SEED LONGEVITY AND CLIMATIC TOLERANCE OF SAN JOAQUIN WOOLY-THREADS (*Monolopia congdonii*; Asteraceae) AN ENDANGERED PLANT FROM THE SAN JOAQUIN DESERT, CALIFORNIA

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TITLE: Seed longevity and climatic tolerance of San Joaquin wooly-threads (*Monolopia congdonii*; Asteraceae) an endangered plant from the San Joaquin Desert, California

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ABSTRACT

San Joaquin wooly-threads (*Monolopia congdonii*; Asteraceae) is a federally-listed, endangered annual plant species from the desert areas of the San Joaquin Valley. Its limited range puts it at risk of extinction if the climate changes in such a way as to hinder its growth and reproduction. The primary aims of the study were to 1) determine how long-lived the seeds of the *M. congdonii* are, a key determinant of survival of desert annual plant populations through long droughts and 2) determine how severely hotter, drier conditions impact the ability of emerged plants to grow and reproduce. Secondarily, I aimed to test two hypotheses 1) is seed longevity within the genus *Monolopia* correlated with habitat aridity? 2) do species' geographic range limits represent their climatic tolerances? In testing the viability of seeds of *Monolopia* species collected from herbarium specimens and old field collections, I did not find evidence for the predicted pattern of seed longevity. Though, idiosyncrasies in the data suggest possible issues with the longevity of *M. congdonii* seeds that are collected prematurely and warrant further investigation to develop best practices for seed collections of this species. To test the climatic tolerance of *M. congdonii* and the relationship between geographic range and climatic tolerance, I grew several desert annual species under three manipulated water treatments. And while, *M. congdonii* failed to germinate, the other species showed variable tolerance for the drought treatments but this variability was seemingly unrelated to the species' geographic range. Importantly, *Monolopia lanceolata,* a close relative of *M. congdonii* did not show exceptional vulnerability to the drought-stress conditions relative to other co-occuring species. Taken together, the results of this study enable better informed population viability analyses with the end goal of allowing recovery efforts to succeed.

Keywords: California plants, soil seed bank, deserts, annual plants, climate change, rare plants, drought stress

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Chapter 1

1. INTRODUCTION

In this chapter, I will review seed bank dynamics and the possible implications of predicted climatic changes for native annual plants that rely on persistent soil seed banks. I will introduce *Monolopia congdonii*, the federally-endangered focal species of this study, then review the taxonomy of the genus *Monolopia*, and discuss what role seed longevity may have played in its evolution. Lastly, I will discuss the pronounced difference in the two fruit morphs of *M. congdonii* and its potential adaptive significance. I will aim to address the following questions:

- How long lived are the seeds of *M. congdonii* and what are the implications of this for the recovery of the species under a changing climate?
- Is increased seed longevity an adaptation to arid habitats in the genus *Monolopia* or is it a preadapation?
- Do the distinct disk and ray fruit morphs of *M. congdonii* represent different specializations for dispersal in space and time, respectively?

1.1 Seed banks

Seeds are the longest-lived and most numerous life-stage of most annual plants (Baskin and Baskin 1998, Cypher 1994, Taylor 1989). Since seeds persist in the environment for years, they provide a means by which a population can persist through stressful environmental conditions. Annual plants that experience highly variable environmental conditions rely on the seed bank to persist through years of unfavorable conditions. This is the case for desert annuals and other plant species that follow disturbances (fire, soil, etc.), all of which experience more unfavorable years than favorable years (Parker and Kelly 1989, Saatkamp et al. 2013, Venable and Lawlor 1980). Desert annual plants persist dormant as seeds in the seed bank through years of low rainfall or prolonged drought and only emerge in years with adequate rainfall. As an adaptation to prolonged drought, desert annual seeds have a high degree of dormancy and are presumed to be fairly long-lived, reducing the risk of seeds dying of old age in the seed bank after delaying germination. Even in years of adequate rainfall, a large proportion of the seeds in the soil seed bank in the near surface environment will remain dormant, delaying germination for later favorable years (Saatkamp et al. 2013), an additional fraction can become buried deep in the soil profile due to soil movement, soil freeze-thaw cycles, wetting-drying cycles in expansive soils, or the burrowing action of rodents, with the potential to resurface years or even decades later.

Germination for an annual plant is inherently risky. Once a seed germinates, the plant is obligated to grow and reproduce before it dies at the end of the growing season. If water supply is inadequate post-germination, the plant will die prematurely and fail to reproduce. Delayed germination of desert annuals is a canonical example of diversified bet-hedging, spreading the risk of mortality due to climate variability across multiple years and avoiding catastrophic population crashes (Cohen 1966, Philippi and Seger 1989, Venable 2007).

This life history can make monitoring populations of desert annuals challenging. Observed population sizes of emergent desert annuals will vary widely year to year due to highly variable annual rainfall, but these fluctuations don’t necessarily represent long-term population trends when the non-emergent individuals (seeds in the seed bank) are included. Therefore, the size of the soil seed bank is much more relevant for the long-term fates of species that utilize this life history strategy. Populations persist where the seed bank maintains a positive balance - that is, where the rate of new seeds entering the seed bank is equal or greater than the rate of seeds exiting the seed bank due to germination or death due to age expiration or predation (Fig 1.1). The two key demographic drivers of the soil seed bank are therefore: 1) rate at which seeds are added to the soil seed bank and 2) the rate at which seeds exit the soil seed bank, mostly due to germination or age-related seed mortality (Doak et al. 2002). Persistence of the seed bank through long droughts depends on limited emergence in years of inadequate rainfall to support successful reproduction and maximum seed longevity longer than the duration of the drought.

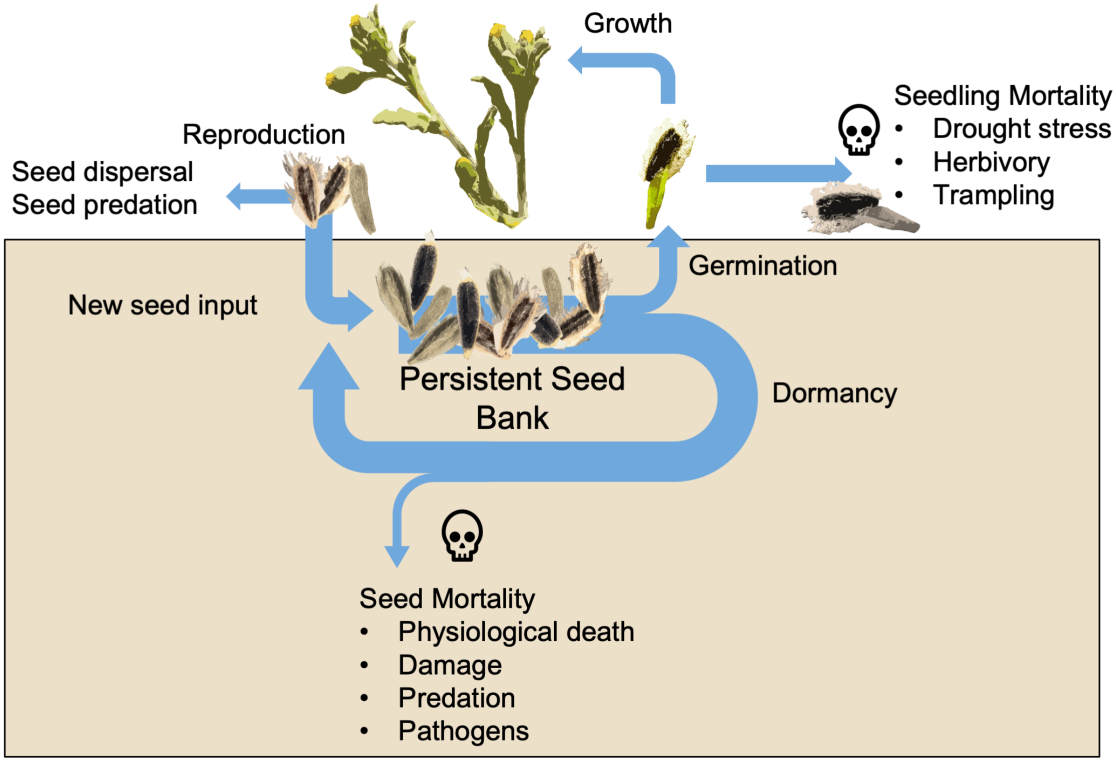

Fig 1.1 Diagram of the soil seed bank dynamics of *Monolopia congdonii*.

Seed banks are inherently difficult to study because seeds are tiny and distributed at low densities throughout the soil profile, making them difficult to detect and quantify. Additionally, the seeds of most annual plant species are relatively long-lived (at least several years), necessitating long-term studies to document their dynamics. Various techniques have been employed to study soil seed banks. Some studies have examined changes in the species composition and/or density of seeds in soil samples from the field over time (Evans et al. 2007, Laforgia et al. 2018, Sotomayor and Gutiérrez 2015), although it can be difficult to determine the age structure of the soil seed bank from such studies. Moriuchi et al. (2000) used radioactive dating with the ^{14}C signature from mid-20th century atmospheric nuclear weapons testing to resolve some of the age structure of seeds of a desert annual retrieved from a soil seed bank, however, the uncertainty of the measurements still spanned multiple years; this technique has not been applied to further studies on this topic since then.

Mesh seed packets buried in the soil profile have been used to track germination and mortality of seed in the soil seed bank (Auld et al. 2000, Hernandez et al. 2020), but these experiments are usually short term (1-5 years). Additionally, the artificially high density of seed in the packets may alter dynamics by negatively density-dependent germination mechanisms and allowing pathogenic fungi to spread more easily between seeds (Van Mourik et al. 2005).

Studies of seed longevity typically depend on the willingness of scientists to undertake studies that take decades to yield results. The Dr. William Beal Seed Longevity Study was initiated in 1879 and is still running today (Brown 2001, Telewski and Zeevaart 2002). It is the oldest study of its kind. Many questions with significant implications for conservation and ecology could be answered with such an approach, but unfortunately such projects which take years or decades to yield results are often not in line with the incentive structures of academia and funding agencies. Additionally, for species imperiled by climate change or other human activities, waiting years for results may hamper conservation efforts. Rapid artificial seed aging—subjecting hydrated seed to hot, humid conditions (Newton et al. 2009)—is one method that has been used to comparatively study phylogenetic, morphological, and environmental correlates of seed longevity (Merritt et al. 2014, Probert et al. 2009), but it is not clear exactly how directly these results compare to decline of seed viability under natural conditions. Opportunistic studies of old seed collections stored dry at room temperature provide an avenue to approach these questions in the short term, but depend on the existence of and availability of such collections, and it can be challenging to obtain a series of seed ages. Recent successes retrieving viable seed from herbarium specimens (Godefroid et al. 2011, Molnár et al. 2015, Nakahama et al. 2015) raise the possibility of using herbaria as a source of a wide range of seed ages for seed longevity studies among many species.

1.2 Climate change

Precipitation in California has historically been highly variable, with several multi-year droughts documented in the past 170 years (Hereford et al. 2006). Several decades-long megadroughts are also apparent in the paleoclimatic record from the past millennium (Cook et al. 2016, Michaelsen et al. 1988, Stahle et al. 2003), although these reconstructions generally lack the resolution to determine whether precipitation remained anomalously below average every year consecutively during these periods. To what extent species in more arid parts of California persisted as dormant seeds through these droughts or were extirpated and subsequently re-colonized via dispersal from more mesic sites is unclear. It is also possible that infrequent wet years may have punctuated these multi-decadal droughts, preventing extinctions of species without seed longevity on the order of the lengths of these megadroughts. Climate models are not in strong agreement on the magnitude or direction of change in average annual precipitation for California over the rest of the 21st century, largely because of difficulties modeling the atmospheric rivers that are responsible for 20 to 50% of annual precipitation in California. A majority of models predict either neutral or slight increases in annual precipitation but generally not enough to offset greater moisture deficits from higher temperatures (Chang et al. 2015, Cook et al. 2018, Dettinger et al. 2011, Polade et al. 2017, Swain et al. 2018). Drought years in central and southern California are expected to become more frequent and severe due to both more frequent years of below average precipitation (Swain et al. 2018) and greater soil moisture deficits because of higher evapotranspiration under warmer temperatures (Cook et al. 2018).

Though there is not clear evidence for an increase in the probability of consecutive dry years (Swain et al. 2018), higher temperatures may render years of average or even above-average precipitation unsuitable for some annuals. High temperatures during early season rains may limit germination, and emergent plants may experience higher mortality rates due to greater evapotranspirative stress. These effects of increasing temperatures may result in longer stretches of years between successful emergence and replenishment of the seed bank which would place greater significance on seed longevity and delayed germination for successful persistence of annuals.

Climate models forecast an increasing probability of extremely wet years driven by more frequent and intense atmospheric river events (Gershunov et al. 2019, Polade et al. 2017, Swain et al. 2018), and also an increase in the probability of so-called precipitation “whiplash” events, like the extremely wet winter of 2016-17 which followed the extremely dry drought of 2012-16 (Swain et al. 2018). While such a precipitation regime will pose extreme challenges for many other natural systems and for human infrastructure, it does not pose an obvious threat to California’s native desert annuals.

Increasing variability has the potential to preferentially reduce populations of invasive Mediterranean grasses (Laforgia et al. 2018, Minnich 2008, Valliere et al. 2019) several of which significantly impact populations of native annuals through competition. Invasive species from the Mediterranean basin are more prone to extreme population crashes during droughts, largely due to their shorter-lived seeds (typically <5 years) that tend to germinate much more readily than the seeds of native desert annuals (Laforgia et al. 2018, Salo 2004). Some of the most successful years for Californian desert annuals are extreme wet years following several years of extreme drought (Minnich 2008). Provided that drought lengths do not exceed the longevity of native annuals' seeds in the soil seed bank, the increased frequency of so-called "precipitation whiplash" events could potentially mitigate some of the fitness losses resulting from a warmer climate. The fitness consequences of a warming climate will be discussed more in Chapter 2.

1.3 The genus Monolopia and M. congdonii

The genus *Monolopia* is endemic to the California Floristic Province (CFP). It is within tribe Baeriinae and phylogenetically closely related to other primarily CFP and Desert Province distributed genera including *Pseudobahia*, *Eriophyllum*, *Syntrichopappus*, *Lasthenia*, *Baeriopsis*, and *Ambyloppapus* (Baldwin 2003). *Monolopia* includes five species including *M. gracilens, M. major, M. lanceolata, M. stricta*, and *M. congdonii* (Baldwin 2003, Jepson Flora Project (eds.) 2022). These five species differ markedly in growth form (erect vs. decumbent), flower head morphology (size and presence/absence of prominent ray corollas) and degree of hairiness (Fig 1.2).

Additionally, all five species differ markedly in their tolerance range with respect to climate (Fig 1.3) and substrate texture.

Monolopia congdonii (A. Gray) B.G. Baldwin (San Joaquin wooly-threads, Asteraceae) is a federally listed, endangered annual plant endemic to the San Joaquin Desert in the Central Valley of California. Compared to the ascending to erect growth form of the other species of *Monolopia*, *M. congdonii* has a decumbent growth form. Compared to the relatively large and showy-rayed flower heads of the other species of *Monolopia*, *M. congdonii* has small, non-showy flower heads with highly reduced ray corollas (Fig. 1.2). The species is primarily self-pollinating (Bainbridge et al. 2017).

Monlopia congdonii occurs within the Köppen-Geiger topoclimates of BSk (cold semi-arid), BWk (cold desert), and BWh (hot desert). It is a strict endemic of sandy soils on stream terraces (alluvial sand) and on low sandstone ridges. The species typically grows in patches with low competition from other annual plant species, such as disturbed soils around rodent burrows (Taylor 1989, R. E. O'Dell, pers. comm., BLM). As a winter annual, *M. congdonii* germinates only with sufficient rain and cool temperatures, typically >3/4 of an inch and < 60 °F (R. E. O'Dell, pers. comm., BLM) and does not emerge in large numbers during extreme drought years (Mazer and Hendrickson 1993, Taylor 1989).

