

# GERMINATION AND ECOPHYSIOLOGICAL RESPONSES OF SAN BERNARDINO MOUNTAIN PLANT SPECIES

A Thesis By

MARISOL SANCHEZ

California State University, Fullerton  
Fall, 2025

---

**In partial fulfillment of the degree:**

Master of Science in Biology, Plant Biology

**Department:**

Department of Biological Science

**Approval Committee:**

Darren Sandquist, Department of Biological Science, Committee Chair

Joshua Der, Department of Biological Science

Trevis Matheus, Department of Geography & the Environment

**DOI:**

10.5281/zenodo.17162600

**Keywords:**

*Bouteloua gracilis*, seed germination, climate change, montane plants, California native plants

**Abstract:**

Limited gene flow and small population sizes make montane plant species, like many of the species found in the San Bernardino Mountains, vulnerable to rising temperatures and other environmental changes predicted to occur over the coming 30 years. The influence of rising temperatures on montane species was tested by conducting a germination experiment with variable temperature treatments on six representative species. The physiological responses of adult *Bouteloua gracilis* plants from two distinct populations grown under different temperature treatments were also investigated and compared based on net photosynthesis and growth. Germination rates for three of the six species increased with higher temperatures relative to present-day conditions while germination rates for the remaining three species did not change with higher temperatures. Species with wider geographic distributions did not produce statistically significant differences for germination rates under the different conditions. Net photosynthesis values for the San Bernardino Mountain range population of *B. gracilis* decreased with increasing temperature but biomass growth for this population was also highest at the warmest temperatures. These results suggest that higher temperatures alone may not negatively impact native montane plant species, and that they are capable of tolerating warmer temperatures and might even prefer them. However, warming temperatures could still lead to other challenges including increased competition between plants as species that are not cold adapted begin to migrate from lower elevations as well as the potential compounding stressors of higher ambient temperatures, reduced or changed precipitation patterns, and increased frequency of hot daily extreme temperatures.

## TABLE OF CONTENTS

|                                                                                                                 |     |
|-----------------------------------------------------------------------------------------------------------------|-----|
| LIST OF TABLES .....                                                                                            | iii |
| LIST OF FIGURES .....                                                                                           | iv  |
| ACKNOWLEDGMENTS .....                                                                                           | v   |
| 1. OVERVIEW .....                                                                                               | 1   |
| 2. NATIVE PLANT GERMINATION.....                                                                                | 5   |
| Introduction.....                                                                                               | 5   |
| Germination and Dormancy.....                                                                                   | 5   |
| Experimental Goals.....                                                                                         | 7   |
| Hypotheses and Predictions .....                                                                                | 15  |
| Methods.....                                                                                                    | 16  |
| Seed Material .....                                                                                             | 16  |
| Experimental Design.....                                                                                        | 16  |
| Sampling and Measurements .....                                                                                 | 17  |
| Data Analysis .....                                                                                             | 18  |
| Results.....                                                                                                    | 18  |
| Discussion .....                                                                                                | 22  |
| 3. TESTING ECOPHYSIOLOGICAL FUNCTION IN TWO POPULATIONS OF BLUE GRAMA GRASS ( <i>BOUTELOUA GRACILIS</i> ) ..... | 26  |
| Introduction.....                                                                                               | 26  |
| Experimental Goals.....                                                                                         | 29  |
| Hypotheses and Predictions .....                                                                                | 29  |
| Methods.....                                                                                                    | 31  |
| Plant Materials .....                                                                                           | 31  |
| Experimental Design.....                                                                                        | 32  |
| Sampling and Measurements .....                                                                                 | 33  |
| Data Analysis .....                                                                                             | 34  |
| Results.....                                                                                                    | 35  |
| Discussion .....                                                                                                | 38  |
| 4. CONCLUSIONS AND BROADER IMPLICATIONS.....                                                                    | 41  |
| REFERENCES .....                                                                                                | 46  |

## LIST OF TABLES

| <u>Table</u>                                                                                                                                                                                                | <u>Page</u> |
|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------|
| 1. Additional Information on Selected Species.....                                                                                                                                                          | 14          |
| 2. Pretreatments Used on Seeds of the Six Trial Species .....                                                                                                                                               | 17          |
| 3. Number of Replicates and Seeds of the Six Trial Species per Temperature Treatment .....                                                                                                                  | 17          |
| 4. One-way ANOVA Analysis on Germination Rate ( <i>Boechera californica</i> ) .....                                                                                                                         | 20          |
| 5. One-way ANOVA Analysis on Germination Rate ( <i>Calyptidium parryi</i> ).....                                                                                                                            | 20          |
| 6. One-way ANOVA Analysis on Germination Rate ( <i>Eriophyllum lanatum</i> var. <i>obovatum</i> ) .....                                                                                                     | 20          |
| 7. One-way ANOVA Analysis on Germination Rate ( <i>Hulsea vestita</i> ssp. <i>parryi</i> ) .....                                                                                                            | 21          |
| 8. One-way ANOVA Analysis on Germination Rate ( <i>Phacelia mohavensis</i> ) .....                                                                                                                          | 21          |
| 9. One-way ANOVA Analysis on Germination Rate ( <i>Monardella breweri</i> ssp. <i>lanceolata</i> ).....                                                                                                     | 21          |
| 10. Estimated Mean Temperature Optimum and Estimated Mean Max Net Photosynthesis with 95% Confidence Intervals of SBMT <i>Bouteloua gracilis</i> Population under Experimental Temperature Treatments ..... | 35          |
| 11. Estimated Mean Temperature Optimum and Estimated Mean Max Net Photosynthesis with 95% Confidence Intervals of Utah <i>Bouteloua gracilis</i> Population under Experimental Temperature Treatments ..... | 35          |
| 12. One-Way ANOVA Temperature Optimum ( $T_{opt}$ ) SBMT Population <i>Bouteloua gracilis</i> .....                                                                                                         | 36          |
| 13. One-Way ANOVA Peak Photosynthesis ( $A_{max}$ ) SBMT Population <i>Bouteloua gracilis</i> .....                                                                                                         | 36          |
| 14. One-Way ANOVA Temperature Optimum ( $T_{opt}$ ) Utah Population <i>Bouteloua gracilis</i> .....                                                                                                         | 36          |
| 15. One-Way ANOVA Peak Photosynthesis ( $A_{max}$ ) Utah Population <i>Bouteloua gracilis</i> .....                                                                                                         | 36          |
| 16. One-Way ANCOVA Living Mass SBMT Population <i>Bouteloua gracilis</i> .....                                                                                                                              | 37          |
| 17. One-Way ANCOVA Living Mass Utah Population <i>Bouteloua gracilis</i> .....                                                                                                                              | 37          |
| 18. <i>Bouteloua gracilis</i> Adjusted Means for Living Mass .....                                                                                                                                          | 37          |

