Mojave Desert: *Larrea tridentata* (creosote bush) and *Ambrosia dumosa* (Gray) Payne (white bursage or burro-weed). The *L. tridentata*–*A. dumosa* community covers *c*. 70% of the Mojave Desert typically between 375 m and 500 m elevation (MacMahon, 1988). Both species are highly drought-tolerant shrubs, but *L. tridentata* is a long-lived, deep-rooted evergreen shrub with a potential life span of several 100 years, while *A. dumosa* is a shallow-rooted drought-deciduous short-statured shrub with a typical life span of several decades (Bowers, 2005; Cody, 2000; Schwinning & Hooten, 2009).

The critical water potential threshold for the loss of hydraulic conductivity is similar for the two species, well below −10 MPa and perhaps somewhat lower for *A. dumosa* (Huxman et al., 2004; Mencuccini & Comstock, 1997). Shallow-rooted, deciduous species tend to have steeper declines in water potential, which end in leaf xylem embolism and leaf abscission. Non-phreatophytic evergreen species tend to maintain wider safety margins against hydraulic failure (Hacke et al., 2000). However, under conditions of extreme drought, both species experience canopy dieback and mortality, *A. dumosa* more so than *L. tridentata*, and mortality in *A. dumosa* declines with greater plant size (Hamerlynck & McAuliffe, 2008).

There is almost no information on genotypic and phenotypic differentiation in the two species across their ranges, except for ploidy differences. *Ambrosia dumosa* diploids occur throughout its range, hexaploids occur only in southern California and tetraploids across the range except in southern Baja California and Owens Valley (Raven et al., 1968). *Larrea tridentata* has ploidy differences across the Chihuahuan (diploid), Sonoran (tetraploid) and Mojave Deserts (hexaploid) of North America (Hunter et al., 2001) with very limited co-occurrence in the transition zones (Laport et al., 2012). In *L. tridentata*, cytotype races are correlated with seedling and adult traits (Laport & Ramsey, 2015; Walters & Freeman, 1983), but there are no reports on genotype differentiation within cytotype for this species. For *A. dumosa*, one study reported differentiation between extreme northern and southern populations of *A. dumosa* grown in the greenhouse (Comstock, 2000). Populations of *A. dumosa* from the southern edge of the range, which is hotter but has two rainy seasons, had higher rates of leaf gas exchange but less biomass allocation to leaves and more allocation to tap roots compared to plants from the northern edge of the range.

A recent study showed that *L. tridentata* can shift hydraulic strategy seasonally and with antecedent soil moisture (Guo et al., 2020) in a manner consistent with limiting the risk of hydraulic failure when potential carbon gains do not warrant such risk taking. Control over risk exposure, including changes in fine root dynamics (Wilcox et al., 2004) and leaf cover (Kurc & Benton, 2010) could have a genetic component and produce between-population variability in mortality and growth under shared conditions.

In drought-deciduous species, hydraulic failure occurs annually and results in leaf abscission, which protects the remaining hydraulic architecture from permanent damage (Bucci et al., 2013; Pivovaroff et al., 2014; Zhang et al., 2017). Plants may therefore be more likely to die from insufficient carbon supply to other life-supporting functions, such as tissue maintenance and repair, enemy defence, the volume of leaf and fine root flushing at the beginning of the next growing season (McDowell et al., 2008; Wiley, 2020).

The objective of this study was to document, for the first time, phenotypic differences among Mojave Desert populations of *L. tridentata* and *A. dumosa* and to examine whether they exhibited a trade-off between growth under more benign environmental conditions and survivorship under harsher environmental conditions. With the primary growing season in winter/spring, we hypothesized that populations from winter-wetter regions would have higher growth rates in wetter gardens but higher mortality rates in the driest gardens compared to populations from winter-drier regions. However, we did not expect growth and mortality to be necessarily correlated with the same traits in both species. We thought it likely that, to avoid hydraulic failure, populations of the evergreen species *L. tridentata* differed in the regulation of leaf cover, so that populations with higher average leaf cover (from winter-wetter homesites) would have higher growth rates under favourable conditions and lower survivorship under harsh conditions. We expected *A. dumosa* to differ more strongly in leaf productivity traits; SLA, leaf N content (%N) and intrinsic water use efficiency (iWUE), to maximize leaf carbon returns and minimize the risk of death by carbon starvation. Although we expected leaf phenological and structural traits to be plastic across gardens, population × garden interactions should favour the growth of populations from winter-wetter regions in the more productive gardens, and disfavour growth and survivorship in the driest garden.

2 | MATERIALS AND METHODS

2.1 | Seed sources and seedling propagation

Ripened fruits of *Ambrosia dumosa* Gray (white bursage) and *Larrea tridentata* (DC.) (creosote bush) were collected across the Mojave Desert Ecoregion during the summers of 2010 and 2011 (Figure 1) and cleaned at the Bend, Oregon Seed Extractory (US Forest Service). Fruits were collected and pooled from 50 adult plants spaced at least 10 m apart per population and across broad precipitation and temperature gradients in the ecoregion (n = 19 populations for *A. dumosa*; n = 12 populations for *L. tridentata*; Table A1).

Seeds were stored at 4°C until germinated in a greenhouse between January and March 2013 (College of Southern Nevada, Henderson, NV, USA). To overcome dormancy, seeds were cold, wet stratified for 30 days prior to planting (*A. dumosa*) or soaked in water for a minimum of 12 hr with the water changed every 3 hr (*L. tridentata)* before sowing into 72-cell (2.5 cm × 2.5 cm) flats. Upon the development of two true leaves, seedlings were transplanted into

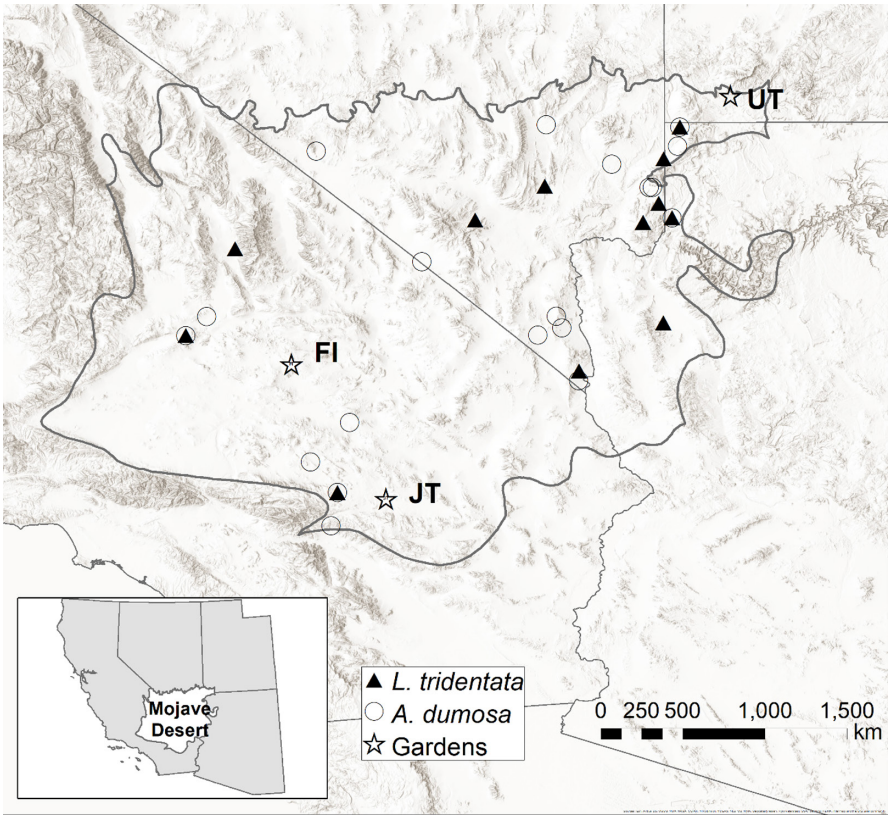

FIGURE 1 Map of the Mojave Desert in North America. The terrain is coded by elevation. Sample and garden locations are indicated

7.62 cm × 7.62 cm × 30.48 cm plant bands (Monarch Manufacturing, Inc.) with a growing mix of 3:1:1 ratio of sand, sterile mulch and perlite.