The species is endangered due to conversion of habitat to agriculture, urban development, fossil fuel extraction, and non-native annual plant invasion (USFWS 1998). Most populations on the San Joaquin Valley floor have been extirpated. Remaining extant populations are scattered in the foothills of the Inner South Coast Ranges including at Panoche Creek, Monocline Ridge, Jacalitos Creek, Kettleman Hills, Lost Hills, Antelope Plain, Carrizo Plain, Elkhorn Plain, and Cuyama Valley (Taylor 1989, USFWS 1998). Conservation and recovery of the species is focused on protecting extant populations, potential current habitat, and reintroduction of new populations to suitable habitat (R. E. O'Dell, pers. comm., BLM, USFWS 1998). However, it is uncertain how climate change will impact the viability of these remaining populations and if locations of current potential habitat for re-introductions will be rendered unsuitable by a shifting climate.

Fig 1.2. Photos of the five species of *Monolopia*. **a** *Monolopia congdonii*, **b** *Monolopia lanceolata,* **c** *Monolopia stricta*, **d** *Monolopia major*, **e** *Monolopia gracilens* by Morgan Stickrod. All other photos by the author.

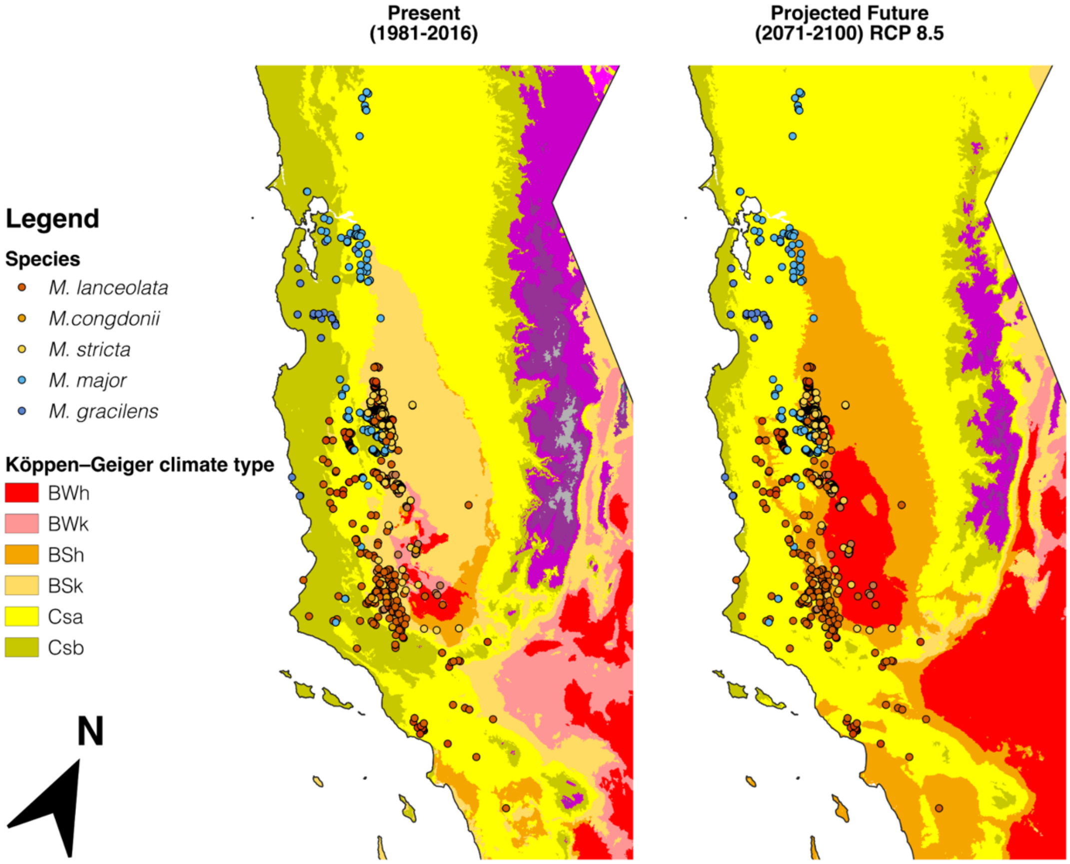

Fig 1.3. Georeferenced occurrence data for species of *Monolopia* (GBIF 2021, CCH2 2022, Calflora 2022) superimposed on maps of current and projected future Koppen–Geiger climate types from Beck et al. (2018)

1.4 Other species of Monolopia

Monolopia stricta has a short (<30 cm), erect, branching growth form and medium-sized (1 cm wide), relatively showy flower heads bearing short (1 cm), bright yellow rays. It is a strict endemic of clay soils in the San Joaquin Desert. Most occurrences are within the BSk climate (Calflora 2021, CCH2 2022, Jepson Flora Project (eds.) 2022).

Monolopia lanceolata has a tall (>>30 cm), erect, growth form and large (2 cm wide, very showy flower heads bearing long (2 cm), bright yellow rays. *Monolopia lanceolata* has a similar core range to *M. congdonii*, centered on the San Joaquin Desert, but it extends beyond as scattered populations on steep south facing slopes of the Csa hot summer Mediterranean climate in the Inner South Coast Ranges (SCoRI), Transverse Range (WTR), and Riverside Valley (Calflora 2021, CCH2, Jepson Flora Project (eds.) 2022). A few populations in the BWh hot desert climate of the western Mojave Desert occur on steep north facing slopes. The largest populations occur in BSk, BSh hot semi-arid, and BWk. Steep south facing slopes within the Csa topoclimate and steep north facing slopes within the BWh topoclimate are effectively BSk, BSh, and BWk microclimates. Unlike *M. congdonii*, the species is a soil texture generalist, occurring on most soils of different textures including sand, loam, and clay.

Monolopia major has a tall (>>30cm), erect, growth form and large, very showy flower heads bearing long, deep yellow rays. *Monolopia major* is a strict clay soil endemic occurring in generally more mesic habitat of the South Coast Ranges (SCoRO, SCoRI, SnFrB) and Inner North Coast Ranges (NCoRI). Most of the occurrences are within the Csa climate (Calflora 2021, CCH2, Jepson Flora Project (eds.) 2022).

Like *Monolopia major*, *M. gracilens* has a tall (>>30cm), erect, growth form and large, very showy flower heads bearing long, deep yellow rays. *Monolopia gracilens* is also a strict clay soil endemic. Most occurrences are in the San Francisco Bay Area (SnFrB) and Central Coast (CCo). Most occurrences are within the Csb warm summer Mediterranean climate (Calflora 2021, CCH2, Jepson Flora Project (eds.) 2022).

Published phylogenies of Madieae only include *M. gracilens, M. major, and M. congdonii*, and they show *M. gracilens* as basal and *M. major* and *M. congdonii* as sister (Baldwin and Wessa 2000, Baldwin et al. 2000). Morphological similarities (hairy cypselae) and similar geographic ranges suggest that *M. congdonii* is most closely related to *M. stricta* and *M. lanceolata.* Baldwin and Wessa (2002) hypothesize that the common ancestor of Madieae was a perennial, montane herb and that the many desert annuals in the group represent multiple developments of an annual habit and multiple radiations into semi-arid and arid habitats, with *Monolopia* appearing to represent one of those radiations.

1.5 Evolution of seed longevity

While seed longevity clearly varies across plant species (Telewski and Zeevaart 2002, Molnár et al. 2015, Went 1969) and is a key trait for annuals to escape frequent drought in arid climates (Probert et al. 2009, Venable and Lawlor 1980), few studies have examined whether this trait is variable at a fine phylogenetic scale. As a result, it is unclear if extended longevity is a derived adaptation to arid climates, or merely a preadaptation that allows certain plant species to pass an ecological filter and expand into arid climates. By also testing the longevity of three other species of *Monolopia,* I hope to provide some insights into this question.

1.6 Heterocarpy

Monolopia congdonii is the only species in the genus which exhibits pronounced heterocarpy, the production of multiple distinct types of fruit (Fig 1.4). In *M. congdonii,* there is strong differentiation between the cypselae produced by the ray and disk flowers.

Disk fruits are flattened with glabrous faces and a fringe of long hairs. Ray fruits are three-angled, more massive, and covered in short hairs on all surfaces, similar to the cypselae of *M. lanceolata.* Ray fruits are attached more firmly to the receptacle, dispersing more slowly than disk fruits, as the plant senescence. Mass measurements from a small number of fruits averaged 0.34 mg each for disk fruits (n=10) and 0.57 mg each for ray fruits (n=7). On average, the ray fruits were about 67% more massive. Due to the lower surface-area-to-volume-ratio of the ray fruits, a larger fraction of the mass of the ray fruit is likely made up of energetically expensive oils and starches, rather than dry pericarp. Seed mass has been found to correlated with longevity when comparing among species (Merritt et al. 2014), but it is unclear if this correlation will hold within two different morphs within a species.

The pronounced heterocarpy appears to be a derived trait and may represent adaptation for the two fruit morphs to specialize in dispersal, alternately, in space and time. The larger, energetically expensive ray fruits likely remain close to the parental site, where reproductive success has proven possible, exhibiting a more conservative strategy, and ensuring persistence at the site. The lighter disk fruits have a fringe of hairs which is most likely a specialized adaptation for animal dispersal (Vittoz and Engler 2007). The hairy disk fruits could become lightly entangled in the fur of rodents and other small mammals for local dispersal, or even possibly the downy feathers of songbirds for longer-distance dispersal. Animal dispersal represents a riskier strategy, since it depends on chance dispersal to suitable habitat, but opens up the possibility of colonizing new sites and the ability of the species to expand its range. *Monolopia congdonii* is strongly associated with rodent burrows within its habitat, especially those of giant kangaroo rat (*Dipodomys ingens*; Taylor 1989, Mazer and Hendrickson 1993, Cypher 1994). Given this affinity, giant kangaroo rats may be (or historically may have been) the primary vector for seed dispersal in *M. congdonii*. Its decumbent stems may also represent adaptation to reduce clipping by kangaroo rats in these habitats and/or adaptation to increase the likelihood that the disk cypselae contact and adhere to passing kangaroo rats.

Heterocarpy was noted in the original description of *M. congdonii* (Gray 1884), but the functional significance of this trait has not been empirically examined, and only rarely discussed in the existing literature (Taylor 1989). Heterocarpy or seed heteromorphism in other species has been documented to allow dispersal of seeds and fruits by multiple vectors and different distances (Ruiz De Clavijo 2005, Mandák and Pyšek 2001). Additionally, seeds of heterocarpic or heteromorphic species often show differential germination cues, phenology, and germination fraction (Tanowitz et al. 2018). These two are often interrelated, with dispersal ability of a seed typically being negatively related to its germinability (Mandák 1997). Heterocarpy in *M. congdonii* potentially could represent a form of bet-hedging, where many short-lived, less energetically-costly fruits are made that disperse through space with a lower individual probability of landing in new suitable habitat and a few expensive long-lived, highly dormant remain close to the parental site anchoring the population in space and dispersing through time.

1.7 Objectives

The primary objective of this study is to obtain an estimate for the maximum seed longevity of *M. congdonii* to help provide insight on how future droughts may impact the survival of existing or re-introduced populations of *M. congdonii*. Secondarily, I hope to provide insight into whether seed longevity is a trait that varies at a fine phylogenetic scale and test the hypothesis that the species of *Monolopia* from more arid climates should have longer-lived seeds than those from more mesic climates. Lastly, I aim to investigate heterocarpy of *M. congdonii* and test whether the seeds within the ray fruits are longer-lived than the disk fruits, representing specialization to disperse through time.

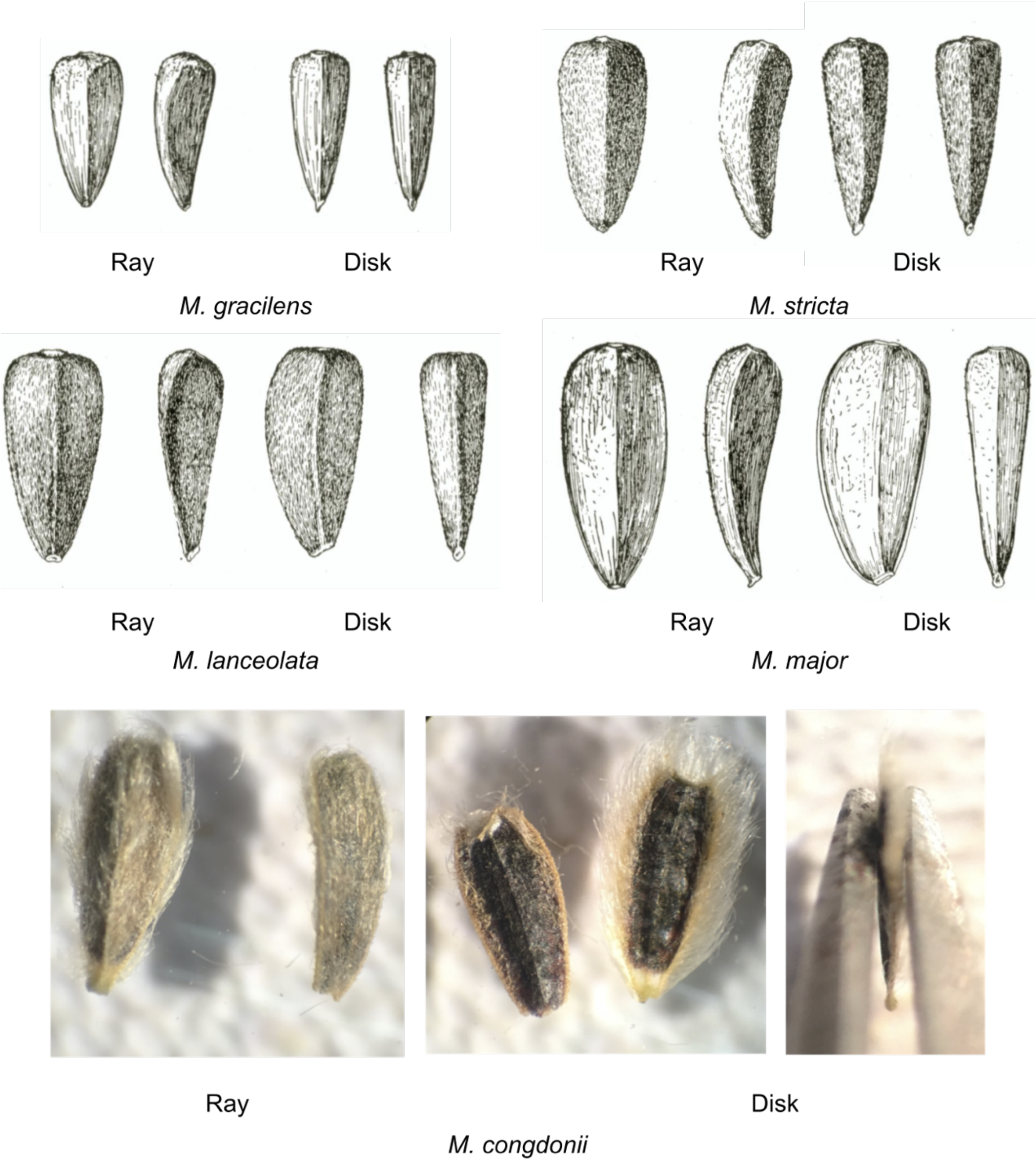

Fig 1.4. Drawings from Crum (1940), reproduced with permission (*Madroño*, ed. J. B. Whittall 2022). Disk and ray cypselae of the then-recognized species of *Monolopia* and photos of the disk and ray cypselae of *M. congdonii*. *Monolopia congdonii* was formerly *Lembertia congdonii* and not reclassified until 1999 (Baldwin 1999).