## LIST OF FIGURES

| <u>Figure</u>                                                                                            | <u>Page</u> |
|----------------------------------------------------------------------------------------------------------|-------------|
| 1. Observation data and photograph of <i>Phacelia mohavensis</i> .....                                   | 8           |
| 2. Observation data and photograph of <i>Monardella breweri</i> ssp. <i>lanceolata</i> .....             | 9           |
| 3. Observation data and photograph of <i>Boechea californica</i> .....                                   | 10          |
| 4. Observation data and photograph of <i>Eriophyllum lanatum</i> var. <i>obovatum</i> .....              | 11          |
| 5. Observation data and photograph of <i>Calyptridium parryi</i> .....                                   | 12          |
| 6. Observation data and photograph of <i>Hulsea vestita</i> ssp. <i>parryi</i> .....                     | 13          |
| 7. Current geographic distribution of <i>Bouteloua gracilis</i> within the continental United States ... | 27          |
| 8. Observation data of <i>Bouteloua gracilis</i> within California.....                                  | 30          |
| 9. Example A-T Curve with Labeled $A_{\max}$ and $T_{\text{opt}}$ Values.....                            | 34          |

## **ACKNOWLEDGMENTS**

I know for a fact that I would not have been able to get this far without the unyielding support from my family, friends, academic colleagues, work colleagues, and many loving pets. Even though most of my family has remained predominantly unaware of what exactly obtaining a master's degree means, my mother, sister, stepfather, and partner have been supportive every step of the way. My dog, Ivy, and cats, Osito and Naranja, reminded me that to fund the lifestyle they are accustomed to, I better finish the degree and get a raise. My friends, Mo and Marjorie, remained consistent sources of reprieve when things became especially overwhelming. My work colleagues frequently reminded me that doing a graduate degree and working full time was crazy and I should go easy on myself. And lastly, I wanted to give a special shout out to my therapist Stacia for keeping me sane throughout this process and not letting me give up despite my continued complaints. Thank you all.

## CHAPTER 1

### OVERVIEW

Sky islands (SIs) are generally identified as isolated mountain peaks surrounded by dispersal barriers such as lowlands or deserts. Despite their solitude, SIs contain immense biodiversity in terms of flora and fauna (Love et al., 2023). SI species found at high elevations are typically isolated from neighboring populations, similarly to those on traditional islands but with unique risks that do not threaten island species (Warshall, 1995). SI plant populations can be isolated from other populations of the species due to specific environmental needs, such as the need for colder climates and snow cover, which might only be found at high mountain peaks. In some cases, certain SI species may have such restricted distributions that they are only found at one site (Lomolino, 2001). Regardless of whether additional populations of a species exist, the major issue seen with SI plants is the lack of gene flow due to geographic isolation, which can limit environmental plasticity and adaptability. The geographic isolation that SI species experience in conjunction with smaller habitats and more extreme climate conditions tends to also lead to smaller population sizes (Atwood et al., 2011; Love et al., 2023). As such, SI species are often more vulnerable to environmental disturbances due to their small population sizes and lack of gene flow (Atwood et al., 2011; Hoffman and Sgro, 2011; Love et al., 2023). These limitations can lead to genetic homogenization and a reduced ability to bounce back after a disturbance or tolerate changing environmental conditions (Valencia et al., 2020; Love et al., 2023). This is of particular concern given the potential impacts of anticipated climate change. However, not all plant species that are found atop mountains can be considered SI species. With over 5,000 native California plant taxa, there are many plant species that have adapted to survive in a wide range of environments (Loarie et al., 2008). Some species can be found alongside SI species but also persist throughout California and inhabit lower elevations with warmer climates. This persistence in a wider range of environments suggests that these species might have more environmental plasticity than SI species. If these more widely distributed species do have higher environmental plasticity, they may also be better

able to tolerate changing climate conditions without facing losses in their distribution ranges (Hoffman and Sgro, 2011).

Climate change is occurring worldwide, but it is characterized differently depending on geographical region. Global climate change models predict an average temperature increase of 1.4° C by the end of the century under conservative greenhouse gas emission scenarios (GHG including carbon dioxide (CO<sub>2</sub>)) and an average temperature increase of 4.4° C under extreme emission scenarios (IPCC, 2021). Similarly, climate change scenarios that have been modeled for California predict a 1.7° C increase by the end of the century under conservative GHG emissions and up to a 5.8° C increase under extreme GHG emissions (Cayan et al., 2008). Conservative emissions refer to emissions below current averages that approach net zero around the year 2050 and even broach into net negative GHG emissions whereas extreme emissions refer to quantities that are double what global emissions currently stand at now (IPCC, 2021).

Most warming in California is predicted to occur during the summertime; however, the overall increase could have extreme impacts on snowfall and snowpack in the mountains with an up to 70% reduction in snow cover at moderate elevations and 100% reduction of snow below 1,000 meters (Cayan et al., 2008, Tague and Dugger, 2010). The reduction in snowpack is concerning because certain plant species require an extended period of cold stratification<sup>1</sup> lasting anywhere from a couple weeks to several months to break dormancy and begin germination (Loayza et al., 2023). The presence of snowpack generally provides these consistent cold conditions, but with higher temperatures and reduced snowfall, the snowpack would likely melt earlier in the season than what is currently considered normal. Additionally, the onset of snowfall would probably begin later in the season which, coupled with the

---

<sup>1</sup> Cold stratification is a method of breaking seed dormancy by simulating cold winter conditions prior to germinating under warmer, spring temperatures. Seeds are typically stored moist at temperatures ranging from -2 to 5° C for two to four months (Emery, 1988).

earlier than normal snowmelt, would collectively reduce the duration of snowpack. This in turn means that seeds from species that need prolonged periods of cold temperatures would not experience them, which could halt germination entirely. For example, the germination rates of three montane species that are accustomed to spending the winter season under snow were generally higher for trials under which their seeds experienced the longest cold stratification period (Bernareggi et al., 2016). Germination rates were overall low for trials that ran with fresh seeds (i.e., seeds that had not experienced any cold stratification) (Bernareggi et al., 2016).