Prior to planting in the gardens, seedling heights were measured (January 2014), grouped into three height classes and tagged with a unique ID number. Seedlings of a given population were randomly assigned to gardens by height class, to safeguard against unintentionally distributing transplant sizes unevenly among gardens. *Ambrosia dumosa* stems were clipped to 10 cm height prior to transplanting to prevent breaking entangled stems during transport and planting. *Larrea tridentata* stems were not clipped. In February 2014, after 1 year in the greenhouse, all seedlings were moved outside to acclimate for 1 month prior to garden transplanting.

2.2 | Common gardens

Three fenced gardens approximately 50 m × 50 m were positioned across the Mojave Desert (Figure 1). Relative to one another, a garden north of St. George, Utah (UT garden) represented a cool-wet climate, a garden north of Joshua Tree National Park, California (JT garden) represented a hot and dry climate and an intermediate climate was represented by a garden on the grounds of the Fort Irwin National Training Center, California (FI garden). All locations had previously been cleared of vegetation and abandoned for at least a decade. Soils varied among gardens with soil derived from Navajo sandstone in UT; a sand with low clay content, decomposed grussy granite in FI; and gravelly, sandy loam granitics in JT. Based on volumetric soil moisture data collected onsite between October 2014 and September 2018, soils at FI and JT were similar in saturation water content at 20 cm depth and had similar rates of soil water decline in spring and summer given the same water content. Soil water dynamics at UT were different, indicating a lower saturation water content, rapid infiltration and drainage past 20 cm depth. Because of the coarser soil texture and higher precipitation at UT, moisture would have infiltrated to much greater depth.

In early to mid-March 2014, plants were transported to the gardens for transplanting. Holes were dug approximately 30 cm deep to accommodate the root plug and spaced approximately 1 m apart in a square lattice design. *Ambrosia dumosa* and *L. tridentata* sections of the garden were spatially separated but within these areas, plants were planted at random with respect to population source. Each hole was prepared by moistening it with water prior to planting. Seedlings were watered with a portable sprinkler system during establishment. Afterwards, transplants were watered monthly on each visit from April to June 2014 for the UT garden, April to July 2014 for the FI garden and April to August 2014 for the JT garden. In total, gardens received the equivalent of 70 mm, 73 mm and 86 mm of water subsidy respectively.

2.3 | Climate variables

Weather stations were installed at each garden to log air temperature (°C), rainfall (mm) and soil moisture (g/g) at depths of 5 cm and 20 cm every half-hour beginning February 2014 (Upward Innovations Inc.). Climate normals for each seed source were obtained from the PRISM

Climate Group, Northwest Alliance for Computational Science & Engineering based at Oregon State University (www.prism.oregonstate.edu; accessed 07/28/2020). The database was queried to provide 30-year normals (1981–2010) for mean monthly precipitation and maximal and minimal temperatures. From this, we calculated mean annual precipitation (MAP), winter precipitation (WP: November to April), summer precipitation (SP: May to October), the coefficient of variation in monthly average summer precipitation (SPCV), annual maximum (July) temperature (T_{max}), annual minimum (January) temperature (T_{min}) and the average monthly temperature difference (TD) between T_{min} and T_{max}.

2.4 | Seedling survivorship and growth

Live and dead plants were recorded monthly for the first 3 months after outplanting, from April to June 2014, then continued monthly from February 2015 to October 2018 to determine survivorship. Growth was monitored as canopy cover and stem diameter. Live canopy cover was estimated as the area of an ellipse using the greatest width and its perpendicular width. Canopy cover on live plants was measured at least once per year from 2014 to 2018 during spring when plants were actively growing. Additionally, stem diameters were measured at ground level with digital calipers on live plants once per year in April 2015 and in March from 2016 to 2018.

2.5 | Leaf productivity traits

Leaf samples for the determination of leaf traits were collected once in March (*A. dumosa*) and June (*L. tridentata*) 2016. SLA was determined for a subset of at least six populations that had live individuals in all gardens and together spanned the range of the Mojave Desert climate gradients. Permanent images of the leaf samples were created just after sampling using blueprint paper, and leaf images were later scanned using WinFOLIA software (Regent Instruments Inc. Canada). Leaf samples were collected in coin envelopes and air-dried in the field and later oven-dried at 70°C to a constant weight. SLA was calculated by dividing leaf area by the final dry mass.

Leaves to measure the carbon isotope ratio ($\delta^{13}C$) and per cent N content by mass (%N) were collected once from all live plants in March (*A. dumosa*) and June (*L. tridentata*) 2016. Several of the youngest, fully mature leaves were collected from each canopy and dried. Dry leaves were ground to a fine powder, subsamples weighed into tin foil sample cups and submitted for analysis to the University of Wyoming Stable Isotopes Facility (Laramie, WY, USA). Carbon isotope ratios are expressed in per mille:

$$\delta^{13}C = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1{,}000\,‰, \quad (1)$$

where R is the molar ratio of heavy to light isotope and $R_{standard}$ is based on Pee Dee Belemnite. A more negative value of $\delta^{13}C$ indicates lower intrinsic water use efficiency at the leaf level (iWUE) in C_3 plants (Farquhar et al., 1989).

TABLE 1 Component scores of the principal component analysis

Year	WP (mm)	SP (mm)	SPCV	T_{max} (°C)	T_{min} (°C)	TD (°C)
PC1	0.443	−0.079	0.449	−0.380	−0.052	0.081
PC2	−0.043	−0.021	0.022	0.139	0.618	−0.529
PC3	0.004	−0.664	0.309	0.17	0.218	0.401

Abbreviations: SP, summer precipitation (May to October); SPCV, coefficient of variation in the monthly variation of SP; TD, average monthly difference in T_{max} and T_{min}; T_{max}, average maximal temperature of the hottest month; T_{min}, average minimal temperature of the coldest month; WP, winter precipitation (November to April).

2.6 | Data analysis

Six climate variables across the *L. tridentata* and *A. dumosa* collection range, previously identified as characteristics of Mojave Desert climate variation (Shryock et al., 2017), were reduced to three principal components with eigenvalues greater than 1 (Table 1).

In January 2014, approximately 3 months before outplanting, we used ANOVA of seedling height values to check for population effects on seedling growth in the greenhouse, which could potentially affect their later field performance. Populations of *A. dumosa* and *L. tridentata* did grow to significantly different heights in the greenhouse prior to outplanting, although there was a substantial overlap in the height distributions of populations with the population factor explaining only a small fraction of the variation (*A. dumosa*: adj. $R^2 = 0.092$; *L. tridentata*: adj. $R^2 = 0.041$). However, the greenhouse heights of individuals did not significantly affect stem diameter growth, leaf and reproductive phenology, nor the values of the leaf productivity traits.