2. MATERIALS AND METHODS

2.1 Seed sourcing

Bulk seed collections of *M. congdonii, M. lanceolata, M. stricta,* and *M. major* were provided from the BLM Central Coast Field Office Conservation and Research Seed Bank (USFWS Recovery Permit TE-163671). These collections had been cleaned by size and density before storage. The fringe of hairs on the cypselae of *M. congdonii* allowed immature cypselae to adhere to other cypselae. A significant portion of *M. congdonii* seeds in the samples was immature. These samples required extra hand sorting to extract the mature seed. An additional seed collection of *M. congdonii* from 2005 was provided by Ellen Cypher (retired, California Department of Fish and Wildlife).

Additional samples of seed were collected from herbarium specimens housed at the California Academy of Sciences Herbarium (CAS-BOT), the Hoover Herbarium at California Polytechnic State University (OBI), the Clifton Smith Herbarium at Santa Barbara Botanic Garden (SBBG), the California Botanic Garden Herbarium (RSA), and the University of California, Riverside Herbarium (UCR). Collection targeted loose cypselae entangled in the foliage hairs of the plants, loose cypselae in fragment packets, and cypselae from flower heads with wilted or deciduous ray corollas to ensure maturity.

2.2 Seed testing

Seeds were tested for viability at the Oregon State University Seed Laboratory by tetrazolium chloride staining, which detects the presence of a live embryo within the seed (Lakon 1949, AOSA 2010). Data were reported as percent viability rounded to the nearest integer for all but the last batch of samples which were reported as raw counts of viable and nonviable seed.

2.3 Data analysis

Seed viability graphs and logistic regression curves were generated with package ‘ggplot2’ the species (Wickham 2022). Binomial confidence intervals for the possible ranges of viability represented by each sample given its sample size and reported viability were computed in R with package ‘Hmisc’ (R Core Team 2020, Harrell 2021) and added to the species-specific graphs. Fisher’s Exact Test was used to compare the viability between selected outliers and samples with similar characteristics. A t-test was used to test the significance of the difference between ray and disk cypselae.

3. RESULTS

A total of 85 samples were tested from 46 lots of seed. The average sample size was 133 seeds. Samples from herbarium specimens were generally smaller, 21 (15 lots) were from herbarium specimens with a mean size of 43 seeds (*SD* = 19, max = 84, min = 6). For bulk seed collections, 64 samples, from 31 lots the mean sample size was 162 seeds (*SD* = 96, max = 660, min = 12). Viability results are presented below in Figs 1.5 and 1.6 and broken down by species in the following sections and Figs 1.7-1.10.

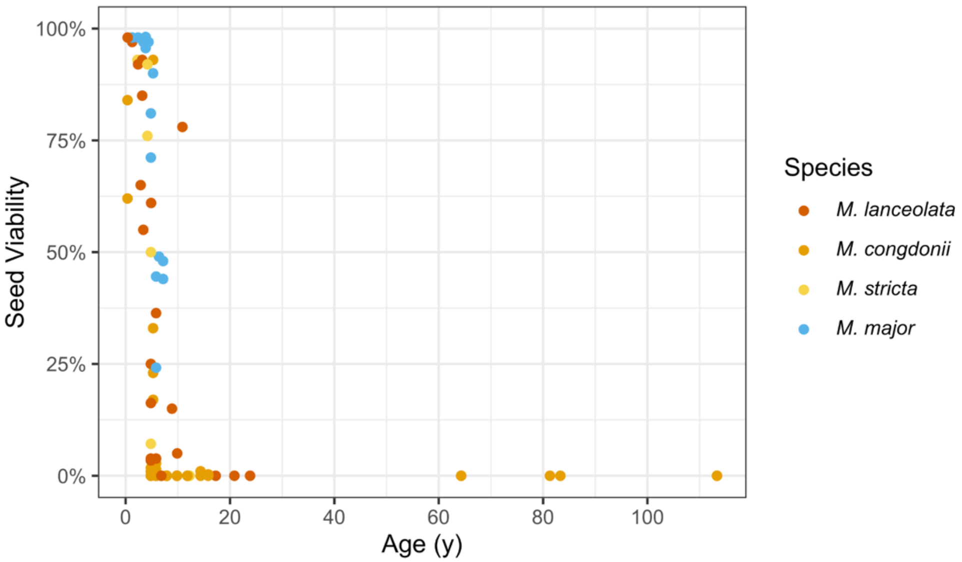

Fig 1.5. Viability of seeds, aged 0 - 113 years, tested at OSU Seed Laboratory of *M. lanceolata*, *M. congdonii*, *M. stricta*, and *M. major*.

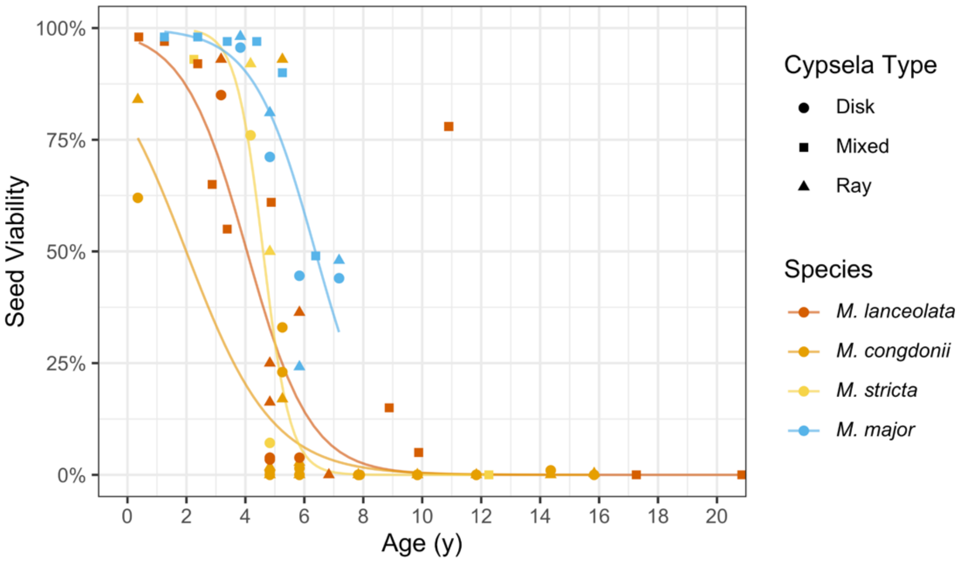

Fig 1.6. Viability of seeds, aged 0 - 20 years, tested at OSU Seed Laboratory of *M. lanceolata*, *M. congdonii*, *M. stricta*, and *M. major*. Binomial regression lines were merely added to assist with visualizing trends and should not be treated as predictive.

3.1 Monolopia congdonii

Monlopia congdonii samples were tested at 0, 5, 6, 8, 10, 12, 14, 16, 64, 81, 83, and 113 years of age (Figs 1.5 and 1.7). Seeds from ray and disk cypselae were tested separately for all samples. Viability of *M. congdonii* at 0 years was lower than for other species from 0-2 years, 84% and 62% for disk and ray cypselae, respectively. It is not clear from the data if this viability begins declining immediately, or if there is a plateau. By 5 years, there is a large decline in viability to an average of 13% (max 93%, min 0%), but with significant variation. Six out of 10 of the samples had <2% viability. Only one sample had >50% viability, a sample of ray cypselae at 93%, a substantial outlier. No viable seeds were found at any other time point beyond 5 years except in samples taken from Ellen Cypher's 2005 collection. When tested in 2021 (16 years), two viable seeds were found in a sample of 660 ray cypselae (0.3%). No viable seeds were detected in a sample of 306 disk cypselae tested at the same time. A test of samples from the same collection in 2019 (14 years) found no viable seed in a sample of 200 ray cypselae and 1% viability (which may represent one or two viable seeds) in a sample of 202 disk cypselae.

The outlier with 93% viability came from one of two seed lots collected from Lost Hills in 2013. The sample of ray achenes from the other seed lot, tested at the same time as the outlier had only 17% viability. Comparing these two samples with Fisher's Exact Test yields an odds ratio of 64.12 corresponding to a p-value $<2.2 \times 10^{16}$ suggesting it is extremely unlikely to be a probabilistic fluke.

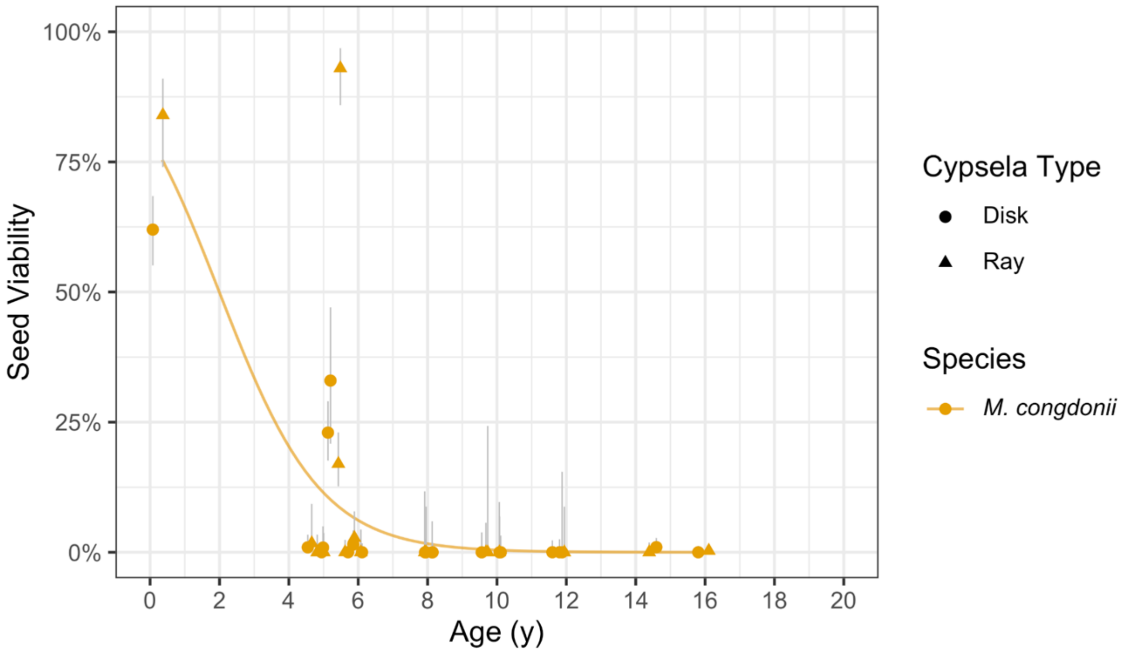

Fig 1.7. Viability of *M. congdonii* seeds, aged 0-20 years. Gray bars represent 95% confidence intervals for each sample. Datapoints have been randomly shifted a maximum of ±0.3y to reduce overlap.

3.2 Monolopia lanceolata

Monolopia lanceolata samples were tested at 0, 1, 2, 3, 5, 7, 9, 10, 11, 17, 21, and 24 years (Fig. 1.8). Most samples were a mixture of disks and ray cypselae. Young seed samples had very high viability. At 0, 1, and 2 years samples were 98%, 97%, and 92% viable. At 3 years viability begins to decline substantially, it was on average 72% (4 samples, max 93%, min 55%). At 5 years, viability was on average 14% (5 samples, max 61%, min 3%). At 6 years, viability (2 samples) was an average of 10% (max 36% min 4%). At 9 years, the one sample was 15% viable. At 10 years, the one sample was 5% viable. At 11 years the one sample was 78% viable, a significant outlier. No viable seeds were detected at 17, 21, or 24 years, although these samples were relatively small. If these three are pooled, 0 viable seed in 154 total seeds could represent a true viability of as high as 2.4% at a 95% confidence threshold. Comparing the number of viable and nonviable seeds from the 9- and 10-year old samples (pooled) to the 11-year old sample with Fisher's Exact Test yields an odds ratio of 32.16 corresponding to a p-value of $<2.2 \times 10^{-16}$, suggesting it is extremely, extremely unlikely that such an outlier would appear by random chance alone.

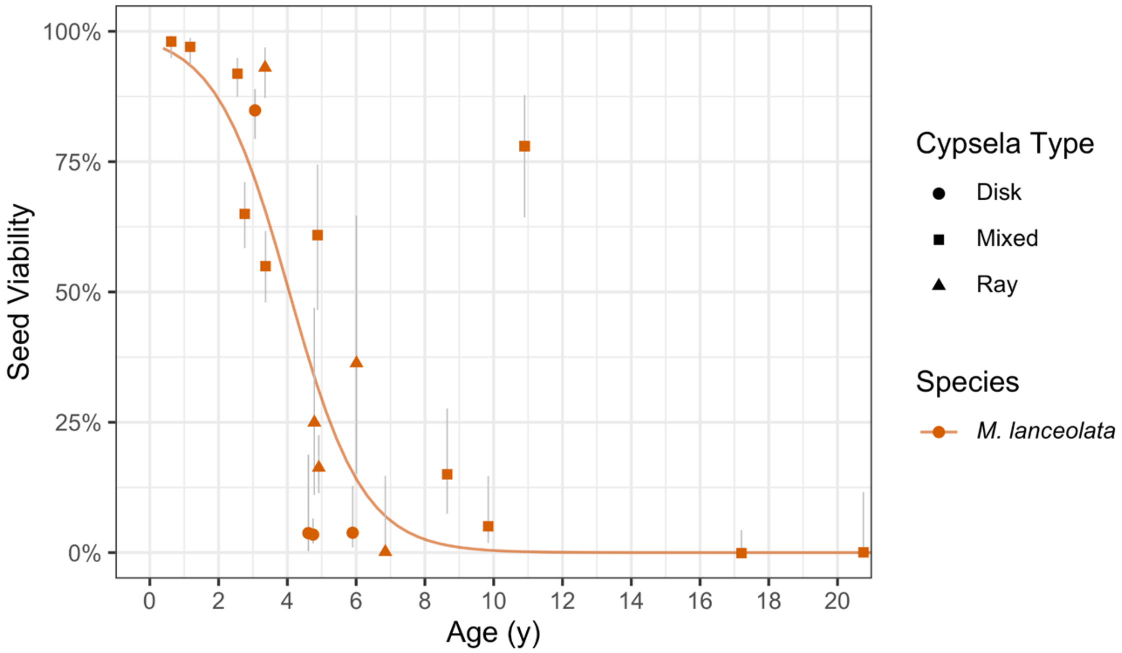

Fig 1.8. Viability of *M. lanceolata* seeds, aged 0-20 years. Gray bars represent 95% confidence intervals for each sample. Data points have been randomly shifted a maximum of ±0.3y to reduce overlap.

3.3 Monolopia stricta

Monolopia stricta samples were tested at 2, 4, 5, and 12 years (Fig 1.9). Viability is fairly high in the youngest samples. At 2 years, viability was 93%. At 4 years, viability was an average (2 samples) of 81% (max 92%, min 76%). At 5 years, viability was an average of 15% (2 samples, max 50%, min 7%), suggesting a rapid exponential decline. No viable seeds were detected at 12 years, though this sample was relatively small (95%ci from 0% to 6.6%).