Another study conducted at the Santa Rosa Mountains in southern California has already shown a steady upwards migration of plants into higher elevations, where temperatures are cooler, over the past three decades as they migrate to more suitable habitat amidst rising temperatures (Kelly and Goulden, 2008). Although the plant species that were studied persisted at their original lower range, they were sparser there, and more prevalent towards their upper range limit. The researchers noted that the general makeup of the plant community had shifted in unison with rising temperatures (Kelly and Goulden, 2008). Other researchers attempted to model how different climate change scenarios will impact California's vast endemic plant species. These researchers used models that covered extreme GHG emissions (4 times present-day) and another scenario where GHG emissions rise slightly beyond present-day levels before dropping to below present-day levels by the year 2100 (Loarie et al., 2008). They combined climate models with models that estimated the likelihood of a plant species being found in a region based on variable climatic conditions and known range data from specimen records sourced from the Consortium of California Herbaria. Overall, the results from their modeling supported the theme that plant species would likely migrate towards higher elevations or towards the coast as temperatures continue to rise. They also suggested that, at a certain point, plant species would be unable to find suitable higher-elevation habitat and would essentially migrate "off the mountain" and face local extirpation. A study by Loarie et al. (2008) supports this possibility and suggested that mountainous

areas would contain a disproportionate amount of plant species with shrinking ranges and species losses (Loarie et al., 2008).

As mentioned earlier, the lack of gene flow seen in many of these plant populations, and their limited distributions, are cause for concern (Valencia et al., 2020; Love et al., 2023), because, for most of these species, it is unclear how their geographic ranges and/or population sizes will respond to the continuing rise in temperature seen in the mountain ranges of California.

The main goal of this study was to investigate how SI plant species and more widespread montane plant species from the local San Bernardino Mountains (SBMTs) might be affected by environmental disturbances in the form of rising temperatures due to climate change. The global average surface temperature has increased by 0.6 to 0.7 ° C since the start of the 20<sup>th</sup> century, however it is not well understood how the diverse flora of southern California will adapt to these and future changes (Cayan et al., 2008).

To address this goal, I conducted two experiments. The environmental plasticity of local montane plant species was tested by conducting germination experiments under increasing temperature conditions on six representative species native to the SBMTs. Furthermore, one additional species that currently inhabits the SBMTs, but is more commonly found throughout the Central Plains, was selected for a growth experiment under variable temperature conditions. This two-part study will evaluate the environmental adaptability of native plant species that reside in the San Bernardino Mountain range of California and help determine whether isolated plant species with narrow distributions and/or small population sizes are particularly susceptible to impending climate change when compared with plant species that have wider geographic ranges.

## CHAPTER 2

### NATIVE PLANT GERMINATION

#### Introduction

##### **Germination and Dormancy**

Germination is considered one of the most sensitive parts of a plant's life cycle and can be particularly responsive to climate change due to the particular environmental requirements seeds often need to break dormancy (if present) and germinate (Walck et al., 2011). Generally, soil temperature and water stress are two of the most important abiotic factors that influence germination in plants (Bokhari et al., 1975). The most current climate change predictions suggest that temperatures will continue to rise, with higher occurrences of hot daily extremes (IPCC, 2021). Concerns exist regarding the potential future mismatch between temperature conditions that are needed to promote germination and temperature conditions that will be experienced by seeds (Cochrane et al., 2011; Fernandez-Pascual et al., 2015). For example, if there is unnaturally warm weather in late winter that triggers germination, followed by renewed cold or freezing temperatures, seedlings could germinate but not survive the subsequent freezing conditions (Orsenigo et al., 2015). With the impending threat of climate change, it is unclear how the seeds and seedlings of species that have adapted to their unique environments, such as SI species, might respond regarding germination rates and seedling survival. If temperatures continue to rise and water regimes change, germination could be severely impacted, causing the rapid depletion of the existing seed bank which could lead to diminishing population sizes and reductions in ranges – a concern that is especially threatening for already rare species (Orsenigo et al., 2015).

Seed dormancy is another condition that could be affected by climate change and thus influence long-term germination success. Dormancy in seeds is a phenomenon that occurs to ensure that environmental conditions are favorable prior to germination and seedling establishment. Seed dormancy is most often seen for plants that exist in unstable environments, such as cold mountains where the growing season is typically short. Types of dormancies observed in plants can be broken down into five

general groups including morphological dormancy, physical dormancy, physiological dormancy, morphophysiological dormancy, and combinational dormancy (Baskin and Baskin, 2014; Loayza et al., 2023). There are many factors that contribute to breaking seed dormancy in plants, which depend on the type of dormancy being experienced. Physiological dormancy is one of the more common types and is often only broken when the seeds experience adequate temperature conditions (Fenner and Thompson, 2005).

Like dormancy, the process of germination is temperature dependent, with different species having different temperature optima. However, it is unknown what this range of adequate temperatures (thermal germination niche) is for most species, and it could be a very narrow range in cold-adapted species (Oliveira et al., 2021).

Two common strategies that plants employ when faced with changing climatic conditions are adapting to the new environment or migrating to a new area with a suitable climate (Oliveira et al., 2021). Unfortunately, many montane plant species have already been shown to harbor low genetic diversity, thus limiting adaptability. These species have limited options, due to a lack of higher elevations, of finding regions that support the conditions needed for them to thrive (Valencia et al., 2020; Oliveira et al., 2021; Love et al., 2023). Much speculation and uncertainty exist regarding how plant distributions might fluctuate with anticipated changes in montane climates.

One way that plant distributions could change would be if seeds or seedlings of a species no longer survive in certain regions due to climatic changes. If new individuals of a species cannot establish, it would be a matter of waiting until adult specimens die out, resulting in geographic range reductions. Additional research will help us gain a better understanding of how the germination rates from the seeds of montane plant species, which are already at higher risks of extinction or local extirpation, will respond in the long-term to rising temperatures (Loarie et al., 2008).

## Experimental Goals

The goal of this research was to assess germination responses to increased temperatures from a group of representative species from the local SBMTs to help determine how narrowly distributed and isolated montane species will perform over time as temperatures continue to rise due to climate change. The selected species were the following: *Phacelia mohavensis*, *Monardella breweri* ssp. *lanceolata*, *Boechera californica*, *Eriophyllum lanatum* var. *obovatum*, *Calyptridium parryi*, and *Hulsea vestita* ssp. *parryi* (See Figures 1-6). The six species were chosen based on certain plant characteristics including their locality, elevation preferences (> 1500 m), and life form (see Table 1). The species are an assortment of perennial herbs and annual herbs. The six plant species are all found locally in the SBMTs based on collections and distribution data retrieved from Calflora (Calflora, 2025).