Vegetative growth was quantified as the difference in the log basal stem diameters between April 2015 and March 2018. Stem diameters were chosen because they are least affected by seasonal change and integrate above- and below-ground vegetative growth due to their central position in the vascular architecture (Grossnickle, 2012). Survivorship was quantified either as the average number of days survived (survival time) or as the fraction of individuals surviving to the last observation day in October 2018. Phenology was quantified by assigning a score between 0 and 5 based on a visual estimate of canopy cover by leaves or reproductive organs (buds, flowers, fruits). A score of 0 was assigned for cover <1%, 1 for 1 to <10%, 2 for 10% to <25%, 3 for 25% to <50%, 4 for 50% to <75% and 5 for 75% to 100%. These scores were then averaged over the observation interval for each plant. The averaging procedure represented both differences in the average duration of the foliated state and differences in the density of foliage.

The study included 19 populations of *A. dumosa*, with initially 1,102 individuals of which 626 survived until October 2018. Four populations had not a single survivor in JT garden, but all populations had

at least one survivor in FI and UT gardens. *Larrea tridentata* had initially 12 populations with 277 individuals of which 176 survived to the end. Although all populations had at least one survivor in every garden, only nine populations were originally planted into all three gardens. Statistical comparisons involving all gardens included only populations for which data were available in all gardens.

Stem growth, leaf and reproductive scores and the three leaf trait values were examined by ANCOVA, using garden, population and their interaction as fixed effects and the last height measured in the year of transplanting (2014) as a covariate—May for *L. tridentata* and June for *A. dumosa*. The covariate was used to disentangle potential plant-size effects on plant performance and functional traits from garden and population effects. Size differences could have been random or they could have been influenced by transplanting procedures in a population- and garden-specific manner. To determine if plant height in the year of transplanting was influenced by population and garden, we also conducted an ANOVA on 2014 plant height. We attributed a fixed effect to the garden factor and a random effect to the population factor in the ANOVA and ANCOVA models because garden locations were deliberately picked to represent contrasting locations along Mojave Desert climate gradients, whereas populations were widely and randomly sampled across the Mojave Desert to represent the species within the Mojave Desert.

Survivorship was examined by Kaplan–Meier survivorship analysis, either by pairwise comparisons of pooled survival times between gardens or by testing if the pooled sample of all populations within gardens had equal survival curves. Pairwise comparisons between populations were not possible for FI and UT, because in some populations all individuals survived until the end of the observation interval and we did not consider pooling across gardens a sensible alternative, given the substantially different environmental conditions at the three gardens.

We conducted a model selection analysis (Burnham & Anderson, 2002) to determine the influence of homesite climate. Initially, we compared three approaches for the representation of homesite climate norms in the model: (a) distance in three-dimensional principal component space between actual garden climate over 5 years and homesite, (b) a linear combination of climate principal components and (c) a linear combination of raw climate data. The last approach yielded consistently better results (lower AIC_c values) and we omitted reporting the results for the other modelling approaches. Based on previous analysis, we included relevant individual plant metrics into the climate regression models, the 2014 plant height for *A. dumosa* and the leaf score for *L. tridentata*. All analyses were conducted in SPSS Version 26 (IMB).

3 | RESULTS

3.1 | Climate variation across seed collection sites

Three principal components with eigenvalues above 1 were identified across seed collection sites. PC1 (39% of variance) was strongly influenced by average total winter precipitation (WP), the average coefficient of variation in monthly summer precipitation (SPCV) and the average monthly maximal daytime temperature (T_{max}). In general, PC1 was highly correlated with site differences ranging from moister, cooler uplands to drier, hotter basins (Table 1). PC2 (24% of variance) was strongly influenced by the average monthly minimal night-time temperature (T_{min}) and the average monthly difference between T_{max} and T_{min} (TD). Thus, seed collection sites varied from winter-cooler sites with larger temperature differences between day and night to winter-warmer sites with less diurnal temperature variation. PC3 (19% of variance) was most strongly influenced by average total summer precipitation (SP), likely associated with the influence of the North American monsoon system.

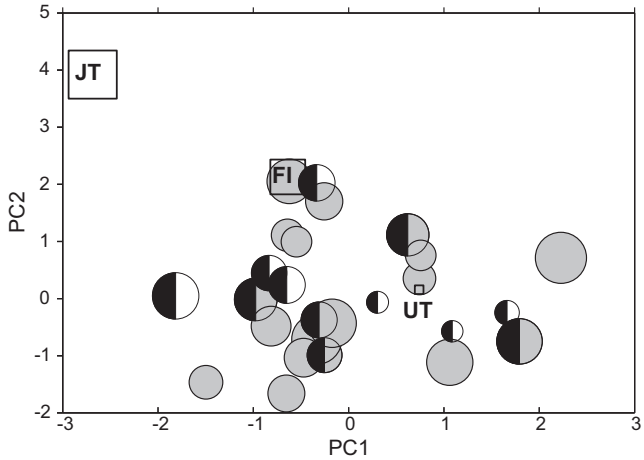

FIGURE 2 Principal component values for climate variation between sample sites and gardens. Symbol sizes are proportional to the value of PC3. Grey circles for *Ambrosia dumosa*, black and white circles for *Larrea tridentata* and squares for garden locations. PCA values for the gardens were calculated from the average climate conditions for 2014–2018. However, the value of SPCV, the CV of summer precipitation, was set to the collection site average

The three gardens varied substantially along all three PC axes (Figure 2; Table 1). JT had the lowest score on PC1 and the highest score on PC2, indicative of exceptionally low winter rainfall, high summer temperatures and large differences between monthly T_{min} and T_{max} (TD). UT was an outlier on PC3 with far more summer precipitation than most Mojave sites (Table B1).

3.2 | Garden effects on growth and survival

Stem diameters increased between 2015 and 2018 (Figure 3A). *Ambrosia dumosa* grew fastest in UT, followed by FI and JT. Relative stem growth rates over 3 years followed a sigmoidal growth model (Table C1), and the 3-year stem growth increment was significantly *negatively* correlated with individual plant heights after outplanting in 2014 (Table 2; Table C3). Plant height in June 2014 had already been marginally significantly affected by population effects and garden × population interactions (Table 2) with effect sizes (η^2) exceeding those on growth in subsequent years (Table 3).