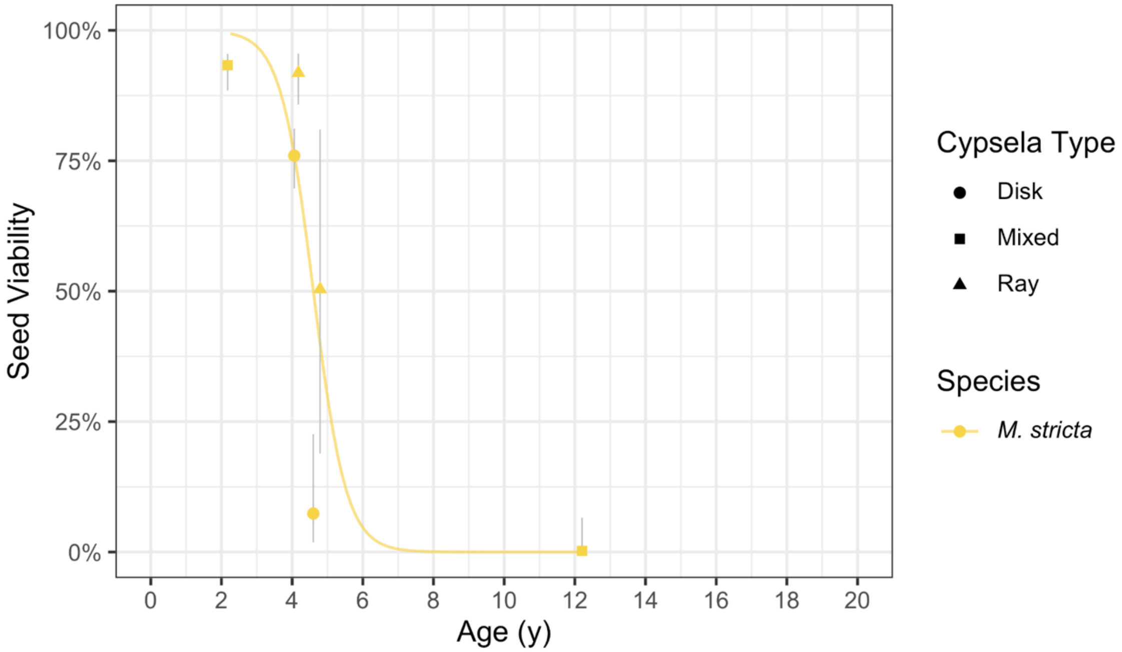

Fig 1.9. Viability of *M. stricta* seeds, aged 0-20 years, Gray bars represent 95% confidence intervals for each sample. Data points have been randomly shifted a maximum of ±0.3y to reduce overlap**.**

3.4 Monolopia major

Monolopia major samples were tested at 1, 2, 3, 4, 5, 6, and 7 years (Fig. 1.10). All samples 4 years and younger had viability ≥95%. At 5 years, viability was an average (3 samples) of 80% (max 90%, min 71%). At 6 years, viability was an average (3 samples) of 42% (max 50%, min 24%). At 7 years, viability was an average (2 samples) of 44% (max 48% min 44%).

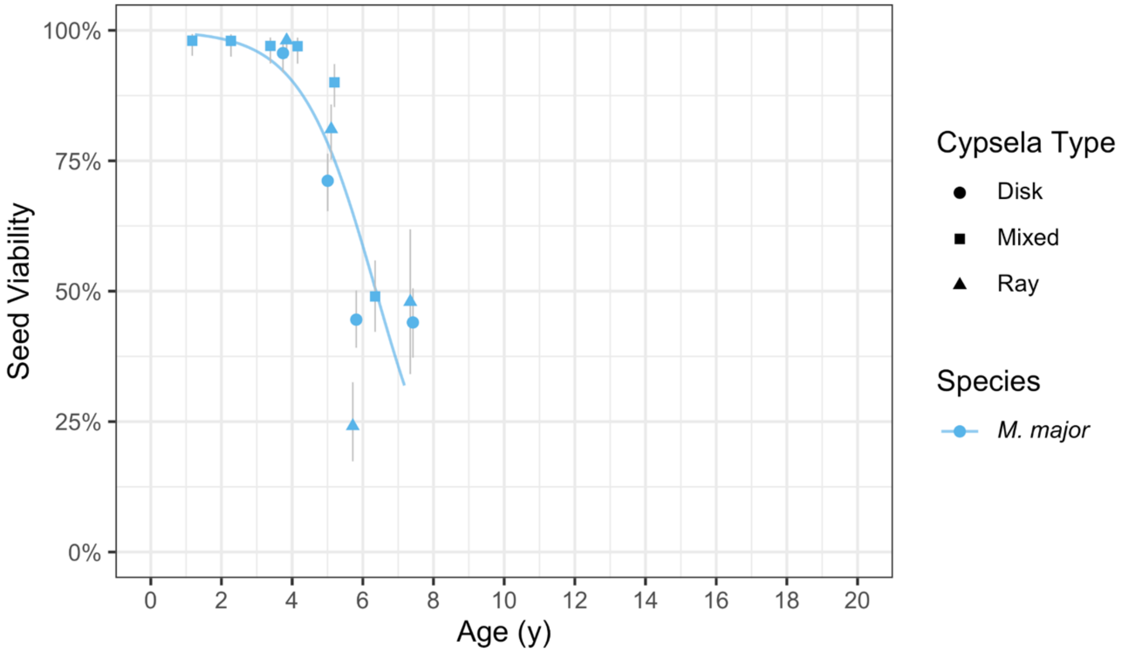

Fig 1.10. Viability of *M. major* seeds, aged 0-20 years, Gray bars represent 95% confidence intervals for each sample. Data points have been randomly shifted a maximum of ±0.3y to reduce overlap.

3.5 Heterocarpy

Across all species, the proportion of viable seed in samples of ray cypselae was on average higher than in samples of disk cypselae (Fig. 1.11). In 18 pairs of disk and ray samples from the same collections tested at the same time with viability >0% in one or both samples, the ray sample had higher viability in 14 cases. Restricting analysis to the 8 pairs of samples with >5% viability in either the disk or ray sample, the average difference between ray and disk samples was 16 percentage points (t= 2.74, p = 0.017). There does not appear to be evidence for this difference increasing with sample age.

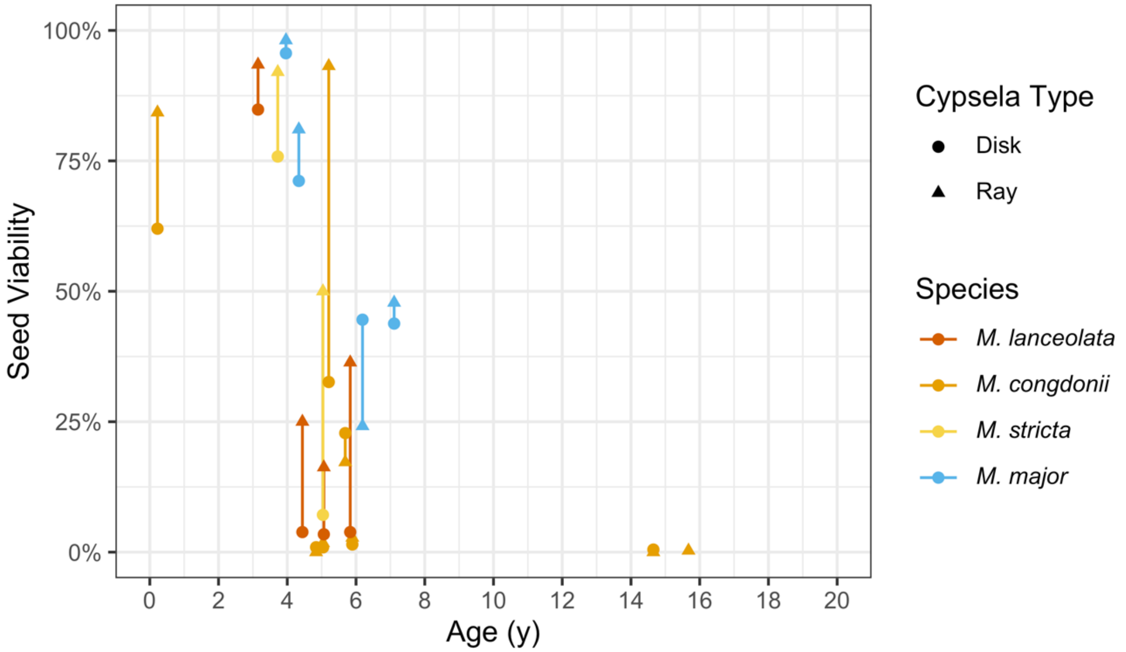

Fig. 1.11. Viability of pairs of disk and ray samples from the same lots of seed tested at the same time. Positions have been randomly shifted by a maximum of ±0.5y to reduce overlap

4. DISCUSSION

4.1 Lower initial viability of M. congdonii

Samples *of M. congdonii* had lower viability at all ages than the other species examined, but the low viability of seeds <2 years old relative to other species (Fig 1.6) suggests that this difference stems from a greater proportion of immature, nonviable seed being incorporated into samples of *M. congdonii* sent to the lab rather than from a shorter lifespan. This increased proportion of immature seeds is likely caused the inability to easily clean the seed collections by density like with the other species due to the longer hairs on the cypselae. An additional potential source of difference relative to other species is the lack of prominent ray corollas which are often used as an indicator of head phenology while collecting seed from other species of *Monolopia.*

4.2 Higher viability in ray cypselae

If the seeds of ray cypselae were longer lived, greater difference in viability between disk and ray samples would be expected to increase as seeds age. Qualitatively, this does not seem to appear in the data. Instead, I found a fairly constant difference in viability between ray and disk cypselae, which suggests that there are simply more immature disk cypselae in each collection. This is likely an artifact of the acropetal maturation of cypselae from outside of the head inward, leading to ray cypselae being on average more mature than the disk cypselae at the time of collection, when collecting whole heads before they shatter. Based on the data presented here, I hypothesize that this difference would likely not be observed or would be much reduced if cypselae were collected by allowing bagged heads to shatter naturally.

The pattern of higher viability in samples of ray cypselae appears to occur in all species tested, so it is likely unrelated to the pronounced heterocarpy of *M. congdonii*. Instead of differing in longevity, it may be the case that the two fruit morphs of *M.*

congdonii differ in how readily their seeds germinate, with the energetically cheaper seeds from disk cypselae employing the riskier strategy of germinating relatively readily while the more massive, energetically expensive seeds from ray cypselae germinate more conservatively. Alternatively, the unique morphology of the disk fruits may simply represent selection for improved animal dispersal (epizoochory), with lighter seeds being able to adhere longer to rodents or songbirds and disperse longer distances (Vittoz and Engler 2007).

4.3 Outliers: are the rest of these seeds fully mature?

The high viability outlier samples of *M. congdonii* and *M. lanceolata* require some explanation. Both were significantly different from samples tested at the same time which had comparable (or identical) storage histories and chains of custody. If there was not some fundamental difference between these sets of samples, the probability of obtaining both of these results would be astronomically small, so they cannot be dismissed as probabilistic flukes. Likewise, given that storage conditions were well-controlled for within these comparisons, storage conditions are not a satisfying explanation for these outliers either.

Outside of cold storage, it is difficult to explain what would cause just a few samples to far exceed the optimal viability for seeds of their age. This would seem to leave the possibility that the outliers are closer to the real optimal viability for their age. This would mean that either the rest of the seeds had never been viable in the first place, which is unlikely because of the high viability in young samples, or that the rest of the seeds tested declined abnormally quickly.

The *M. lanceolata* outlier was collected in early May, while most other samples taken from herbarium specimens were collected in April or March and most of the bulk samples were collected in mid-April. These should, in theory, represent mature seeds based on the phenology of *M. lanceolata* and *M. congdonii*, but seed longevity and desiccation tolerance generally have been shown to be acquired during the late maturation phase of seed development—after the seeds have become germinable (Hay and Probert 1995, Leprince et al. 2017, Newton et al. 2013, Zinsmeister et al. 2020). In some cases, the acquisition of longevity can happen even after the seeds have dispersed (Ali et al. 2007, Newton et al. 2013), which can result in differing longevity under storage based on when (phenologically) the seeds were collected and how they were handled post-collection (Probert et al. 2007). However, most of this research has been done on European temperate woodland species and not desert annuals.

Therefore, it is possible that *M. lanceolata* and *M. congdonii* (and maybe *M. stricta*) have a novel requirement for complete senescence of the plant and/or sustained exposure to hot, dry conditions at the onset of summer for the seeds to properly complete late maturation and acquire their greatest possible longevity.

A similar phenomenon may have been partially documented by Capon et al. (1978), who found seed of *Salvia columbariae* (Lamiaceae) from sites in the Mojave Desert stored at 20 °C for 5 years did not germinate readily, while seed from sites in the San Gabriel Mountains remained germinable. High summer temperatures have been shown to play a role in shifting seeds of winter annuals from dormancy to conditional dormancy, increasing the effectiveness of cold stratification in triggering germination, but it is unclear how or if this would relate to lower-than-expected longevity in seeds deprived of the natural extremes of their environment (Baskin and Baskin 1976, 2014, Capon et al. 1978).

Further research should test the effects of different harvest techniques, timings, and post-harvest treatments on the longevity of *Monolopia* seed. This could include bagging plants or heads and returning later, after the heads have shattered, to collect seed, collecting just persistent ray achenes after the disk achenes disperse, or allowing collections of seeds exposure to field conditions for various periods of time post-harvest. Artificial aging experiments as described by Newton et al. (2009) could be used to gauge the relative effectiveness of these various strategies and treatments. Studies such as this would help inform best practices for seed collection and banking of *M. congdonii,* ensuring that seeds removed from wild populations by collection have the best chances of remaining viable to serve a useful conservation purpose.

In preparing seed for my other experiments, I noticed that the mature-looking seeds I extracted from bulk samples of *M. congdonii* almost all sank in water, and the immature-looking seeds left behind almost all floated water. It is probably worth investigating if there are any negative impacts on seed quality for storage of a brief immersion in water to sort by density if followed promptly by drying. Such a float-sink test could potentially save many person-hours of work over cleaning seed by hand under a microscope and would potentially yield more consistent results. However, reducing the amount of immature seed collected in the first place would also reduce the need to clean seed.

4.4 Apparent longer-lived seeds in Monolopia major

It seems very unlikely that *M. major* seeds would be truly longer-lived than the other species, like the data here appear to suggest. The ability to persist as a seed for several years without significant mortality should be much more important for the persistence of species from arid climates, but it is not clear that any one cause can explain the differences observed. Aside from *M. congdonii*, all the other species had >90% viability in samples ≤2 years old. So, the differences cannot just be attributed to a uniformly higher fraction of non-viable seed at collection. It is possible that the hairiness of the seeds of *M. congdonii* causes greater variability in the fraction of immature seed that makes it through cleaning, but it seems unlikely to be able to explain the size of the difference, and would still not explain the difference between *M. major* and the two other arid habitat species, *M. stricta* and *M. lanceolata*. Another possibility is that the seeds of *M. major* achieve maximum longevity at senescence of the plant, without requiring any additional after-ripening in the hot, dry temperatures of summer. If true, this would suggest that this requirement of exposure to hot conditions to acquire maximum longevity is a novel trait in the arid-climate species.

That the data points for *M. major* form a curve much closer to the typical negative sigmoidal longevity curve expected for orthodox seeds, would seem to provide some tentative evidence that the curves obtained for the other species may not represent the full potential longevity (Baskin and Baskin 2014). This should provide a cautionary note that these curves presented here might not be perfect reflections of the actual longevity of seeds in the seed bank .

4.5 Implications for evolution of seed longevity in Monolopia

The data presented here do not provide support for the hypothesis that increased seed longevity evolved in *Monolopia* as it colonized more arid habitats and speciated. There are two possibilities, taking the data presented here at face value, which would suggest that the seed longevity these species possess is a conserved ancestral trait rather than a novel adaptation related to the habitats the species have diversified into. Data from *M. gracilens* and other species in closely related genera would help provide more insight, but it seems plausible that an early origin of increased seed longevity was a preadaptation that facilitated the several parallel colonizations of arid habitats by other annuals in the Baeriinae.

Alternatively, as discussed in section 4.3, the two extreme outliers seen in the data could represent a novel hot, dry maturation requirement for the seeds of the arid climate species of *Monolopia.* Under natural conditions, rather than room temperature storage, this additional maturation requirement may result in the expected longer-lived seeds for these arid climate species.