Some of these species, including *H. vestita* ssp. *parryi* and *E. lanatum* var. *obovatum*, are endemic to the SBMTs and a few other mountain ranges, while others have a wider range consisting of additional non-montane environments throughout California. The diversity in the distributions seen from the selected plant species helped guide the formation of hypotheses and could eventually be used to generalize the responses of additional species with similar distribution patterns.

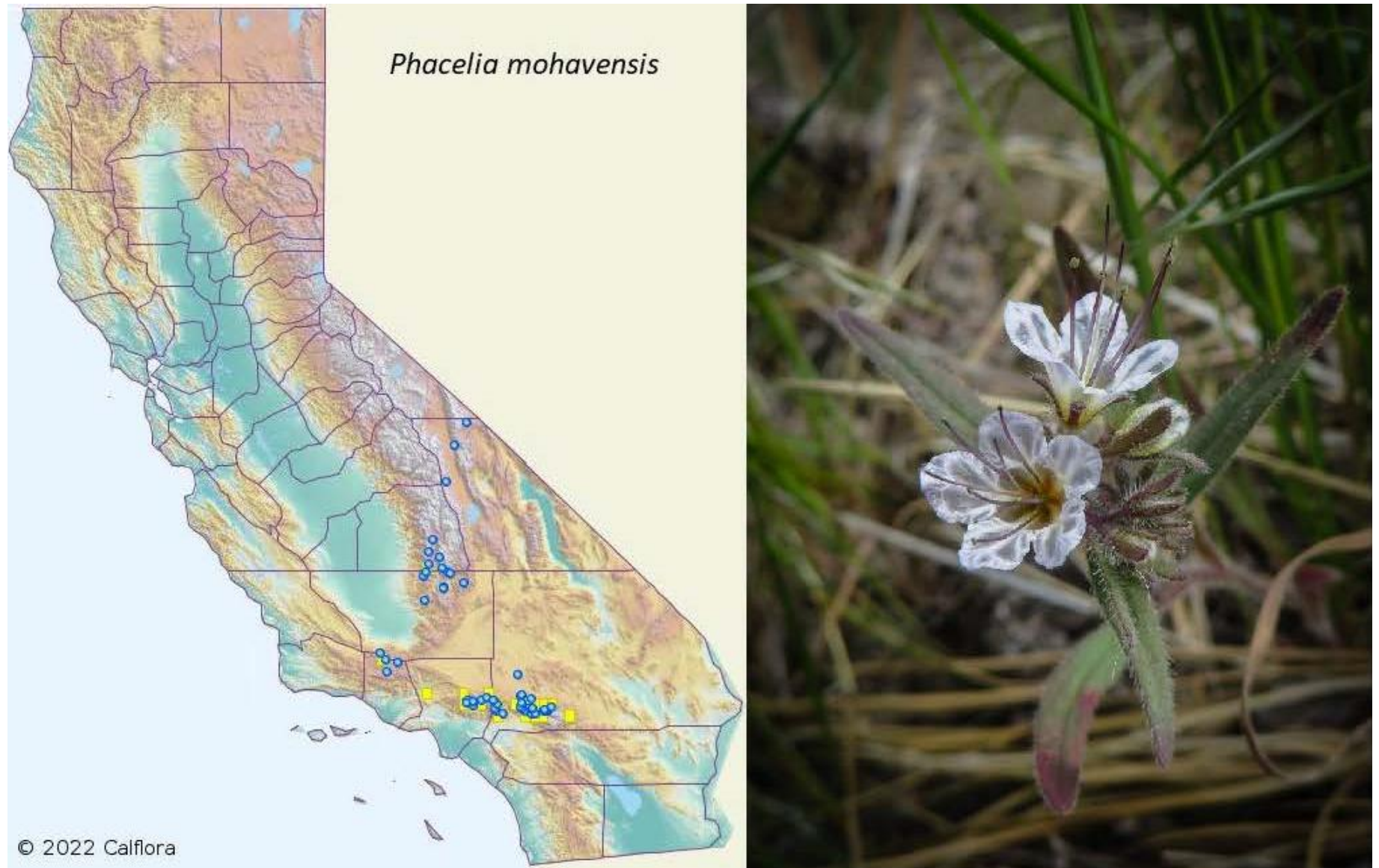


Figure 1. Observation data and photograph of *Phacelia mohavensis* (Calflora, 2022; John L. Thompson, 2017).