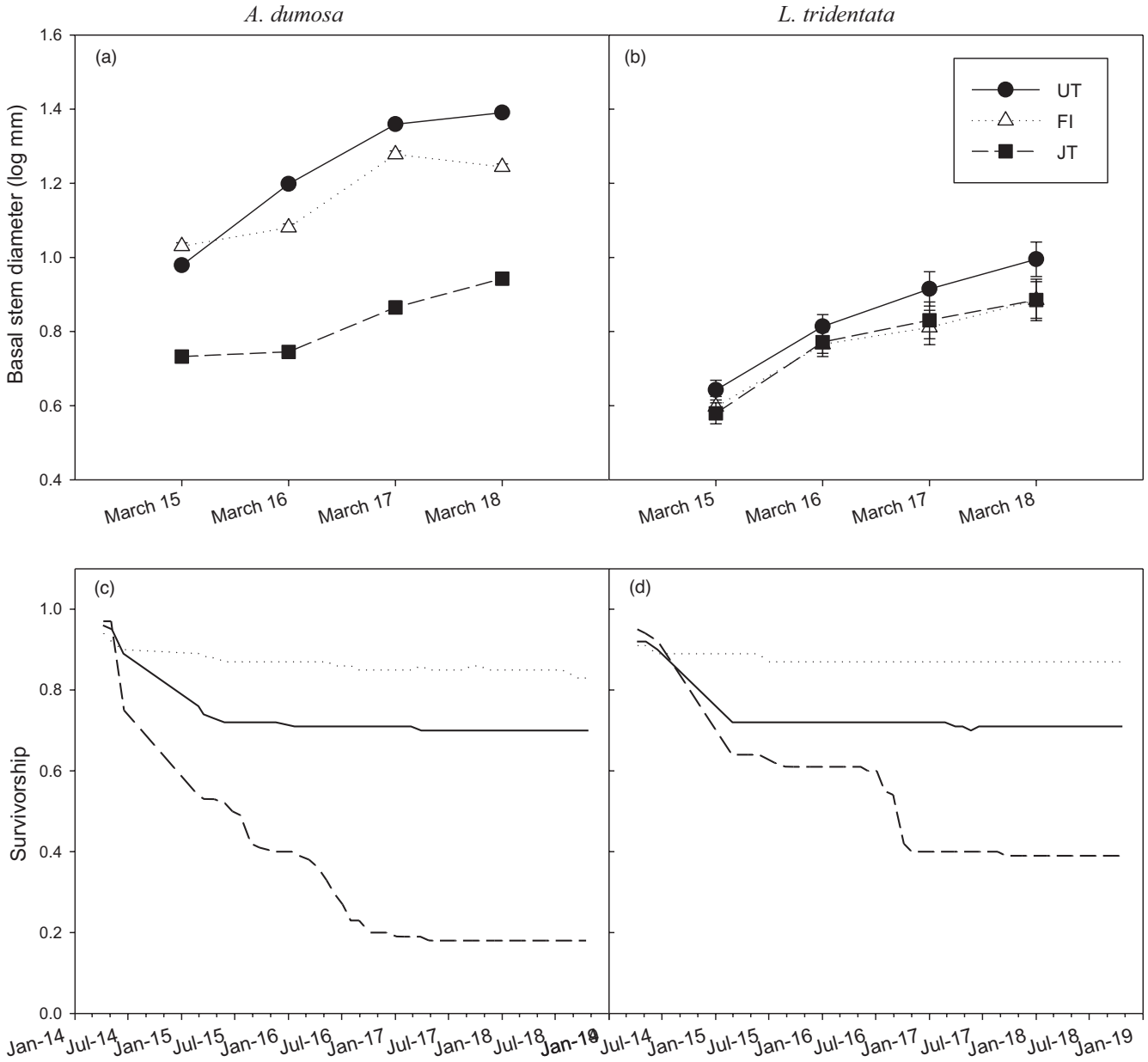

FIGURE 3 Garden effects on the growth and survivorship of *Ambrosia dumosa* (A, C) and *Larrea tridentata* (B, D). Top panels: Log stem diameters measured annually between March 2015 and March 2018; shown are the means and standard errors of the population means. Bottom panels: overall survivorship for *A. dumosa* (C) and *L. tridentata* (D)

	Ambrosia dumosa				*Larrea tridentata*			
Factors	**SS**	***df***	***p***	η^2	**SS**	***df***	***p***	η^2
Garden	6	2	0.917	0.005	32	2	0.803	0.019
Population	936	13	0.076	0.487	1,423	8	0.046	0.553
G × P	982	26	0.065	0.065	1,077	16	0.917	0.047

TABLE 2 Mixed effects ANOVA of plant height 2014, several months after transplanting. Only populations represented in all gardens were included in the analysis. Garden was modelled as a fixed effect, population as a random effect. η^2 is the partial eta squared or the proportion of the variance accounted for by the respective effect

By contrast, *L. tridentata* stem diameter growth was not significantly affected by garden conditions, nor by 2014 plant height (Figure 3B, Table 3; Table C3) and stem diameters grew linearly over 3 years (Table C1). Population effects on stem growth were significant.

In both species, survivorship ranked FI > UT > JT and *A. dumosa* had lower survivorship in JT than *L. tridentata* (Figure 3C,D). Survival times across gardens were significantly different among populations for *A. dumosa* but not for *L. tridentata* (Table C2), at least in part due

to lower sample sizes for *L. tridentata*. In both species, individual plant height in 2014 had a significantly positive effect on survival in October 2018 (Table C4).

Leaf phenology was significantly affected by garden and population in both species, but again, with dominant garden effects on *A. dumosa* and dominant population effects on *L. tridentata* (Table 3). The leaf cover of deciduous *A. dumosa* fluctuated greatly over the course of a year, usually declining after May and increasing by January (Figure 4). In JT, leaf cover was more erratic, particularly during the summer months when leaf cover was at the lowest of the year. Evergreen *L. tridentata* maintained an average leaf score >3 throughout the observation period in every garden.

Reproductive phenology in *A. dumosa* was also affected primarily by garden conditions and a significantly positive effect of 2014 plant height (Table 2; Table C6). In *L. tridentata*, only garden × population interactions were significant (Table 3). On average, *A. dumosa* reached maturity earlier than *L. tridentata*—by 2015, 74% of all *A. dumosa* plants flowered in FI, 66% in UT and the percentages increased to 84% and 73% by 2017. However, very few plants flowered in JT; 4% in 2015, none in 2016 and 10% in 2017. For *L. tridentata*, the percentage of flowering increased from 14% to 51% in FI and JT, and in UT from 31% to 56% between 2015 and 2017. In 2018, the flowering percentages were lower than that in the previous year for both species across gardens. Both species peaked in reproductive cover between April and June across gardens (Figure 4).

Garden conditions dominated the leaf traits SLA, δ^{13}C and %N in both species (Table 3; Tables C7–C9, Figures D1 and D2). Befitting the more mesic conditions, *A. dumosa* had the highest leaf %N and SLA values and the most negative δ^{13}C values in UT (Figure D1). The converse held for the driest garden JT, while trait values for FI were intermediate but closer to JT than to UT. Garden effects on *L. tridentata* were similar in direction and magnitude, except for %N, in part because leaf samples for UT were excluded from analysis due to sample loss (Figure D2).

In *A. dumosa*, there were small but significant population effects on δ^{13}C and a marginally significant effect on SLA that was absent in *L. tridentata*. A highly significant garden × population interaction on δ^{13}C in *A. dumosa* could be attributed to a difference between UT and JT, in which some populations that were among the highest ranking in JT (high iWUE) were among the lowest ranking in UT (Figure D3). The spread of δ^{13}C values was higher in JT and correlated positively with stem growth (Figure D1d).

3.3 | Correlations between growth, survivorship and average trait values

The hypothesis of a negative relationship between growth under fair conditions and survivorship under harsh conditions was supported in *L. tridentata* but was only partially supported in *A. dumosa*. Pooled across all gardens (because growth rates were not different), the average stem growth rates of *L. tridentata* populations were negatively correlated with the average survival time in JT (Figure 5A). The correlation appeared to be mediated by leaf phenology—populations with a higher leaf cover score had shorter survival times in JT (Figure 5B) but higher stem growth rates across gardens (Figure 5C). No other leaf traits were significantly correlated with stem growth or survival time (Figure D2).