4.6 Implications of climate change for M. congdonii

For projecting how long droughts will impact populations of *M. congdonii*, the data presented here, which suggest a rapid decline to well below 50% in under 5 years, are likely not representative of the longevity of seeds in the soil seed bank. More research is clearly needed, but it seems reasonable to treat the more consistent results from *M. major* (negligible decline for 4 years, 50% decline by 6-7 years) as a working estimate for the rate at which seed viability in *M. congdonii* declines due to aging, with a possibility of being a conservative estimate. It is clear that some number of seeds can survive at least 16 years, though exactly how many is not clear due to variability in the initial viability and maturity. How far beyond 16 years seeds of *Monolopia* can survive is not clear due to low availability of samples of adequate size to confidently rule out survival of older seed.

Based on the available data, populations of *M. congdonii* should be able persist as a dormant seed bank through the maximum drought lengths forecast for the 21st century, assuming minimal germination during the drought years, and assuming that good reproductive output in non-drought years can be maintained (seeds in ≥ seeds out). The increasing variation in rainfall predicted for 21st century southern California, while likely problematic for other ecosystems, has the potential to reduce competition from some non-native species and the projected increased frequency of very high seasonal rainfall events may be able to buffer against the increased water stress that accompanies higher temperatures.

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Chapter 2

1. INTRODUCTION

Monolopia congdonii is a federally-listed endangered plant endemic to the San Joaquin Desert (*sensu* Germano et al. 2011) in Central California. It is primarily threatened by habitat loss due to land-use changes to agriculture, urban development, and oil and gas development (USFWS 1998). However, the threat of climate change remains largely unknown and could prove to be as or more devastating than habitat development. Conservation and recovery of the species is currently focused on protecting extant populations, as well as (re)introduction of new populations to potential habitat (R. E. O'Dell, pers. comm., BLM, USFWS 1998). However, it is unclear if the extant populations are located in areas where the climate will remain within the range of suitable climatic conditions for this species in the future, and if *M. congdonii* cannot tolerate the projected climate where it occurs, the focus of recovery efforts will need to shift to include more direct measures such as assisted migration by population introductions at new sites on the climatic leading edge of the San Joaquin Desert.

Water-energy balance, the interaction between evaporative demand and water supply, is the primary climatic factor driving vegetation distributions on global and local scales (Stephenson 1990, 1998, Neilson 1995). Additionally, the distribution of plant species largely reflects the climatic tolerance limits of the species with respect to water-energy relations (Billings 1952, Boyko 1947, Sommer et al. 2010).

Anthropogenic climate change is expected to dramatically alter the climate of California by the end of the century. The magnitude and direction of change in average annual precipitation (water supply) are uncertain over the coming decades (Chang et al. 2015, Polade et al. 2017, Cook et al. 2018). However, the magnitude of predicted warming will speed evapotranspiration, reducing water available for growth. Increased evapotranspiration will result in plants in the San Joaquin Desert experiencing more arid conditions, more similar to those currently found in the Mojave or even Sonoran Deserts by 2100, depending on the trajectory of atmospheric CO_2 (Fig 1.3, Ackerly et al. 2010, Beck et al. 2018).

If the relatively narrow range of average temperatures and precipitation present within the geographic range of *M. congdonii* and other San Joaquin Desert endemics represent the absolute limits of their climatic tolerance, this would bode poorly for their survival in a more arid future. Other species present in the San Joaquin Desert have broader ranges extending into the progressively more arid Mojave and Sonoran Deserts (average annual rainfall ~50 - 250 mm and ~50 mm - 100 mm, respectively, compared to ~150 - 250 mm in the San Joaquin Desert) (PRISM 2022). If climatic tolerance primarily varies at the species-level—as is commonly assumed for the sake of species distribution modeling (Anacker et al. 2013, Loarie et al. 2008, Parmesan and Hanley 2015)—the broad-ranging species that extend across more than one of these deserts should be expected to have a competitive advantage in a more arid future San Joaquin desert.

I aimed to test the effects of drier climates on the performance of *M. congdonii*, as well as ten other desert annuals that have ranges spanning one, two, or all three of California's deserts (Fig 2.1). I hypothesized that desert annuals with ranges spanning all three of these deserts would have the highest tolerance to drought, as compared to San

Joaquin Desert endemics, but will show comparatively lower fitness than these species under less stressful conditions, due to a tradeoff between water-use efficiency or growth rate (Gremer et al. 2013). To test this, I conducted a greenhouse pot study to simulate increasing intensity of drought. I examined the growth and reproduction of 11 different winter annuals species under three different drought treatments. I predicted an interaction between geographic range of a species and the response to the amount of water given. With species from the least arid San Joaquin desert having a steeper slope with respect to water and species from the most arid Sonoran desert having a shallower slope with respect to water.

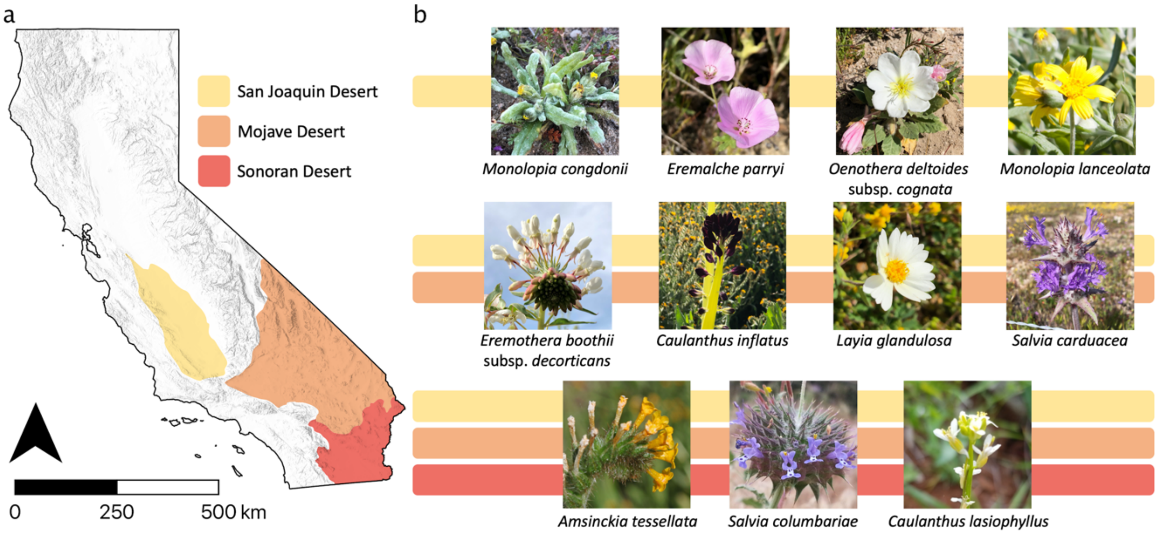

Fig 2.1. a The geographic extents of the three deserts within California. San Joaquin Desert *sensu* Germano et al. (2011), Mojave and Sonoran Deserts *sensu* Jepson Flora Project 2022. **b** The 11 species tested in this experiment. Species shown in yellow only are primarily restricted to the San Joaquin Desert. Those in yellow and orange have

ranges that include both the San Joaquin and Mojave deserts. Species in yellow, orange, and red have ranges spanning all three deserts.

2. MATERIALS AND METHODS

2.1 Study species and plant materials

I included 11 species in the study, all of which grow on sandy soils within the San Joaquin Desert. Four species included in the study are strictly endemic—or very nearly so—to the San Joaquin Desert including *Monolopia congdonii* (A. Gray) B. G.Baldwin, *M. lanceolata* Nutt. (Asteraceae), *Eremalche parryi* (Greene) Greene (Malvaceae), and *Oenothera deltoides* subsp. *cognata* (Jeps.) W.M. Klein (Onagraceae). Four of the species have ranges extending from the San Joaquin Desert into the Mojave Desert, including *Caulanthus inflatus* S. Watson (Brassicaceae), *Salvia carduacea* Benth. (Lamiaceae), *Layia glandulosa* (Hook.) Hook. & Arn. (Asteraceae), and *Eremothera boothii* subsp. *decorticans* (Hook. & Arn.) W.L. Wagner & Hoch (Onagraceae). Lastly, three of the species in the study span all three of California's deserts, including *Amsinckia tessellata* A. Gray (Boraginaceae), *Salvia columbariae* Benth. (Lamiaceae), and *Caulanthus lasiophyllus* (Hook. & Arn.) Payson (Brassicaceae) (Fig 2.1). I obtained seeds for these species from the BLM Central Coast Field Office Conservation and Research Seed Bank. All seeds were collected by BLM from within the San Joaquin Desert. The bulk seed collections included mixed seeds from a minimum of 100 individuals, but more typically 1000+ individuals.

2.2 Greenhouse design

The experiment was conducted outdoors at the Environmental Horticulture Unit on California Polytechnic State University Campus in San Luis Obispo, CA (Lat: 35.308873, Lon: -120.662438). The Köppen-Geiger climate at San Luis Obispo is Csb warm summer Mediterranean (Beck et al. 2018). A temporary greenhouse was constructed of a transparent vinyl tarp top and fine garden netting sides (Fig 2.2). Metal chicken wire was added around the bottom of the greenhouse part-way through the study to prevent rodent intrusion. Polyethylene drop cloths were attached to the sides of the greenhouse which were unfurled and secured to the ground during precipitation events to fully exclude natural precipitation, which would have altered the water regime of the study. The sides were only briefly rolled down to fully enclose the greenhouse during occasional rain events and were rolled up as soon as feasible after each of these events to allow for good airflow and ambient temperature/humidity. Plants were therefore exposed to ambient temperatures and light levels in San Luis Obispo, with only moisture being varied.

2.3 Pot study assembly

A fine, sandy soil (Monoridge soil series) derived from sandstone was collected from within the San Juaquin Desert at Panoche Creek (Lat: 36.605663, Lon: -120.754961) and sieved to < 2 mm to remove stones and other debris. Square 13 x 13 x 30 cm (5 L) plastic pots (Stuewe & Sons CP512). A 13 cm square piece of paper (fine porous) was moistened and stuck to the inside bottom of the plastic pot. This prevented the dry sand from leaking out of the pot drain holes when they were filled.

2.4 Water treatments

Previous studies of desert annual plant communities demonstrate widespread failure to reach maturity and reproduce when the water supply is less than 78 mm of rainfall and marginal growth between 78 and 127 mm of rainfall (Turner and Randall 1989, Beatley 1967, 1969, 1974; DeFalco et al. 2003; Went and Westergaard 1949). Therefore, I simulated water availability treatments of 76 mm annual rainfall (low water), 127 mm annual rainfall (medium water), and 178 mm annual rainfall (high water).

Seeds were planted on December 18th, 2019 and each pot was initially watered with 410 mL to trigger germination. I then monitored plants for germination. Seeds germinated within 10 days from the first watering. At day 11, each pot was thinned down to a single individual per pot. However, several species showed poor (*Caulanthus lasiophyllus, Eremalche parryi, Layia glandulosa,* and *Eremothera boothii*) or no germination (*Monolopia congdonii*, *Salvia columbariae*, and *Salvia carduacea*). For these species, seeds were given treatments previously found to be effective and either re-sowed into a ~2 cm indentation made in the center of the pot, or germinated on filter paper in a growth chamber and transplanted into the pots.

Small supplemental waterings were provided to the plants during the several weeks it took to establish seedlings of the species which failed to germinate. All pots had been given a total of 775 mL of water total by the end of the 5th week, (mid-January). Plants were assessed for phenology and size and grouped into blocks with similar plants before being randomly assigned to low, medium, or high water treatments. For species with low numbers of plants (*Eremalche parryi*, *Layia glandulosa*, and *Eremothera* *boothii*) , due to poor germination, mortality, rodent damage, or aphid damage only the medium and high treatments were given (Table 2.1). During the treatment phase, the plants were watered three additional times. The low treatment received a total of 1220 mL, the medium treatment received 2065 mL, and the high treatment received 2870 mL (Table 2.2).

Table 2.1 Numbers of plants of each species randomized to each treatment. Treatments are listed from low water (1) to high water (3). Species are colored and ordered by range limit from San Joaquin-endemic in yellow to species with range limits in the Mojave Desert in Orange, and species with range limits in the Sonoran Desert in red.

Species	**Treatment 1**	**Treatment 2**	**Treatment 3**
E. parryi		11	8
O. deltoides subsp. *cognata*	6	6	5
M. lanceolata	8	8	8
E. boothii subsp. *decorticans*		3	2
C. inflatus	6	6	7
L. glandulosa		3	3
S. carduacea	8	6	8
A. tessellata var. *tessellata*	7	8	7
S. columbariae	7	7	7
C. lasiophyllus	5	8	5

2.5 Study climate data

Local climate data within the greenhouse was recorded by a HOBO H21Datalogger with a S-THB-M002 temperature and relative humidity sensor and a S-LIA-M003 photosynthetic light sensor (Onset Computer Corporation). To prevent sunlight from heating the temperature probe, it was mounted in a RS3-B radiation shield and attached to a post several inches above the soil level in the pots, on the north side of the greenhouse. This orientation prevented shading the plants. The light sensor was placed within the grid of pots. The Cal Poly Weather Station (CIMIS station #52) is located approximately 400 meters away from the greenhouse. This weather station provided additional local climate data. Solar radiation (W/m^2) from the weather station was converted to photosynthetically active radiation ($\mu mol/m^2 s$) using a conversion factor of 2.04 μmol/s per W (Meek et al. 1984) and integrated over the course of the day. These data can be seen in tables 2.3 and 2.4.

Fig 2.2. Overview of the study design. Pot study in a temporary greenhouse.

Table 2.2. Water treatment schedule for all treatment groups. Dates and volumes (ml) of water applied. Across the soil surface of the pot, 16.9 ml of water applied is equivalent to 1 mm of rain. The last watering date was April 1.

		Water Treatments (ml)			
Week	**Date**	**Low**	**Medium**	**High**	
1	12/18/19	410	410	410	Initial watering
2	12/25/19	.	.	.	Germination
3	1/1/20				
4	1/8/20	Supplemental waterings to help re-sowed seeds germinate and transplanted seedlings survive			
5	1/15/20	All pots brought back to same water level — 775 mL			
6	1/22/20	.	.	.	
7	1/29/20	.	.	.	
8	2/5/20	100	100	100	
9	2/12/20	.	.	.	
10	2/19/20	150	150	150	
11	2/26/20	Blocking of similar plants and randomization to treatments			
12	3/4/20	95	515	615	
13	3/11/20	.	.	.	
14	3/18/20	50	260	615	
15	3/25/20	.	.	.	
16	4/1/20	50	265	615	Final watering
	TOTAL	1220	2065	2870	

Table 2.3. Weekly averages of temperature, humidity, and light (PAR) from the datalogger. Temperatures were taken close to soil level of pots, this likely contributed most of the difference from the Cal Poly weather station.

Week	Date	Average High Temp (°C)	Average Low Temp (°C)	Average Relative Humidity (%)	Average Daily PAR mol/(m^2 d)
1	12/18/19	20.7	8.2	76.3	11.0
2	12/25/19	21.1	7.2	70.6	14.2
3	1/1/20	26.9	9.2	57.6	17.2
4	1/8/20	22.9	7.0	63.6	16.0
5	1/15/20	20.9	6.6	70.3	12.1
6	1/22/20	28.0	10.5	67.3	17.0
7	1/29/20	27.8	8.4	51.1	18.7
8	2/5/20	28.7	6.7	49.8	20.8
9	2/12/20	30.4	8.6	56.9	22.3
10	2/19/20	31.3	9.9	55.1	21.3
11	2/26/20	31.7	10.1	44.9	21.6
12	3/4/20	30.2	10.2	64.3	21.7

Table 2.4. Weekly average of temperature, humidity, and light (PAR) from the Cal Poly Weather Station.