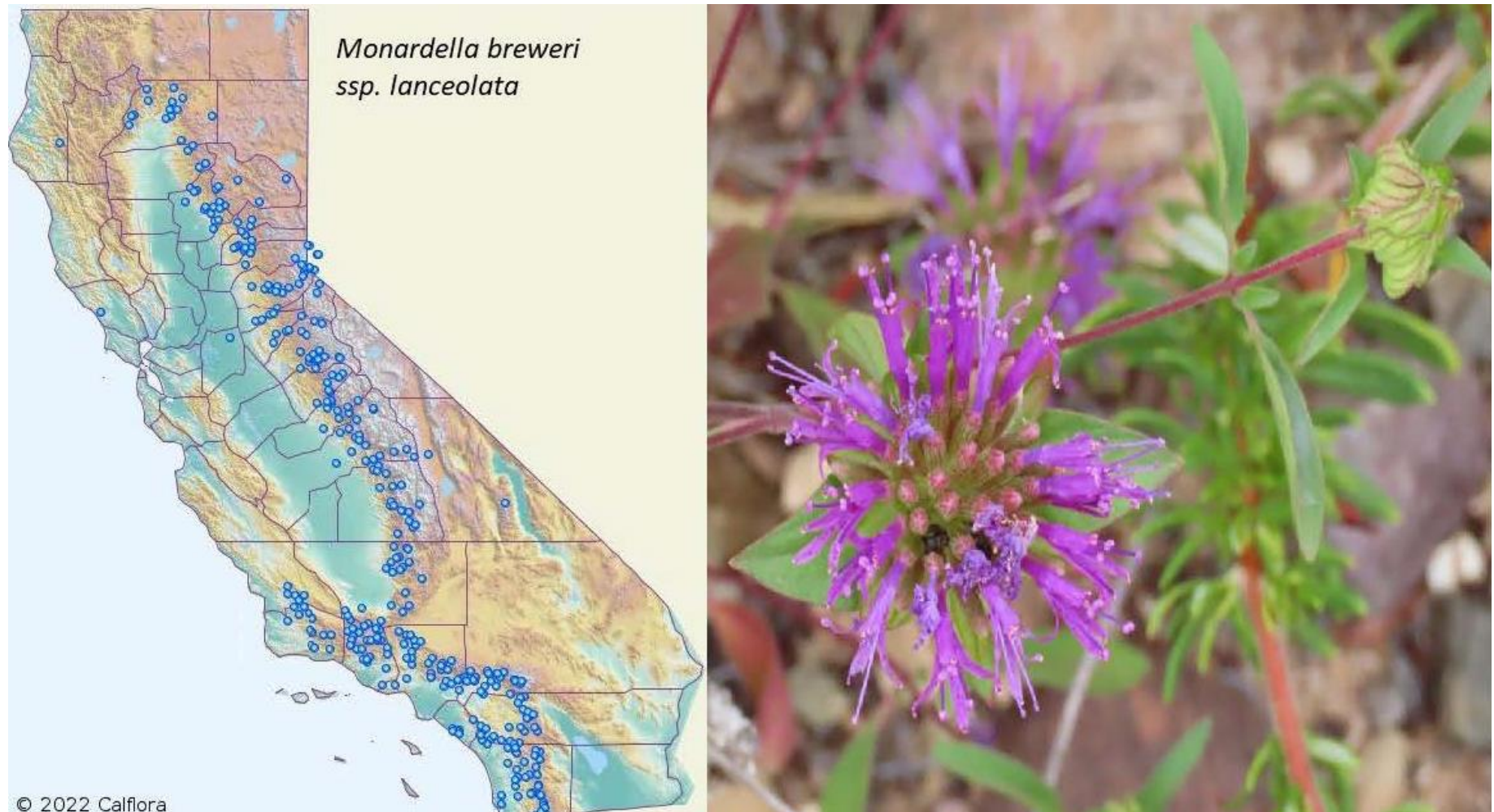


Figure 2. Observation data and photograph of *Monardella breweri* ssp. *lanceolata* (Calflora, 2022; Diane Etchison, 2022).

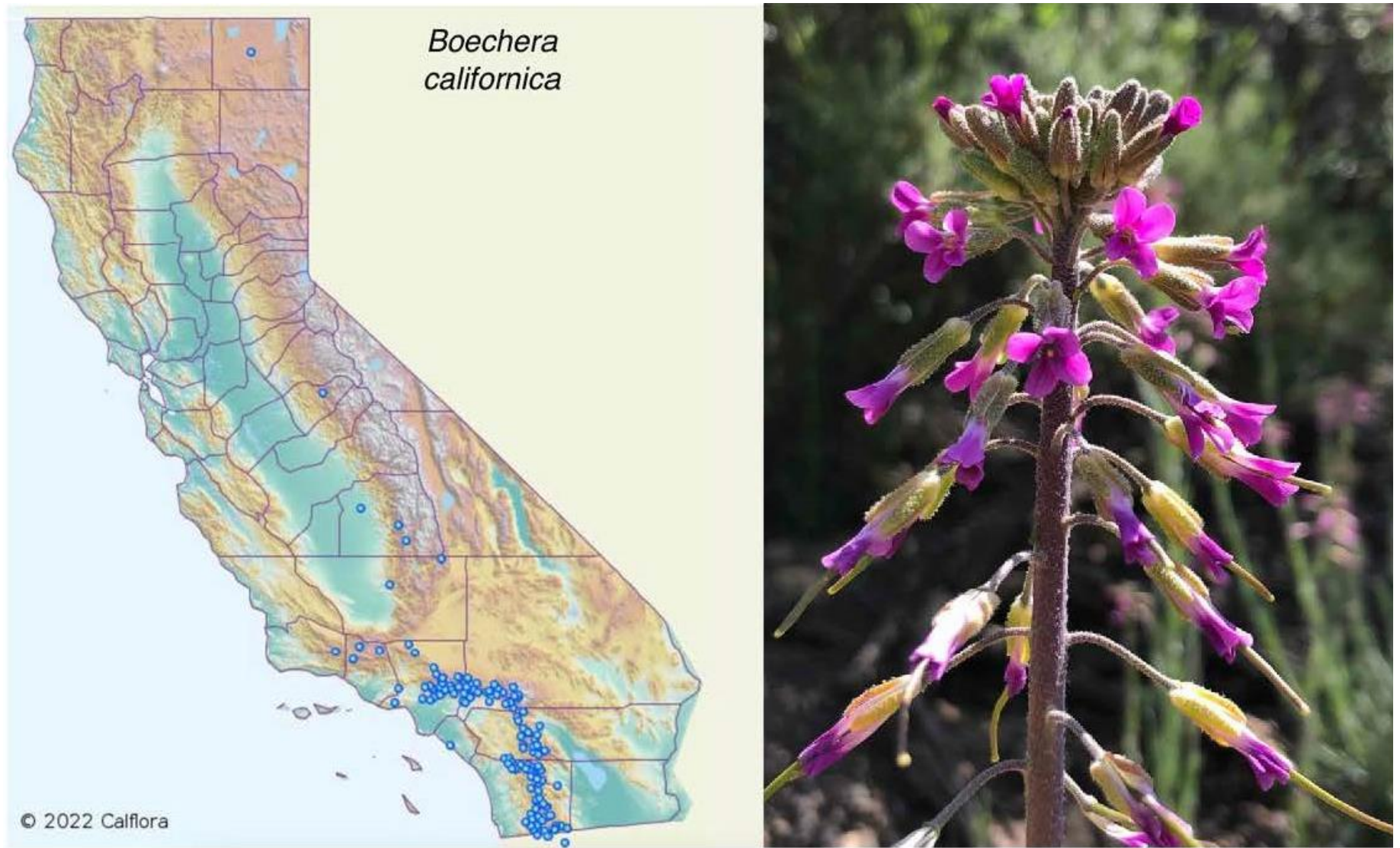


Figure 3. Observation data and photograph of *Boechera californica* (Calflora, 2022; Emily Sluiman, 2022).