In *A. dumosa*, the only significant relationship between growth and survival was a negative correlation between stem growth in FI and survival time in JT (Figure 6A). However, there was no single population trait average that was significantly correlated with both stem growth and survival time in any garden (Figure D1). Individual plant height in 2014 was in fact the only explanatory variable correlated with stem growth (–), reproductive cover (+) and survival (+) (Tables C3, C4 and C6). Though plant height in 2014 was marginally affected by population effects (Table 2) and the average 2014 height

TABLE 3 Overview of garden (fixed) and population (random) effects. Shown are the effect sizes (η^2—partial eta squared or the proportion of the variance accounted for by the respective effect). Only populations represented in all gardens were included in the analysis. Corresponding statistical tables are shown in Appendix C. **: $p < 0.005$; *: $0.005 \le p < 0.05$; $^{(*)}$: $0.05 \le p < 0.1$. The analysis of %N and δ^{13}C for *Larrea tridentata* excluded UT due to sample loss

	Log stem diameter growth (2015–2018)	Leaf cover score	Reproductive cover score	Leaf %N	Leaf δ^{13}C	SLA
Ambrosia dumosa						
Height in 2014	0.040**	0.007$^{(*)}$	0.072**	0.011*	0.014**	< 0.001
Garden	0.852**	0.737**	0.842**	0.838**	0.943**	0.964**
Population	0.189	0.313	0.267	0.212	0.345	0.534
G × P	0.040$^{(*)}$	0.069$^{(*)}$	0.061	0.044	0.083**	0.130$^{(*)}$
Larrea tridentata						
Height in 2014	0.001	0.002	0.009	0.002	0.014	0.032
Garden	0.026	0.230$^{(*)}$	0.117	0.134*	0.948**	0.568**
Population	0.484*	0.417	0.273	0.776*	0.179	0.086
G × P	0.138	0.200**	0.252*	0.037	0.089	0.136

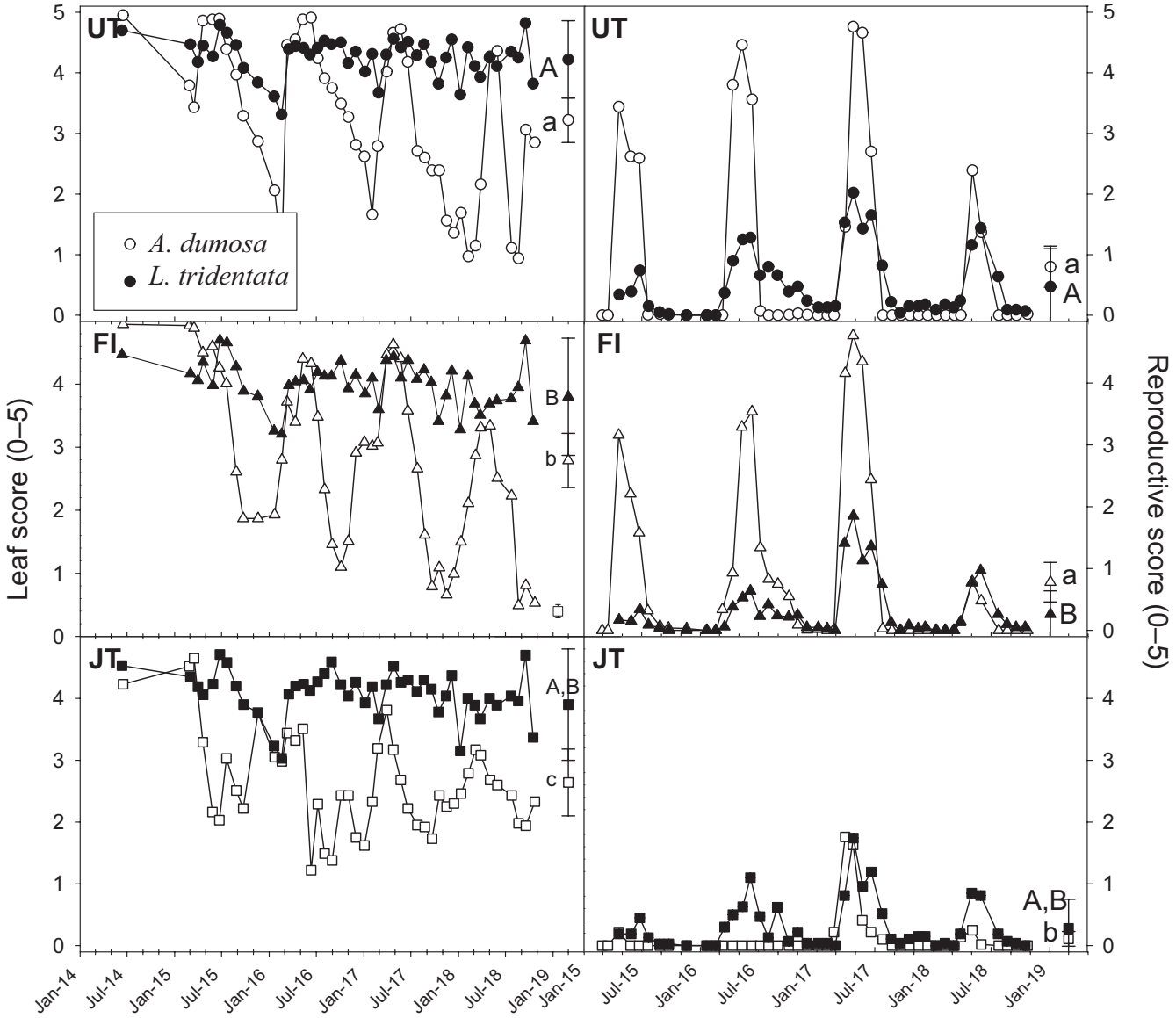

FIGURE 4 Leaf and reproductive phenology in the three common gardens. Scores quantified the relative cover of plant canopies by green leaves or buds/flowers/fruits. Averages were calculated only for plants that survived until October 2018. The terminal symbols represent averages over time and different letter labels indicate significant differences within species between gardens (capital letters for *Larrea tridentata* and lower-case letters for *Ambrosia dumosa*). The error bars are scaled to ±1 *SD*

of populations did correlate negatively with average stem growth in FI (Figure 6C), it did not correlate with survival time in JT (Figure 6B), nor indeed anywhere else.

3.4 | Relationships with homesite climate

The hypothesis that populations from more mesic homesites should grow faster in the more mesic gardens and have higher mortality in the driest garden was generally supported. In *A. dumosa*, stem growth at FI was positively correlated with winter precipitation and maximal temperatures in summer and negatively with minimal temperatures in winter, whereas survival time at JT was oppositely correlated with the same variables (Table 4). Thus, populations from winter-wetter and -colder and summer-hotter homesites grew faster at FI but survived for shorter periods of time in JT. Populations from winter-wetter regions also survived longer in FI. In addition, growth in FI and UT increased with the monthly variability in summer precipitation at the homesite.

Accounting for individual plant height in 2014 improved the fit of the climate regression models and height itself was affected by homesite climate (Table 4). At FI, more winter precipitation, higher maximal summer temperatures and lower minimal winter temperatures affected the 2014 height positively. Although increased individual height had a negative effect on subsequent stem growth, when the height effect was accounted for, winter precipitation, maximal summer