Week	Date	Average High Temp (°C)	Average Low Temp (°C)	Average Relative Humidity (%)	Average Daily PAR mol/(m^2 d)
1	12/18/19	16.6	6.2	73.7	14.8
2	12/25/19	15.4	5.3	68.6	18.2
3	1/1/20	19.3	8.2	59.4	22.5
4	1/8/20	15.3	5.6	66.3	22.8
5	1/15/20	15.3	4.8	70.1	17.4
6	1/22/20	19.8	9.4	69.6	23.6
7	1/29/20	19.5	6.4	53.1	27.5
8	2/5/20	19.3	4.4	54.6	30.9
9	2/12/20	20.6	6.3	64.6	32.9
10	2/19/20	21.5	7.6	61.1	32.1
11	2/26/20	22.5	7.4	50.4	34.8
12	3/4/20	17.9	8.1	75.0	26.5
13	3/11/20	16.2	9.0	80.7	21.8
14	3/18/20	16.3	7.0	77.6	26.9
15	3/25/20	17.4	6.0	70.4	44.4
16	4/1/20	16.5	5.7	72.4	38.7
17	4/8/20	16.4	7.8	82.1	30.9
18	4/15/20	18.7	8.2	74.1	41.3
19	4/22/20	27.7	13.8	54.3	54.7
20	4/29/20	24.8	10.4	59.6	55.7
21	5/6/20	24.7	11.6	58.4	54.5
22	5/13/20	21.5	9.6	72.1	52.4
23	5/20/20	24.7	9.5	64.6	59.8
24	5/27/20	23.0	11.9	74.4	43.2
25	6/3/20	25.3	11.9	59.1	53.9
26	6/10/20	25.8	11.7	58.9	61.9
27	6/17/20	23.6	11.6	72.6	55.9
28	6/24/20	23.0	12.6	74.3	53.4

2.6 Plant biomass harvest

The plants senesced between April and June. Leaves, corollas, fruits, and seeds were collected as they abscised, and the remainder of the aboveground plant biomass was harvested after senescence. Biomass samples were weighed (Mettler Toledo ME54E) and the number of seeds, flowers, and fruits were counted. For species in the Asteraceae, the number of heads was counted instead of the number of flowers.

2.7 Soil water content

Plants were monitored until they naturally senesced after the final watering event. To determine the soil water content at senescence, the top 5 cm were discarded and the soil from 5 cm to 30 cm depth was homogenized. An approximately 1L aliquot was collected into a paper lunch bag and immediately weighed (Ohaus CL201). The samples were then dried at 70 °C for a week and then re-weighed. Gravimetric water content was calculated as the difference between the wet and dry weight divided by the dry weight.

$$\text{Gravimetric water content (\%)} = 100 * \frac{\text{weight}_{\text{wet}} - \text{weight}_{\text{dry}}}{\text{weight}_{\text{dry}}}$$

2.8 Statistical analyses

Statistical analyses included an all-species model to test the hypothesis that desert range breadth would be related to drought tolerance, plus species-specific models to explore species-level variation in drought tolerance. First, total aboveground biomass was used as a measure of overall productivity, in response to the water treatments. A two-level linear mixed-effect model was used to assess if desert provenance explains the plasticity of aboveground biomass across the treatments. Desert provenance, treated as a categorical variable (San Joaquin endemic, San Joaquin and Mojave species, or San Joaquin, Mojave, and Sonoran Desert species, as shown in Fig. 2.1)., total water as a continuous variable, and their interaction were treated as the fixed effects. Blocks were treated as a level 1 random effect with random intercepts to help account for variability that was pre-existing before assignment to treatments. Species were allowed random slopes with respect to water to account for variability between species within each desert category. All models were fitted using R package `lme4` (Bates et al. 2015, R Core Team 2020).

To summarize species-level flowering output and biomass responses, mixed effect models were fitted using treatment as a categorical fixed effect variable. For biomass, linear mixed-effect models were used with block as a random intercept and treatment as a fixed effect. For the species with lower numbers of flowers, generalized linear mixed-effect models (glmm) with Poisson error were used. For species with higher numbers of flowers, the dispersion ratio test as implemented in package `performance` (Lüdecke et al. 2021) suggested that the Poisson glmms models showed evidence of overdispersion. Thus, for these species, I used linear mixed-effect models with natural log-transformed number of flowers as the response. Models with flower number as the response variable had the same random and fixed effects as the biomass models. Given the expectation of a monotonic response to increasing water availability, a significant difference between the high and low treatments would be a trivial finding if either (or both) treatment was significantly different from the medium treatment, so an additional pairwise comparison was conducted between the high and low water treatments only when neither was found to be significantly different from the medium water treatment. Estimated mean responses were calculated using package `emmeans` and graphs were made using package `ggplot2` (Lenth 2021, Wickham 2022).

3. RESULTS

Despite *Monolopia congdonii* being the focal species of study, attempts to propagate the species were unsuccessful. Very few pots had any seedlings emerge naturally and these and the transplanted *M. congdonii* seedlings did not survive long enough to be randomized to treatments. The lack of plants made testing some of my original hypotheses regarding *M. congdonii* impossible. But, the response of *M. lanceolata*—the nearest relative, with a similar geographic range—to the study treatments, can be inferred to apply to *M. congdonii*. However, this should be tested in future experiments.

The majority of plants of the other species senesced in May, although some senesced in late April and a few others senesced as late as the end of June (Fig 2.4). Most species did not reliably set seed, likely due to lack of pollinator access. Many produced fruits with no or few seeds inside.

3.1 Soil Water Content

For most species, soil water content at senescence was less than 2%, on average, with a few outliers for each species (Fig 2.3). Soil water content at senescence was the highest for *Amsinckia tessellata*; however, the variance was high. Many of these outliers are associated with anomalously low biomass and/or flower number relative to other conspecifics in the same treatment, suggesting they died for reasons other than exceeding their tolerance for drought stress.

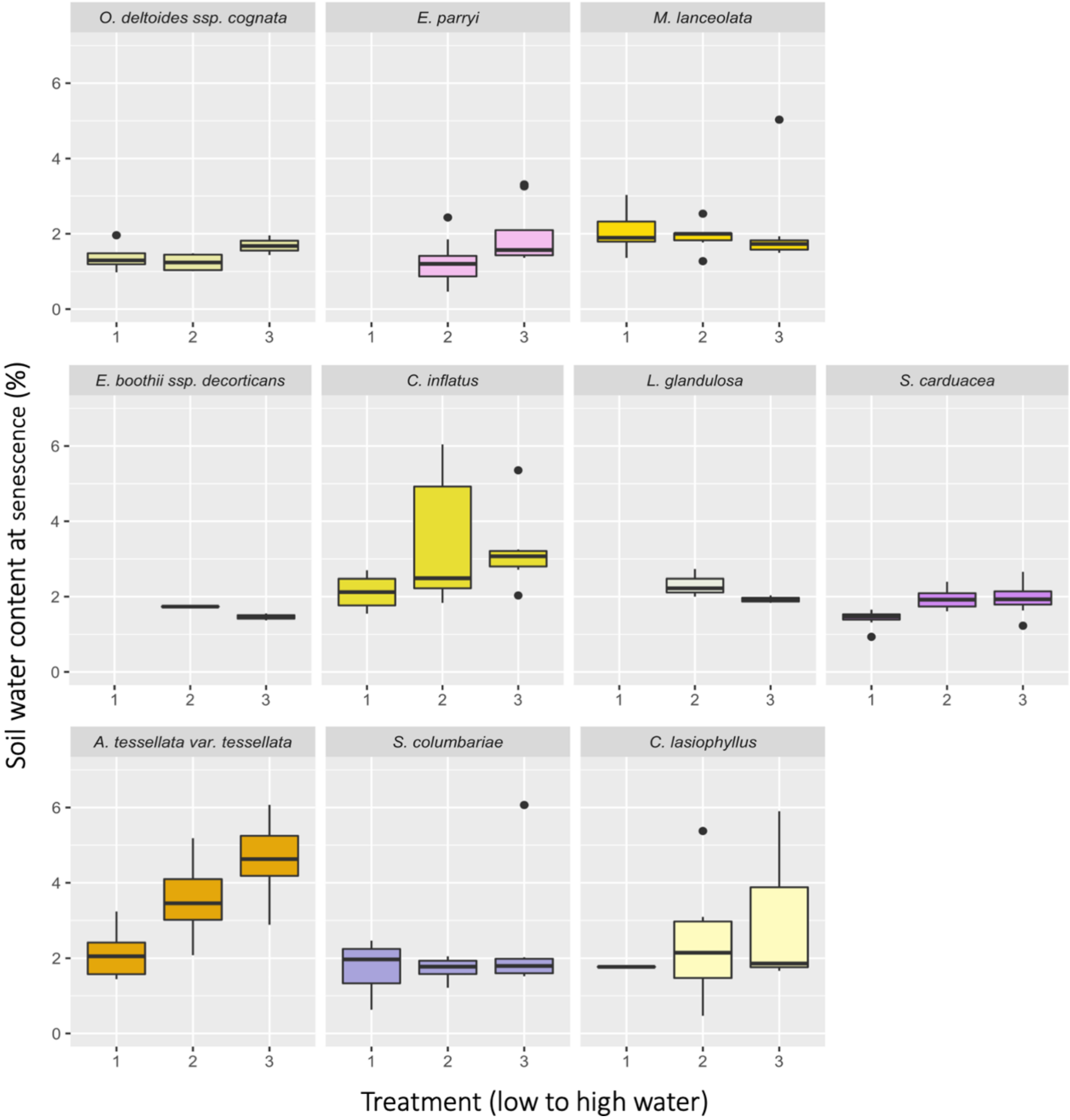

Fig 2.3. Box and whisker plot of gravimetric water content of soil at senescence by species. The center line shows the species median. The boxes span the first and third quartiles and the whiskers extend to the largest and smallest value excluding any outlying

points (defined as any value more extreme than 1.5x the inter-quartile from the first or third quartile).

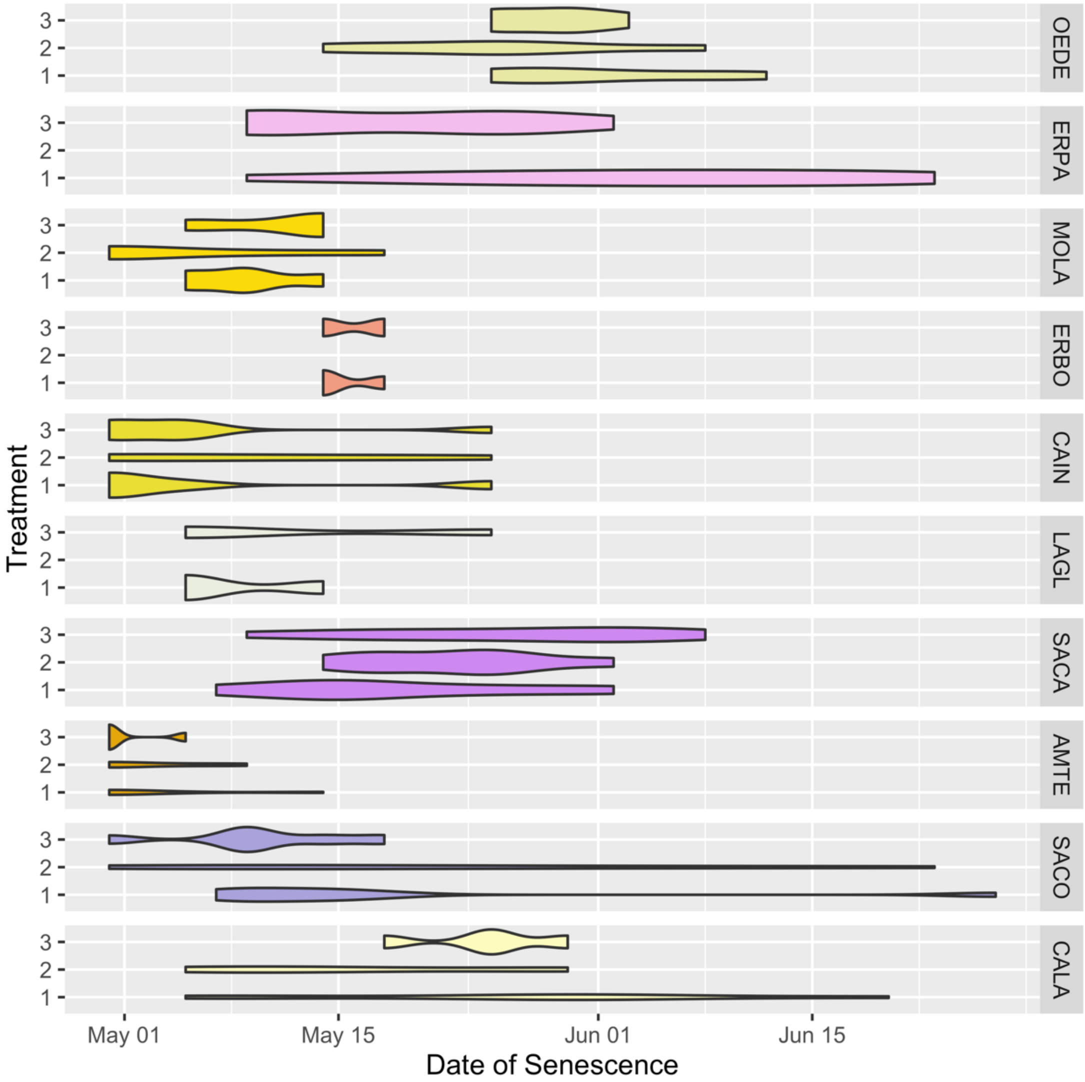

Fig 2.4. Stacked violin plots of senescence dates for each species in each treatment group. Width of the violin represents the proportion of plants senescing in that time period. Data are missing for plants that senesced before May 1. Treatment 1 = 1220 ml (low water), 2 = 2065 ml total (medium water), 3 = 2870 ml total (high water)

3.2 Biomass

There was a significant effect of water on plant biomass. With higher average biomass in response to increased water availability (Table S.1). However, the interactions between species' ranges and water were not significant. That is, the effect of water did not significantly vary by the species' range breadth. San Joaquin endemics did not show a significant positive interaction (steeper slope) relative to the reference group (species occurring in both the Mojave and San Joaquin deserts) and the broadest-ranging species did not show a significant negative interaction (shallower slope).

Despite a lack of influence by desert range breadth, the biomass response of individual species to the treatments did vary. The effect sizes and pairwise comparisons can be seen below in Table 2.5 and Fig 2.5. Of the species with ranges extending into the Sonoran Desert, *A. tessellata* and *S. columbariae*, but not *C. lasiophyllus*, showed a significant decrease in average biomass from the medium to the low treatment corresponding to approximately a 75% and 85% reduction in biomass, respectively. Only *S. columbariae* showed a significant, large increase in biomass of approximately 70% between the high and medium treatments, although *A. tessellata* showed a nearly significant (p = 0.058) increase of about 25%. Biomass of *Caulanthus lasiophyllus* also did not differ between the high and low treatments (p=0.129). Of the species with range limits in the Mojave, only two were given the low water treatment. Both *C. inflatus* and *S. carduacea* showed a significant decrease in average biomass from the medium to the low treatments, approximately a 63% and 66% decrease respectively. None of the four species showed a significant difference in biomass between the high and medium treatments, although the effect for *C. inflatus*, a 57% increase in biomass in the high versus medium treatment, was nearly significant (p=0.095). Of the San Joaquin endemic taxa, the two given the low water treatment—*M. lanceolata* and *O. deltoides* subsp. *cognata*— had significantly lower biomass in low compared to medium water treatments (67% and 73% lower, respectively). All three San Joaquin endemics, *M. lanceolata, O. deltoides,* and *E. parryi*, showed significant increases in biomass from the medium to high water treatments 49%, 102%, and 112%, respectively.