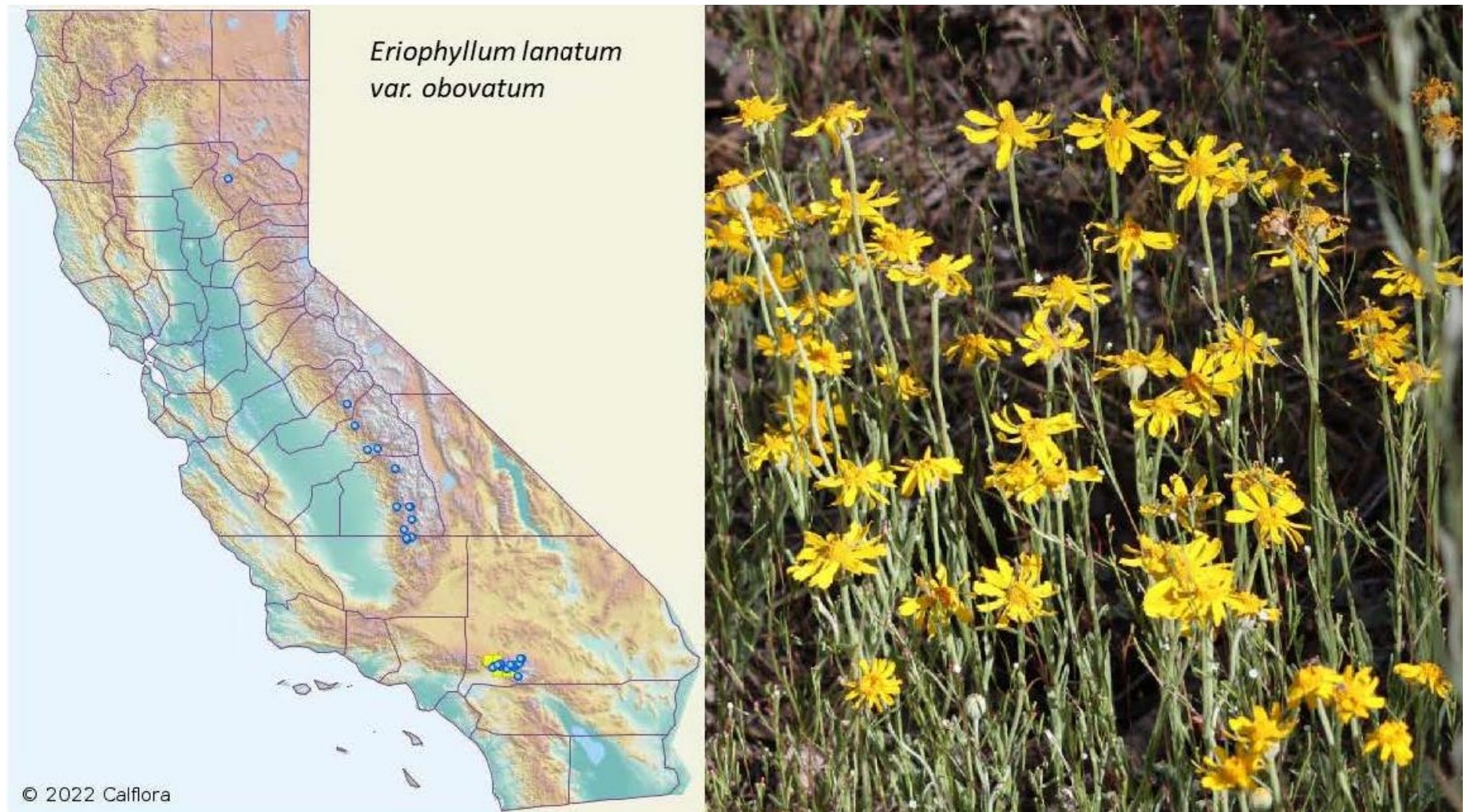


Figure 4. Observation data and photograph of *Eriophyllum lanatum* var. *obovatum* (Calflora, 2022; Diane Etchison, 2023).