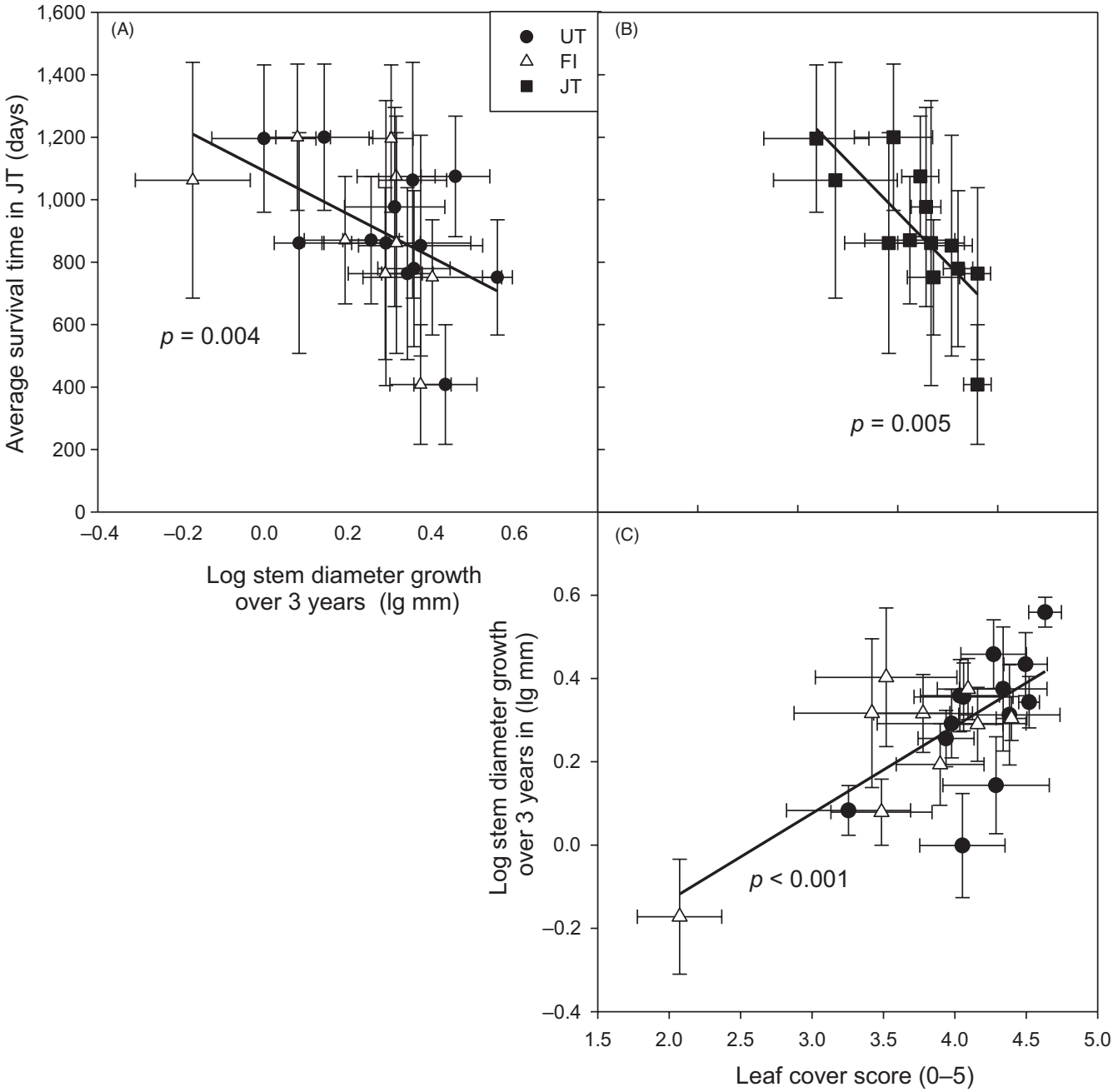

FIGURE 5 Growth versus survival time in *Larrea tridentata*, as related to leaf cover. (A) Average survival time in JT versus stem diameter growth across all gardens; (B) Average survival time in JT versus leaf cover score in JT; (C) Stem diameter growth versus leaf cover score by garden. Populations with greater leaf cover have higher relative stem growth rates and lower survival time in JT

and minimal winter temperatures affected stem growth in the same way as height. In JT, populations from winter-drier and summer-hotter regions were taller in 2014 and taller plants also had higher survivorship. At equal height, populations from winter-drier regions had still longer survival times.

Values of $\delta^{13}C$ were inconsistently affected by homesite climate conditions between gardens. However, it is notable that across all gardens, $\delta^{13}C$ values varied significantly with summer precipitation at the homesite. In FI and JT, $\delta^{13}C$ and iWUE increased with homesite total summer precipitation or summer precipitation variability, whereas it decreased with summer precipitation variability in UT. In *L. tridentata*, stem growth was positively correlated with the leaf score and independently with winter precipitation and the monthly differences between maximal and minimal temperatures (Table 5). Monthly variation in summer precipitation had a negative effect on stem growth. The same climate variables had the exact opposite effects on survival time in JT and the leaf cover score itself increased with winter precipitation and summer maximal temperature at the homesite.

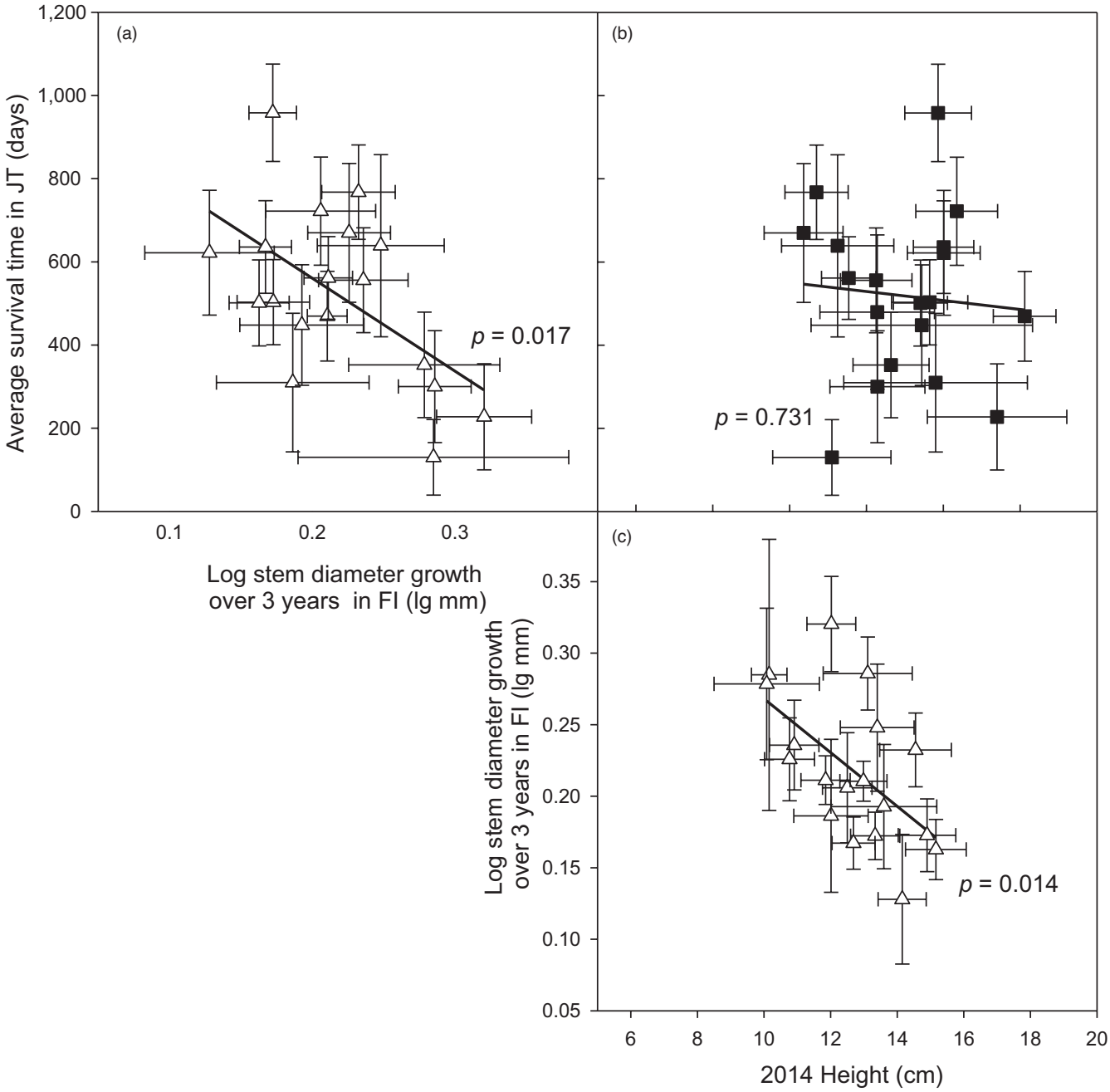

FIGURE 6 Growth versus survival time in *Ambrosia dumosa*, as related to 2014 plant height. (A) Average survival time in JT versus stem diameter growth in FI; (B) Average survival time in JT versus 2014 plant height in JT; (C) Stem diameter growth in FI versus 2014 plant height in FI. Populations with greater height in 2014 have lower relative growth rates in FI and random survival times in JT