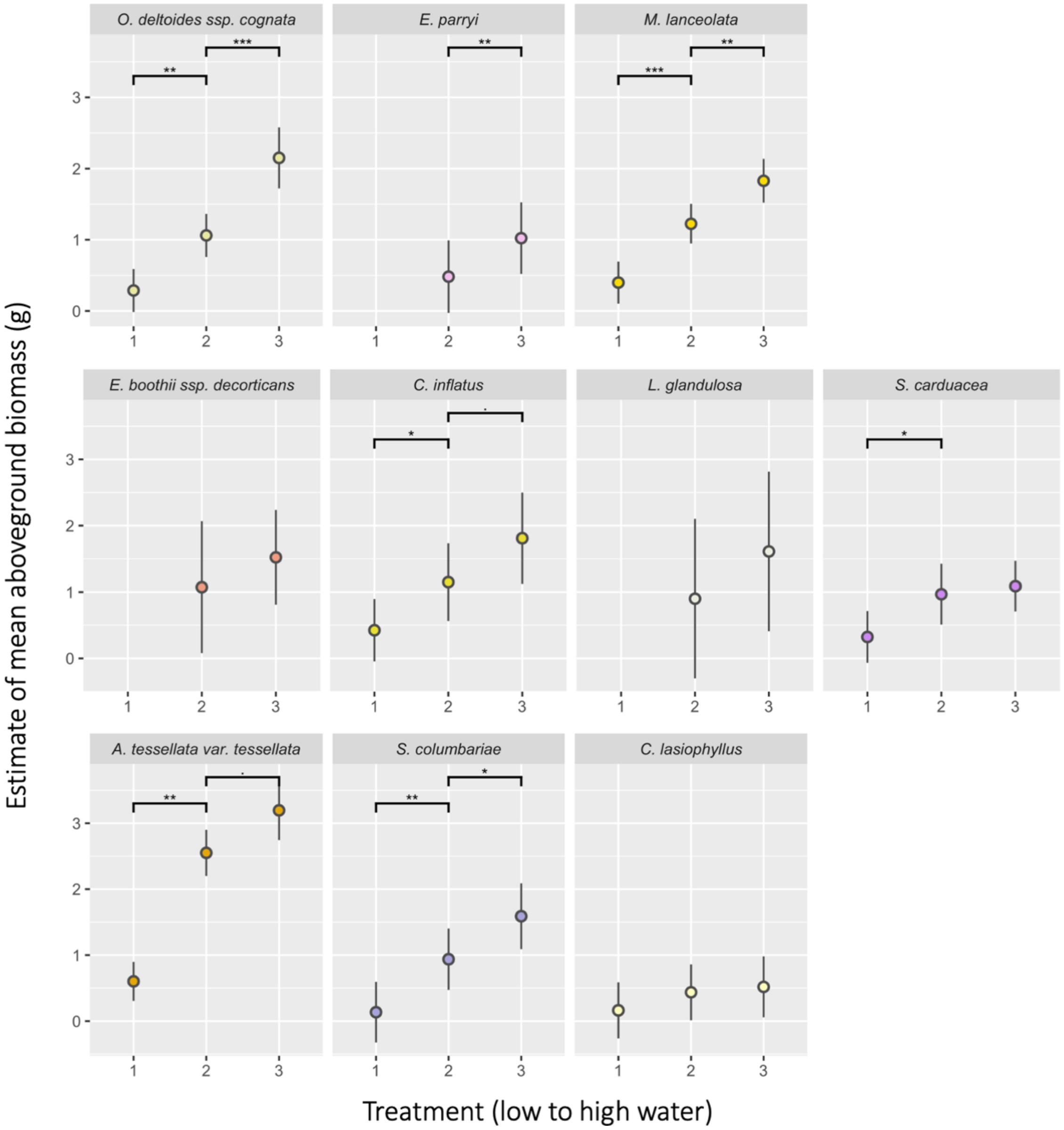

Fig 2.5. Estimated mean aboveground biomass (g) and 95% confidence intervals under three different watering treatments using mixed effect linear models. Treatments 1, 2, and 3 (low, medium, high) = 1220, 2065, and 2870 mL water, respectively. Significant ($p < 0.05$) pairwise comparisons are shown with asterisks, nearly significant comparisons ($0.05 < p < 0.1$) are shown with dots.

Table 2.5. Biomass of each species under three different watering treatments. Intercepts represent the estimated biomass in grams for the medium water treatment, and the estimates for the low and high water treatments represent the estimated differences (in grams) from the medium treatment.

Parameters	Estimate (g)	95% CI	Std. Error	df	t value	p value
Eremalche parryi						
(Intercept)	**0.481**	(0.12 — 0.83)	0.165	3.46	2.92	
High water	**0.541**	(0.27 — 0.83)	0.137	13.1	3.96	**0.002**
Oenothera deltoides* subsp. *cognata						
(Intercept)	**1.062**	(0.81 — 1.31)	0.134	14	7.91	
Low water	**-0.774**	(-1.13 — -0.42)	0.19	14	-4.08	**0.001**
High water	**1.088**	(0.71 — 1.46)	0.199	14	5.46	**<0.001**
Monolopia lanceolata						
(Intercept)	**1.225**	(0.98 — 1.48)	0.128	16.49	9.55	
Low water	**-0.827**	(-1.15 — -0.49)	0.169	15.98	-4.89	**<0.001**
High water	**0.603**	(0.28 — 0.93)	0.167	15.13	3.6	**0.003**
Eremothera boothii* subsp. *decorticans						
(Intercept)	**1.073**	(0.72 — 1.4)	0.155	1.47	6.95	
High water	**0.45**	(0.04 — 0.8)	0.175	2.05	2.57	0.121
Caulanthus inflatus						
(Intercept)	**1.15**	(0.69 — 1.61)	0.245	9.99	4.69	
Low water	**-0.726**	(-1.27 — -0.2)	0.283	6.34	-2.57	**0.041**
High water	**0.661**	(0.04 — 1.37)	0.333	5.95	1.98	0.095
Layia glandulosa						
(Intercept)	**0.9**	(0.12 — 1.68)	0.367	2.85	2.45	
High water	**0.712**	(0 — 1.43)	0.314	2	2.27	0.151
Salvia carduacea						
(Intercept)	**0.968**	(0.54 — 1.37)	0.209	15.74	4.63	
Low water	**-0.645**	(-1.1 — -0.22)	0.223	15.72	-2.88	**0.011**
High water	**0.121**	(-0.32 — 0.54)	0.218	15.69	0.55	0.588

Table 2.5 *continued*

Parameters	Estimate (g)	95% CI	Std. Error	df	t value	p value
Amsinckia tessellata* var. *tessellata						
(Intercept)	**2.55**	(2.27 — 2.85)	0.136	5.99	18.71	
Low water	**-1.947**	(-2.26 — -1.76)	0.108	1.99	-18.05	**0.003**
High water	**0.646**	(0.3 — 0.9)	0.146	1.8	4.42	0.058
Salvia columbariae						
(Intercept)	**0.938**	(0.53 — 1.35)	0.212	13.53	4.43	
Low water	**-0.803**	(-1.27 — -0.33)	0.243	12.42	-3.3	**0.006**
High water	**0.652**	(0.14 — 1.15)	0.262	13.59	2.49	**0.026**
Caulanthus lasiophyllus						
(Intercept)	**0.437**	(0.08 — 0.8)	0.182	7.78	2.41	
Low water	**-0.274**	(-0.63 — 0.1)	0.186	7.59	-1.47	0.18
High water	**0.082**	(-0.36 — 0.44)	0.192	6.89	0.43	0.683

3.3 Flowering

The species-level flowering responses to the treatments were largely similar to the biomass responses. Effect sizes and pairwise comparisons are summarized below in Fig 2.6 and Tables 2.6 and 2.7. Of the Sonoran species, again *A. tessellata* and *S. columbariae* showed significant decreases in median flower number between the medium and low treatments, representing 82% and 74% percent decreases, respectively. Despite showing no significant effect with biomass, *C. lasiophyllus* produced significantly fewer flowers, approximately 78%, in the low water treatment than the medium treatment. Only *S. columbariae* produced significantly more flowers between the medium and high treatments, approximately a 74% increase. Again, unlike with biomass, the effect of the high water treatment on *C. lasiophyllus* was a nearly significant (p=0.053) 57% increase in flower number. Of the Mojave species, *S. carduacea* still showed a significant 65%

decrease in number of flowers in the low water treatment. *Caulanthus inflatus* again showed a significant 87% decrease in flower number that did not appear in the biomass comparison. As with biomass, none of the species showed significant differences between the medium and high water treatments. For the San Joaquin Desert endemic species, both species given the low water treatment (*O. deltoides* and *M. lanceolata*) showed significant decreases in flowering in the low treatment, approximately a 71% decrease for both. Unlike with the biomass, where all species showed significant increases in the high treatment, only *E. parryi* produced significantly more flowers in the high water treatment, approximately 72% more.

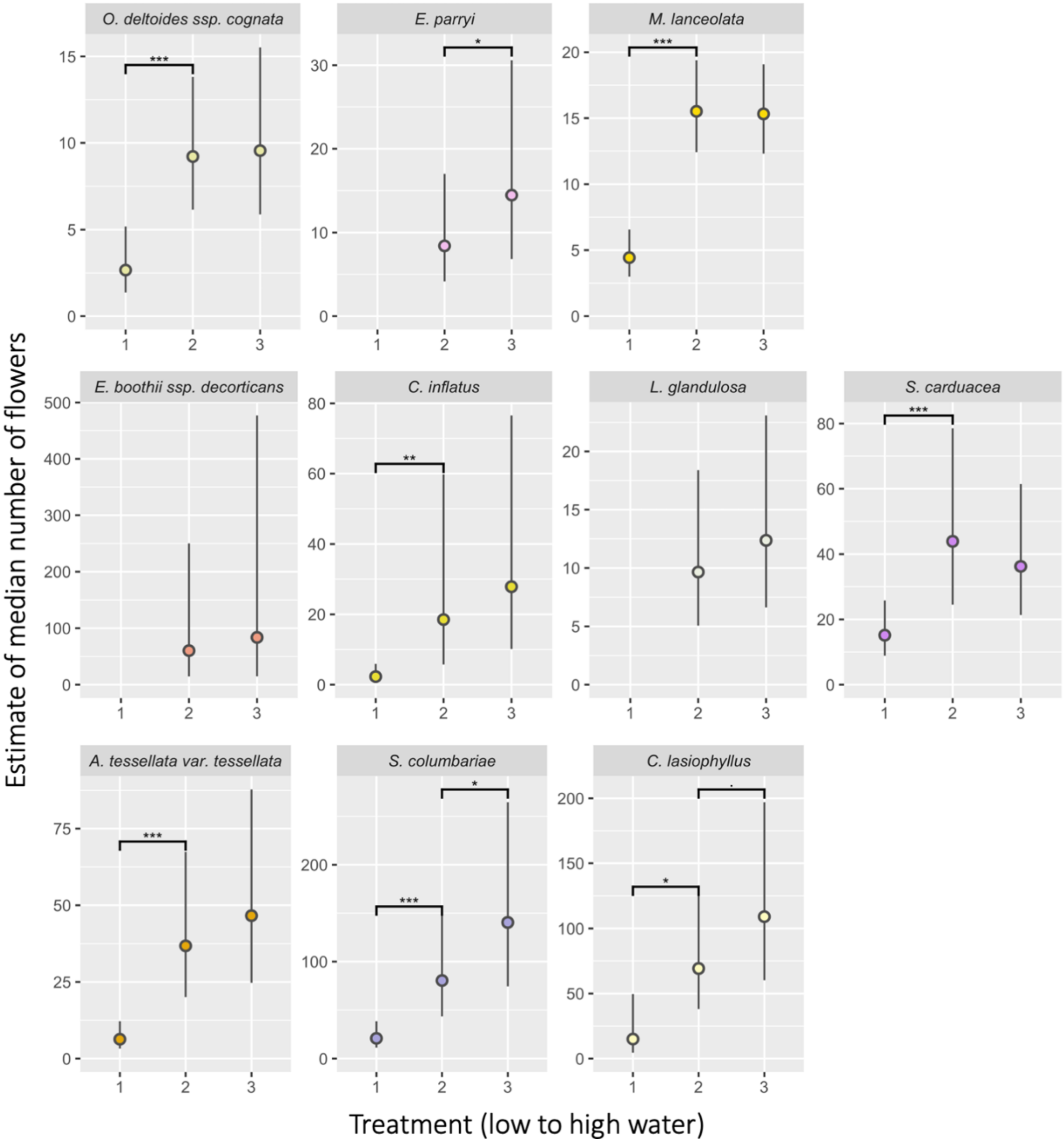

Fig 2.6. Mean flower/flower head number and 95% confidence intervals. Adjusted for variability due to blocks, under three different watering treatments using mixed effect linear models. Treatments 1, 2, and 3(low, medium, high) = 1220, 2065, and 2870 mL water, respectively. Significant pairwise comparisons ($p<0.05$) are shown with asterisks, nearly significant comparisons ($p<.1$) are shown with dots.

Table 2.6. Flower number of each species under three different watering treatments, predicted from species-level mixed linear models using log-transformed number of flowers. Intercepts and estimates are on a logarithmic scale. Intercepts represent the estimated flower number for the medium water treatment, and the estimates for the low and high water treatments represent the estimated relative differences in flower number from the medium treatment.

Parameters	**Estimate**	**95% CI**	**Std. Error**	**df**	**t value**	**p value**
Eremalche parryi						
(Intercept)	**2.129**	(1.63 — 2.61)	0.232	3.78	9.18	
High water	**0.543**	(0.07 — 1.06)	0.242	13.66	2.24	**0.042**
Eremothera boothii* subsp. *decorticans						
(Intercept)	**4.099**	(3.76 — 4.42)	0.141	1.12	28.99	
High water	**0.328**	(0 — 0.45)	0.062	1.05	5.26	0.111
Caulanthus inflatus						
(Intercept)	**2.919**	(1.82 — 3.98)	0.517	12.83	5.64	
Low water	**-2.096**	(-3.22 — -0.75)	0.598	7.85	-3.51	**0.008**
High water	**0.408**	(-0.73 — 1.9)	0.591	7.2	0.69	0.511
Salvia carduacea						
(Intercept)	**3.782**	(3.24 — 4.29)	0.265	12.38	14.26	
Low water	**-1.064**	(-1.55 — -0.62)	0.235	14.61	-4.53	**<0.001**
High water	**-0.192**	(-0.66 — 0.25)	0.229	14.58	-0.84	0.416
Amsinckia tessellata* var. *tessellata						
(Intercept)	**3.605**	(3.07 — 4.14)	0.283	19	12.72	
Low water	**-1.763**	(-2.55 — -0.97)	0.415	19	-4.25	**<0.001**
High water	**0.236**	(-0.55 — 1.03)	0.415	19	0.57	0.575
Salvia columbariae						
(Intercept)	**4.39**	(3.85 — 4.93)	0.273	9.29	16.1	
Low water	**-1.35**	(-1.78 — -0.92)	0.222	11.38	-6.09	**<0.001**
High water	**0.555**	(0.07 — 1.02)	0.243	11.89	2.28	**0.042**
Caulanthus lasiophyllus						
(Intercept)	**4.237**	(3.89 — 4.59)	0.188	3.02	22.53	
Low water	**-1.529**	(-2.31 — -0.75)	0.42	3	-3.64	**0.036**
High water	**0.454**	(0.36 — 0.55)	0.039	1.02	11.5	0.053

Table 2.7. Flower/flower head number of each species under three different watering treatments, predicted from species-level generalized linear mixed effect models (fit with a Poisson distribution). Intercepts and estimates are on a logarithmic scale. Intercepts represent the estimated flower/flower head number for the medium water treatment, and the estimates for the low and high water treatments represent the estimated differences (in flower number) from the medium treatment.