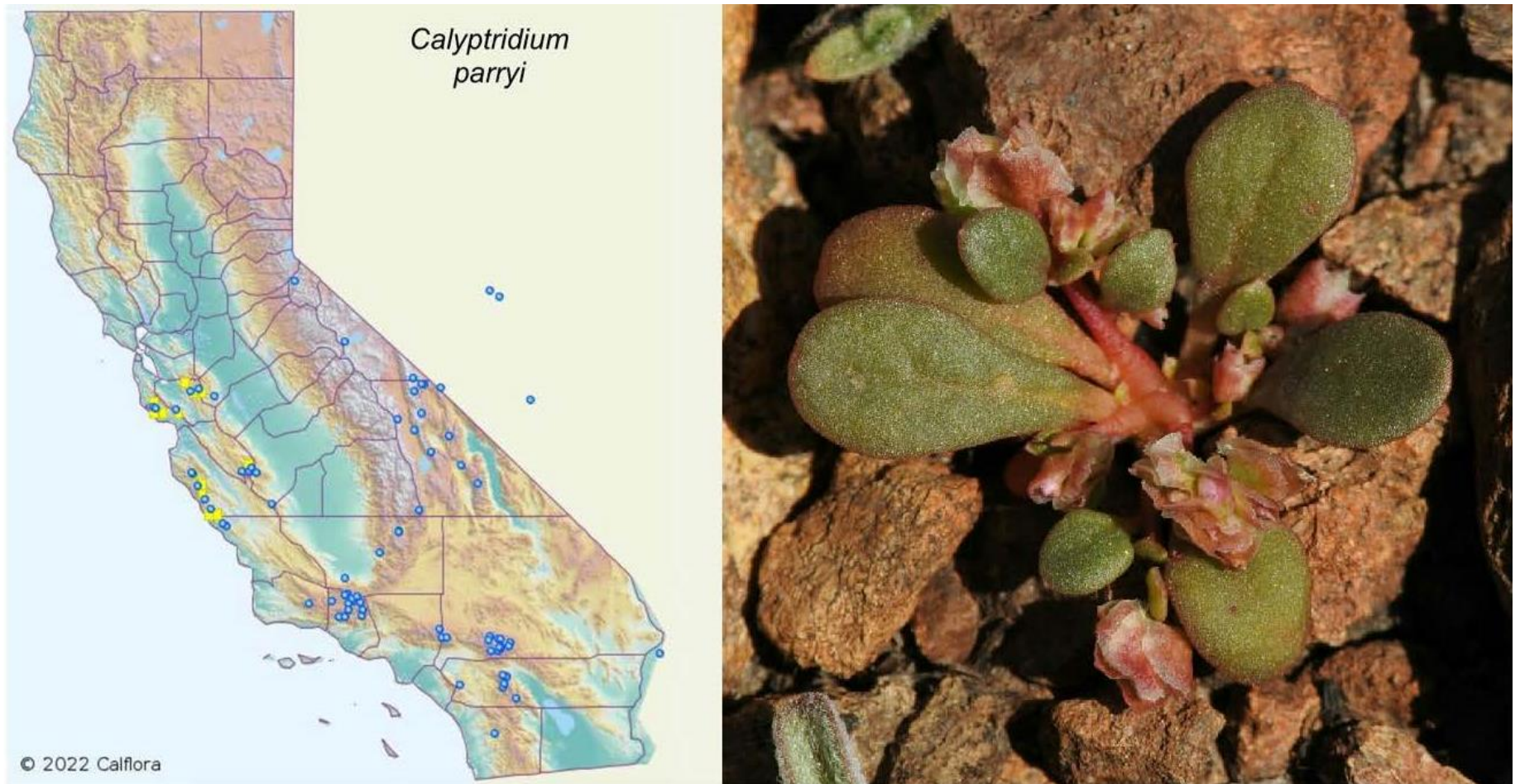


Figure 5. Observation data and photograph of *Calyptridium parryi* (Calflora, 2022; David Greenberger, 2019).

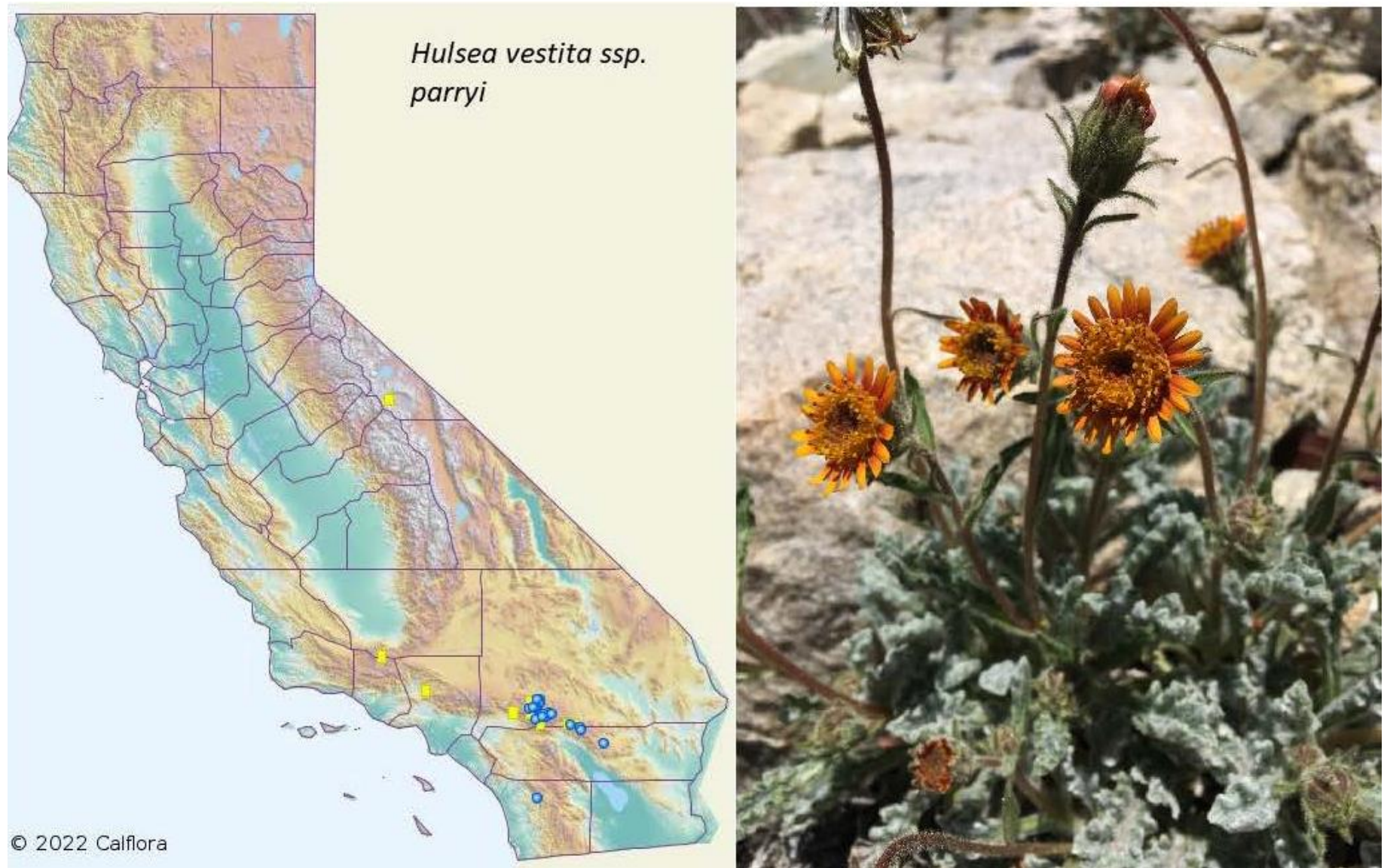


Figure 6. Observation data and photograph of *Hulsea vestita ssp. parryi* (Calflora, 2022; Matt Berger, 2019).