4 | DISCUSSION

This study documented previously unknown intraspecific variation in cytotype races of two dominant shrub species of the Mojave Desert. Both *L. tridentata* and *A. dumosa* exhibited significant population differences in growth, survivorship and trait values (Table 2), with some of the variation correlated with homesite climate (Tables 4 and 5). As predicted, the amount of winter precipitation at the homesite was a common factor correlated with population differences, but so was summer maximal and winter-minimal temperatures. Higher summer temperatures and lower winter temperatures tended to enhance growth, though not in all gardens. In addition, summer precipitation variability had a positive effect on *A. dumosa* growth and a negative effect on *L. tridentata* growth (Table 5). This climate factor in a previous study was also associated with potentially adaptive genetic markers in two other Mojave Desert shrub species, *Ephedra nevadensis* and *Sphaeralcea ambigua* (Shryock et al., 2017). Though shrub productivity in the Mojave Desert is primarily associated with dependable winter precipitation (Biederman, 2018), individual species may have divergent adaptations to less predictable summer

TABLE 4 Climate regression models for stem growth of *Ambrosia dumosa*. Null ΔAIC_c is the difference in the AIC_c values between the intercept-only (Null) model and the regression model with the lowest (best model) AIC_c value. Null models with a $\Delta AIC_c \gg 2$ are considered to have substantially less support than the best regression model (Burnham & Anderson, 2002). n/a indicates that no regression model was substantially better than the null model. Regressions were linear in the case of stem growth and 2014 height and binary logistic with log-link function for survivorship status in October 2018

	Stem growth (UT)		Survival time (UT)		2014 Height (UT)		$\delta^{13}C$ (UT)	
	Effect sign	*p*	Effect sign	*p*	Effect sign	*p*	Effect sign	*p*
2014 Height	−	< 0.001	+	< 0.001			+	0.001
WP							+	0.011
T_{min}								
SPCV	+	0.005					−	< 0.001
T_{max}					−	0.002		
TD	+	0.007						
Null ΔAIC_c	20.9		51.4		7.0		19.1	
	Stem growth (FI)		**Survival time (FI)**		**2014 Height (FI)**		**$\delta^{13}C$ (FI)**	
	Effect sign	***p***	**Effect sign**	***p***	**Effect sign**	***p***	**Effect sign**	***p***
2014 Height	−	0.001	+	0.005				
WP	+	< 0.001	−	0.039	+	0.034		
T_{min}	−	0.002			−	0.010		
SPCV	+	0.040					+	0.024
T_{max}	+	0.012			+	0.037		
TD								
Null ΔAIC_c	20.6		8.8		5.0		3.0	
	Stem growth (JT)		**Survival time (JT)**		**2014 Height (JT)**		**$\delta^{13}C$ (JT)**	
	Effect sign	***p***	**Effect sign**	***p***	**Effect sign**	***p***	**Effect sign**	***p***
2014 Height			+	<0.001				
WP			−	0.005	−	< 0.001		
SP							+	0.012
T_{min}			+	0.002				
SPCV								
T_{max}			−	0.010	−	0.018		
TD			+	0.001	−	0.015		
Null ΔAIC_c	n/a		17.7		13.0		4.2	

precipitation, according to their species-specific constraints and functional trade-offs.

4.1 | *Larrea tridentata*

Larrea tridentata exhibited the predicted negative correlation between growth and survival (Figure 5A). Originally, we expected to see the correlation only between growth in gardens with higher productivity (FI and UT) and survival in the most arid garden (JT), but not necessarily between growth and mortality *within* JT garden, given that slow growth can also negatively affect survival through plant size. In hindsight, since average stem diameter growth of *L. tridentata* was not significantly different among gardens (Figure 3B), it is not surprising that faster growing populations grew faster everywhere, including in JT. This result suggests that population variation in developmental patterns, for example in root:shoot ratios (Walters & Freeman, 1983), had a potentially stronger control on early growth and survivorship than resource availability. Several other studies documented relative insensitivity of *L. tridentata* stem growth to winter/spring precipitation (though not to summer precipitation) for Sonoran and Chihuahuan desert populations of *L. tridentata* (Muldavin et al., 2008; Reynolds et al., 1999; Sponseller et al., 2012). Still, reproductive cover was significantly lower in JT than in UT and FI (Figure 4), suggesting that *L. tridentata* may have compensated for a presumably lower annual carbon gain in JT with reduced allocation to reproduction in favour of stem growth, in accordance with theoretical expectations for long-lived plants (Bialic-Murphy & Gaoue, 2018; Crone, 2001; Dalgleish et al., 2011).

TABLE 5 Climate regression models for *Larrea tridentata*. Null ΔAIC_c is the difference in the AIC_c values between the intercept-only (Null) model and the regression model with the lowest (best model) AIC_c value. Null models with $\Delta AIC_c \gg 2$ are considered to have substantially less support than the best regression model (Burnham & Anderson, 2002). Since Garden is a categorical factor, an effect sign cannot be stated

	Stem growth (all gardens)		Survival (JT)		Leaf score (all gardens)	
	Effect sign	*p*	Effect sign	*p*	Effect sign	*p*
Garden						0.011
Leaf score	+	< 0.001	−	0.044		
WP	+	0.003	−	0.037	+	0.002
SPCV	−	0.036	+	0.010		
T_{max}					+	0.086
TD	+	0.003	−	0.020		
ΔAIC_c	62.3		56.5		11.7	

Larrea tridentata was clearly structured into faster and slower growing populations and faster populations came from regions with wetter-colder winters and less variable summer precipitation (Table 5). Thus, there must be some advantage to faster growth if site conditions allow. Genotypes that are not *overly* resource conservative likely transition into less vulnerable life stages and reproduction earlier (deSoyza et al., 1996) and would be expected to increase in frequency. Genotypes that are not conservative enough may not live long enough to be maintained in the population.

As we hypothesized, the trait most closely correlated with resource conservatism was the average leaf cover, which was dominated by garden and garden × population interactions (Figure 5; Table 3). Leaf cover varied by garden, but within the same garden, more conservative populations stayed in the highest leaf cover category for shorter periods of time, suggesting that plants shed leaves sooner compared to other populations. This would have lowered the risk of hydraulic failure but also decreased whole-plant assimilation and growth (Ocheltree et al., 2020). While leaf productivity traits (SLA, %N and $\delta^{13}C$) were plastic between gardens and %N varied significantly among populations, %N was not significantly correlated with growth or survival time (Table 2; Table D2). In addition, there were no significant garden × population interactions in any of the leaf productivity traits (Table 2), suggesting that leaf structure and physiology took no lead role in the observed growth–survivorship trade-off.