Parameters	**Estimate**	**95% CI**	**Std. Error**	**z value**	**p value**
Oenothera deltoides* subsp. *cognata					
(Intercept)	**2.221**	(1.7 — 2.62)	0.21	10.76	
Low water	**-1.242**	(-1.96 — -0.6)	0.35	-3.6	**<0.001**
High water	**0.036**	(-0.51 — 0.58)	0.27	0.13	0.895
Monolopia lanceolata					
(Intercept)	**2.742**	(2.49 — 2.96)	0.11	24.1	
Low water	**-1.253**	(-1.7 — -0.84)	0.22	-5.7	**<0.001**
High water	**-0.013**	(-0.29 — 0.26)	0.14	-0.09	0.928
Caulanthus inflatus					
(Intercept)	**3.62**	(3.43 — 3.81)	0.09	38.31	
Low water	**-2.773**	(-3.63 — -2.08)	0.39	-7.12	**<0.001**
High water	**-0.079**	(-0.41 — 0.22)	0.15	-0.52	0.606
Layia glandulosa					
(Intercept)	**2.267**	(1.34 — 3.11)	0.33	6.9	
High water	**0.248**	(-0.21 — 0.72)	0.23	1.06	0.29
Amsinckia tessellata* var. *tessellata					
(Intercept)	**5.564**	(4.23 — 8.06)	0.79	7.05	
Low water	**-4.133**	(-6.99 — -2.76)	0.91	-4.54	**<0.001**
High water	**0.19**	(-0.18 — 0.56)	0.19	1.01	0.311

4. DISCUSSION

If these data provided support for the hypothesis that a species' geographic range should predict its drought tolerance, relative to species with range limits in the Mojave, I would expect to find that the species with range limits in the Sonoran Desert show the least variation in biomass by amount of water given (negative interaction) and the San Joaquin endemics show the greatest difference (positive interaction with water). However, in my model of biomass no significant interaction was found between amount of water and a species' geographic range. Relative to the Mojave species, the non-significant interaction of the San Joaquin species with treatment was trending positive, as predicted but, the non-significant effect for the Sonoran species was also trending positive and had a similar estimated magnitude to the San Joaquin interaction term, counter to the hypothesis (Table S.1).

If it is assumed that *Monolopia congdonii* responds similarly to its close relative in this experiment, *M. lanceolata*, large differences in both biomass and flower number would be predicted with decreasing precipitation. While I have not determined the lower climatic threshold for *M. congdonii*, drier conditions are likely to result in smaller plants with fewer flowers, or death prior to flowering and seed set, but not necessarily any more so than other native species in the community.

While I failed to find support for my hypothesis, there are several possible reasons why the predicted effect may not have been detected. These species' range might span several deserts, but each population within those deserts might be locally adapted to the climate of their immediate environment. In this experiment, all seeds were collected from populations within the San Joaquin Desert. If the San Joaquin Desert populations are locally adapted ecotypes, results should match what was observed in this experiment. Population-level variation has been demonstrated in some ecologically important traits of *Salvia columbariae* (Capon et al. 1978), and in other taxa (Cook 1962, Nagy and Rice 1997, Wright et al. 2006). Another possible explanation for the apparent absence of elevated drought tolerance in the Sonoran and Mojave Desert species is that drought tolerance is a phenotypically plastic response to the parental environment, so seeds from parents in the San Joaquin Desert would lack the drought tolerance that they would possess if their parents had experienced different conditions. Such adaptive plasticity has been demonstrated in numerous systems (Galloway 2005, Herman and Sultan 2011).

An alternative explanation (but by no means mutually-exclusive) is that the pattern of drought tolerance is confounded by a bet-hedging strategy in less stress-tolerant species (Venable 2007). In the wild, interannual precipitation variation exposes these species to individual years of dramatically different water-energy balances, greater than the difference in average conditions among the deserts. For species with narrower tolerances, populations may partially or completely escape individual years that fall outside their tolerances by remaining dormant as seeds in the soil seed bank. This may enable persistence in climates where the conditions of an “average” year might be unsuitable if enough surplus seed is produced in wet years to offset any losses due death of ungerminated seed in the seed bank or mortality of emergent plants in poor years. Kimball et al. (2010) demonstrate a counter-intuitive community-wide increase in the abundance of cold-adapted, late-germinating winter annual species in a Sonoran Desert community over a 25-year period of decreasing precipitation and increasing temperature. The delay in the start of the growing season to a colder part of the fall or winter can shift the growing season water-energy balance in a more mesic direction potentially compensating for the effects of a warming, drying climate. Similarly, Thomson et al. (2018) found seedling mortality of an annual *Phacelia* in a Northern California grassland was higher in a moderately dry year than in an extreme drought year due to variation in the timing of the rainfall between the two years. These examples highlight the important role variability of precipitation both within and among years will play in determining the impact of climate change on native annuals like *M. congdonii*.

Atmospheric CO_2 at present is 50% higher than preindustrial levels and will likely increase at least an additional 20% by the end of the century (RCP 4.5) and may as much as triple beyond current levels under a worst-case scenario (RCP 8.5). It's also possible that elevated atmospheric CO_2 may improve the productivity and/or drought tolerance of annuals in arid climates like *M. congdonii* by increasing CO_2 concentrations achievable inside leaves, reducing the amount of water transpired to obtain CO_2 and reducing the rate of photorespiration. The effects of atmospheric CO_2 on plants are an area of ongoing research and they are potentially highly species- and context- specific. These effects may also be nonlinear with CO_2 concentration and change depending on time scale (Medeiros and Ward 2013, Nowak et al. 2022, Smith et al. 2014, Temme et al. 2019, Zavaleta et al. 2003).

The study presented here might also just not have been adequately powered to capture the effect. The initial hypothesis could plausibly be true on average when many species are considered together—but with large variances between species—resulting in a signal that is difficult to detect with a small sample of species such as the one in this study. The longer than intended delay before assignment to treatments likely also limited the opportunity for the species to take advantage of the water in the high treatment. However, the timing of the waterings was similar to the actual timing of rains in the winter and spring of 2020, though this was an unusual precipitation year and fairly stressful for many annuals in the wild. Inadvertently, I tested ability to switch from water stressed to nearly unlimited water which is one element of the predicted pattern of greater growth rates in the San Joaquin species and lower rates in the Sonoran species, but possibly these species would have reacted differently if the plants had not been so drought stressed for so long before being randomized to treatments.

Some of the difficulties with this study, such as low germination rates for some species and failure of seedlings to establish may have resulted from differences between the climate of San Luis Obispo and the climates of the deserts of California. Due to marine influence, average temperatures recorded at the Cal Poly weather station throughout the early weeks of the experiment were several degrees Celsius higher than CIMIS weather stations the San Joaquin Desert (Fig. S.1) near wild populations of *M. congdonii* (Belridge and Cuyama) and stations in the western Mojave Desert (Victorville). Additionally, humidity was 10-20 percentage points lower than sites in the San Joaquin Desert during the same period. The higher temperatures may have inhibited germination of some species, and the combination of higher temperature and lower humidity may have caused greater stress at the early stage of establishment.

Future work should try to replicate these drought tolerance experiments using seeds from various source populations (potential climatic ecotypes), spanning the full range of climatic variability from the climatic trailing edge (warmest, driest), center of climate (average), to climatic leading edge (coolest, wettest). Ideally, growth chamber experiments could be used to explicitly test for the temperature and precipitation limits of *M. congdonii*, but this approach has proved challenging. An alternative could be field experiments in disturbed areas that are candidates for reintroductions of *M. congdonii* and other threatened San Joaquin desert species with experimentally manipulated temperature with heat lamps and/or water using rain exclusion and rain addition (as in Zavaleta et al. 2003 and Harrison et al. 2018, respectively). Future work should aim to examine the impact of the timing and intensity of precipitation events in a warming climate. Given the shift towards a shorter rainy season (Swain et al. 2018) may already be underway and is predicted to strengthen, and the predicted increasing share of annual precipitation arriving in intense atmospheric river events (Polade et al. 2017, Gershunov et al. 2019), the sensitivity of *M. congdonii* to these factors will determine how well its populations can weather the climate of the future.

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APPENDIX

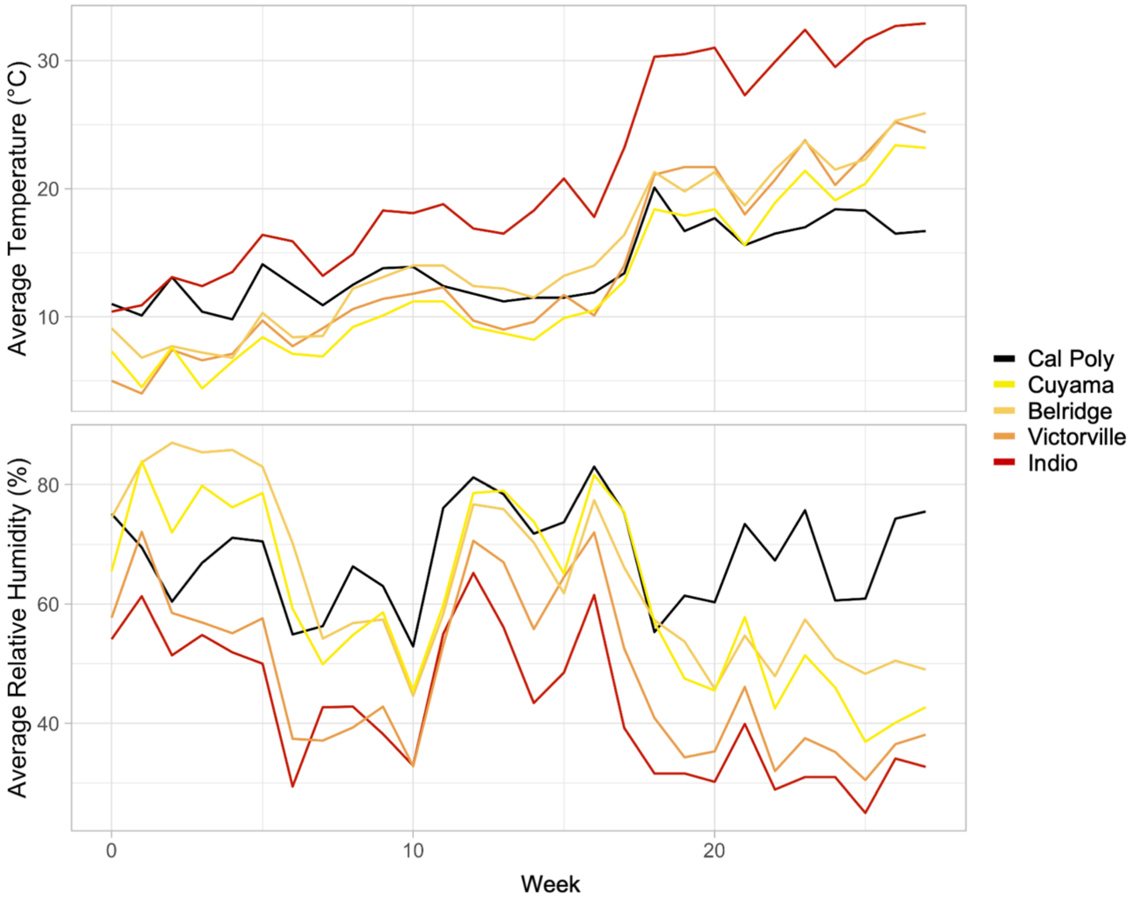
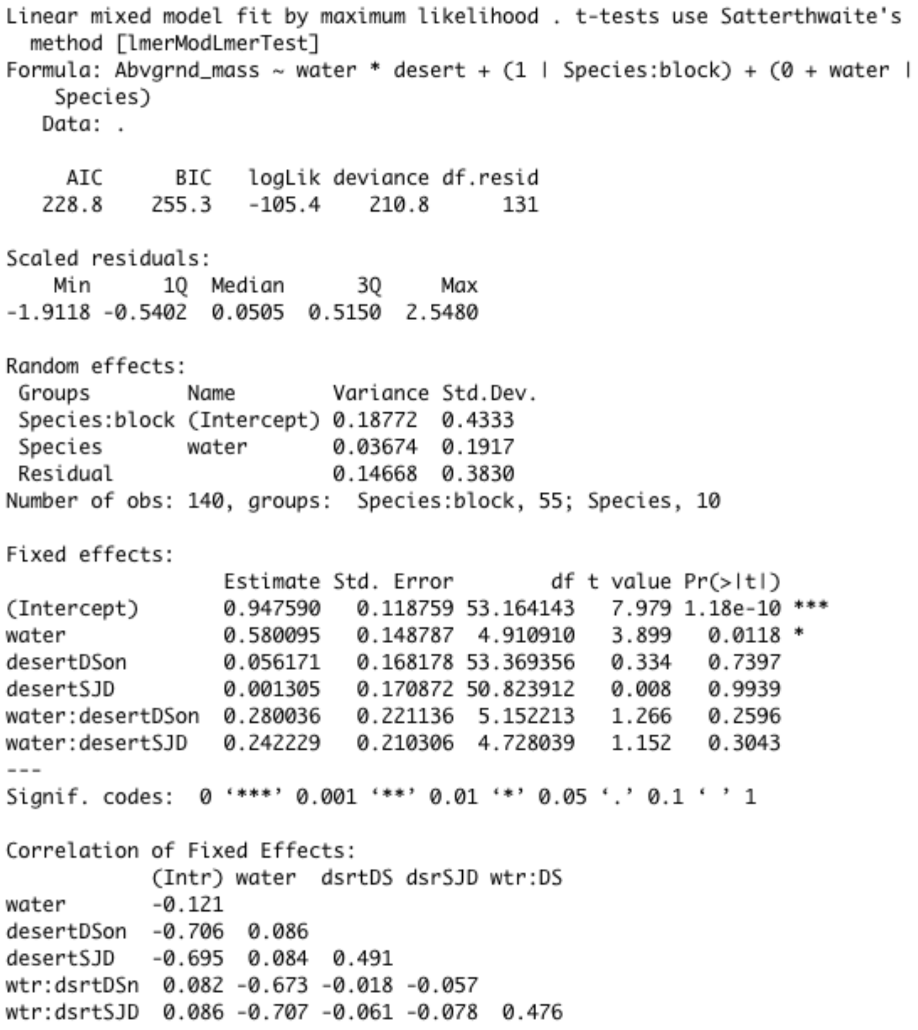


Fig. S.1. Average weekly temperature and relative humidity during the study duration at Cal Poly (CIMIS station #52), and weather stations in the San Joaquin (Cuyama CIMIS #86 and Belridge CIMIS #146), Mojave (Victorville CIMIS #117).

Table S.1. Two-level linear mixed-effect model of aboveground biomass as an effect of treatment group, desert range size, and the interaction of desert range and treatment group. Experimental block was treated as a random effect with random intercepts nested within species which was treated as a random effect with random slopes.



```
Linear mixed model fit by maximum likelihood . t-tests use Satterthwaite's
  method [lmerModLmerTest]
Formula: Abvgrnd_mass ~ water * desert + (1 | Species:block) + (0 + water |
    Species)
   Data: .

     AIC      BIC   logLik deviance df.resid
   228.8    255.3   -105.4    210.8      131

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.9118 -0.5402  0.0505  0.5150  2.5480

Random effects:
 Groups        Name        Variance Std.Dev.
 Species:block (Intercept) 0.18772  0.4333
 Species       water       0.03674  0.1917
 Residual                  0.14668  0.3830
Number of obs: 140, groups:  Species:block, 55; Species, 10

Fixed effects:
                  Estimate Std. Error        df t value Pr(>|t|)
(Intercept)       0.947590   0.118759 53.164143   7.979 1.18e-10 ***
water             0.580095   0.148787  4.910910   3.899   0.0118 *
desertDSon        0.056171   0.168178 53.369356   0.334   0.7397
desertSJD         0.001305   0.170872 50.823912   0.008   0.9939
water:desertDSon  0.280036   0.221136  5.152213   1.266   0.2596
water:desertSJD   0.242229   0.210306  4.728039   1.152   0.3043
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) water  dsrtDS dsrSJD wtr:DS
water       -0.121
desertDSon  -0.706  0.086
desertSJD   -0.695  0.084  0.491
wtr:dsrtDSn  0.082 -0.673 -0.018 -0.057
wtr:dsrtSJD  0.086 -0.707 -0.061 -0.078  0.476
```