With more winter precipitation and the lower winter temperatures, more water is stored deeper in the soil, away from the evaporation zone (Scanlon & Milly, 1994). For a deep-rooted shrub such as *L. tridentata*, this means that water supply declines gradually and predictably over spring and early summer, which can be met with a controlled decline in stomatal aperture and leaf abscission (Evans & Black, 1993). By contrast, the more rapid decline in stored water in winter-drier regions, as well as erratic changes in shallow soil water with summer precipitation, may overwhelm the response time of plants and select a more conservative phenological strategy with perhaps lower physiological thresholds to trigger leaf abscission.

The regulation of leaf cover is almost certainly only one aspect of *L. tridentata*'s full spectrum of climate adaptation. For example, ploidy races of *L. tridentata* differ in root:shoot biomass ratios (Walters & Freeman, 1983) and members of the genus *Larrea* exhibit differences in xylem structure and the degree of plasticity in these characteristics, underscoring the importance of the hydraulic transport safety and efficiency trade-off for climate adaptation among *Larrea* species.

4.2 | *Ambrosia dumosa*

For *A. dumosa*, we did not find a direct correlation between growth and survivorship among populations (Figure 6). At first glance, what appeared to be a potential trade-off between growth in FI and survivorship in JT (Figure 6A) turned out to be a consequence of individual size variation between transplants. Initially taller transplants had longer survival times in JT (though not significantly so at the population level; Figure 6B) and *lower* stem growth rates (Figure 6A) due to sigmoidal growth dynamics.

Individual variation in initial height after transplanting was 87% random and only weakly correlated with population (Table 2). Thus, individual size variation, acquired chiefly offsite and in response to transplant shock, may have obscured mean population effects on growth and survivorship, if they existed. Being taller after transplanting increased subsequent survival across all gardens, curtailed subsequent growth through allometric growth constraints but increased reproductive cover. It is possible that a growth–survivorship trade-off may have been observed in the first year of life, had individuals been raised in the common gardens. However, in the actual experimental design, the only indication of a growth–survivorship trade-off was indirect—after accounting for individual height effects, homesite climate factors with positive effects on stem growth in FI had negative effects on survival time in JT (Table 4). This does suggest that adaptations facilitating growth in more winter-mesic regions have negative consequences for survival in more winter-arid regions and vice versa, though the facilitating mechanisms remain unclear.

We hypothesized that population effects on growth and survival would be largely facilitated by leaf productivity traits, rather than leaf phenology. Leaf traits did in fact exhibit population ×

garden interactions, suggesting that, although garden effects and phenotypic plasticity were dominant, populations exhibited different degrees of plasticity across gardens (Table 3). The most intriguing pattern emerged from the analysis of $\delta^{13}C$, a proxy of iWUE. Some of the populations that achieved the highest iWUE in JT had the lowest iWUE in UT (Figure D3). In addition, $\delta^{13}C$ in JT was positively correlated with stem growth in JT (Figure D1). This suggests that despite prominent phenotypic plasticity, presumably to maximize carbon gain at each site, some adaptations at the leaf level remain genotype specific and are favourable to growth only under dry conditions and neutral or potentially maladaptive for growth under wet conditions. Similar examples of adaptive phenotypic plasticity in iWUE have been reported in several other species (Edwards et al., 2012; Marais et al., 2017; Marguerit et al., 2014; Ponton et al., 2002) and linked to complex mechanisms involving multiple traits responding to multiple stressors.

In comparison, *L. tridentata* and *A. dumosa* adapted differently to homesite climate conditions, supporting our hypothesis that the two species managed different types of risk. In *L. tridentata*, slow growth is an apparently lesser risk to survival than hydraulic failure. This conclusion is underscored by the size insensitivity of mortality, canopydieback and root:shoot partitioning observed in several previous studies (Allen et al., 2008; Hamerlynck & McAuliffe, 2008; Medeiros & Pockman, 2010). Populations from regions with less predictable precipitation maintained lower leaf cover, even at times or in places where higher leaf cover would be viable. By contrast, in *A. dumosa*, plant size dominates all fitness components. Therefore, every opportunity for growth not taken increases the risks of death or inferior reproduction relative to other genotypes. Less threatened by hydraulic failure, populations may be adapted to maximize leaf productivity and to use water wherever and whenever available, including from more erratic summer precipitation. As adults, populations from different climate regions have only minor differences in growth and survivorship when growing together, but, unobserved in this study, differences in the magnitude of phenotypic plasticity maybe more consequential in the seedling establishment phase of the life cycle.

4.3 | Restoration implications

It has been standard practice in the Mojave Desert to collect plant materials for restoration wherever they are available in quantity. Collections often originate outside the ecoregion, and population variation was not considered until recently (Shryock et al., 2018). However, the establishment of transplants originating from other climate zones, while it may appear initially to be successful, may result in populations poorly adapted to local conditions in the long term (Broadhurst et al., 2008).

This study showed not only that *populations* from different climate regions are different, but also that different species employ different strategies for coping with variation in climate patterns. Traits that may be indicative of climate suitability adaptation in one species may not be in another. In *L. tridentata*, populations appeared to balance mortality risk against growth rate, according to average winter precipitation at their homesites. The implication is that mesic genotypes exposed to an exceptionally dry winter could be rapidly decimated. Arid genotypes exposed to wetter winters may, however, endure, being only gradually out-competed by more mesic genotypes, if they are present. We may expect similar responses in other long-lived, evergreen species whose lives are threatened primarily by hydraulic failure.

By contrast, *A. dumosa* presented an example of greater complexity and a cautionary tale for the use of transplants in experiment and restoration. Due to their high degree of phenotypic plasticity, sufficiently large transplants may grow and survive anywhere, irrespective of their climate provenance, but whether they are equally successful during germination and the most vulnerable seedling establishment phase remains an open question. For species with a high degree of phenotypic plasticity, climate adaptations are difficult to recognize and their responses to climate change are difficult to predict. Multiple common garden studies with multiple cohorts may be needed to disentangle predictable population effects from random size effects on early size development.

An understanding of the relationships between trait variation and fitness in relation to the environment in key species, as well as general principles that may apply to the many untested species, will guide how broadly to collect plant materials without jeopardizing the suitability of the materials at restoration sites. In combination with landscape genetic approaches, common garden studies importantly assign fitness costs to genetic distances along marker-based adaptive climate gradients, which will inform seed transfer guidelines and prevent maladaptive outcomes in restoring damaged ecosystems under current and projected climates (Shryock et al., 2018).

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CONFLICT OF INTEREST

Susanne Schwinning is an Associate Editor of *Journal of Ecology*, but took no part in the peer review and decision-making processes for this paper. Lesley DeFalco and Todd Esque were Guest Editors for this *Journal of Ecology* Special Feature, but took no part in the peer review and decision-making processes for this paper. The authors have no other conflicts of interest to declare.

AUTHORS' CONTRIBUTIONS

N.A.C., L.A.D. and T.C.E. led the conception and design of the experiment and contributed substantially to data acquisition; all authors contributed to data analysis and interpretation, as well as the drafting the article; S.S. led the final revisions of the manuscript. All authors gave their approval for this version to be published and agreed to be accountable for the aspects of the work that they conducted and ensuring that questions related to the accuracy or integrity of any part of their work are appropriately investigated and resolved.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13747.

DATA AVAILABILITY STATEMENT

The data is archived with the USGS ScienceBase database: https://doi.org/10.5066/P99F9GDV (Custer et al., 2021).

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