Table 1. Additional Information on Selected Species

| Species                                                                                      | General Elevation<br>Range (m) | Sample<br>Elevation Range | SBMT<br>Elevation<br>Range | Typical Vegetation<br>Community               | Plant Family    | Plant Habit       |
|----------------------------------------------------------------------------------------------|--------------------------------|---------------------------|----------------------------|-----------------------------------------------|-----------------|-------------------|
| <i>Boechera californica</i><br>(California rockcress)                                        | 350-2300                       | 758                       | 0-3504                     | Chaparral, Oak<br>woodland                    | Brassicaceae    | Perennial<br>herb |
| <i>Calyptridium parryi</i><br>(Parry's pussypaws)                                            | 1400-3500                      | 2117                      | 0-3504                     | Chaparral,<br>Conifer forest                  | Montiaceae      | Annual<br>herb    |
| <i>Eriophyllum lanatum</i><br><i>var. obovatum</i><br>(Southern Sierra woolly<br>sunflower)* | 1300-2500                      | 1890                      | 0-3504                     | Conifer forest                                | Asteraceae      | Perennial<br>herb |
| <i>Hulsea vestita ssp.</i><br><i>parryi</i><br>(Parry's hulsea)*                             | 2000-2500                      | 2462                      | 0-3504                     | Sagebrush,<br>Fir forest                      | Asteraceae      | Perennial<br>herb |
| <i>Phacelia mohavensis</i><br>(Mojave phacelia)*                                             | 900-2570                       | 1530                      | 0-3504                     | Conifer forest                                | Hydrophyllaceae | Annual<br>herb    |
| <i>Monardella breweri</i><br><i>ssp. lanceolata</i><br>(Mustang mint)                        | < 3400                         | 1890                      | 0-3504                     | Chaparral,<br>Oak woodland,<br>Conifer forest | Lamiaceae       | Annual<br>herb    |

\*refers to species that are endemic to California and are ranked as a CRPR 4.3

## Hypotheses and Predictions

I hypothesized that germination rates would see a steady decrease as temperatures increase for the species that have the most limited distributions or that have a range that extends into the colder Sierra Nevada Mountains. These species included *Eriophyllum lanatum* var. *obovatum*, *Phacelia mohavensis*, and *Hulsea vestita* ssp. *parryi*. These three species are either only found in the SBMTs, are known from only a small handful of localities, or only persist from the SBMTs northward into the Sierra Nevada. Conversely, I expected that germination rates would moderately improve with increasing temperatures for species that have a broader distribution (i.e., into low elevations and lower latitudes) and less dependence on the cold temperatures typically found at high elevations, particularly those that are also found in the coastal mountain ranges. These species include *Boechera californica*, *Monardella breweri* ssp. *lanceolata*, and *Calyptridium parryi*. These species either have very broad distributions across all of California's mountain ranges or persist in the SBMTs and other warmer coastal mountain ranges.

These predictions assumed that species with broader distributions across a more diverse range of habitats and climates would have more genetic variation or phenotypic plasticity that would allow them to better adapt to changing climatic conditions (Sultan et al., 1998; Pohlman et al., 2005). The species that are particularly isolated, such as *H. vestita* ssp. *parryi*, are expected to have less genetic variation since the populations of this species are small, experience less variability in environmental conditions, and are not connected to a larger metapopulation since other populations do not exist. At the other extreme, *M. breweri* ssp. *lanceolata*, and species like it, are expected to have higher genetic variation due to having a larger number of interconnected populations and over a wider geographic range.

Using various temperature treatments, germination was compared within species to help discern the thermal germination niche for six plant species from the SBMTs. The results from these experiments will help predict how these species might perform over time as the climate continues to warm at higher elevations.

## Methods

### Seed Material

Seeds from the six montane species were sourced from the seed collections of the California Botanic Garden in Claremont, California. The seeds from the selected species were all collected in the SBMTs at elevations that were  $> 750$  m. A total of 400 seeds from each population were used to run the experiments.

### Experimental Design

Germination tests were conducted at four 12-hour day/ 12-hour night temperature cycles: 17.0/1.0, 18.5/2.5, 20.0/4.0, and 21.5/5.5 ° C. The baseline day/night temperatures were selected based on present-day temperature normals (averaged from 2001 to 2010) for the week immediately following the last day of freezing low temperatures (based on 2001-2010 normals; National Center for Environmental Information). Subsequent temperatures increased from this baseline at intervals of 1.5 ° C. These values were based on IPCC estimates for global temperature increases under different carbon emissions scenarios (IPCC, 2021).

Seeds from 3 out of 6 species underwent a pretreatment to break dormancy prior to the start of the germination trials (See Table 2). The pretreatments, or lack thereof, were based on practices and results from germination trials conducted at the California Botanic Garden, where the seeds were sourced.

Each treatment had four or five replicates with a minimum of 15 seeds and a maximum of 20 seeds in each square petri dish (Table 3). Seeds were sterilized and coated using a 20% bleach/1% Tween solution for 60 seconds before being randomly placed in the petri dishes. Petri dishes were sanitized with a 10% bleach solution and dried thoroughly before use. The petri dishes were set up with 1 cm of agar made using BD Difco™ Dehydrated Culture Media: Granulated Agar 500g. Seeds were placed at evenly spaced intervals on top of the agar.

Table 2. Pretreatments Used on Seeds of the Six Trial Species

| Species                                          | Pretreatment                                                               | Baseline Seed Lot Germination Rate – (CBG*) |
|--------------------------------------------------|----------------------------------------------------------------------------|---------------------------------------------|
| <i>Boechera californica</i>                      | None                                                                       | 100%                                        |
| <i>Calyptridium parryi</i>                       | None                                                                       | 45%                                         |
| <i>Eriophyllum lanatum</i> var. <i>obovatum</i>  | None                                                                       | 45%                                         |
| <i>Hulsea vestita</i> ssp. <i>parryi</i>         | Cold moist stratification (2 months)                                       | 76%                                         |
| <i>Phacelia mohavensis</i>                       | 500 ppm soaked overnight Gibberellic acid + high concentration smoke water | 96%                                         |
| <i>Monardella breweri</i> ssp. <i>lanceolata</i> | Cold moist stratification (14 days)                                        | 98%                                         |

\*Germination rate from viability tests conducted at California Botanic Garden for same seed lot and pretreatment

Table 3. Number of Replicates and Seeds of the Six Trial Species per Temperature Treatment

| Species                                          | Number of Replicates | Seeds Per Replicate |
|--------------------------------------------------|----------------------|---------------------|
| <i>Boechera californica</i>                      | 4-5                  | 15-20               |
| <i>Calyptridium parryi</i>                       | 5                    | 20                  |
| <i>Eriophyllum lanatum</i> var. <i>obovatum</i>  | 5                    | 18-20               |
| <i>Hulsea vestita</i> ssp. <i>parryi</i>         | 5                    | 20                  |
| <i>Phacelia mohavensis</i>                       | 5                    | 16-20               |
| <i>Monardella breweri</i> ssp. <i>lanceolata</i> | 5                    | 15-20               |

### Sampling and Measurements

Seed trays for each treatment were randomly arrayed inside a growth chamber (Percival E36HO, Percival Scientific Perry, Iowa) for 6 weeks at the assigned temperature treatment. The “diurnal”

program was used with a 12-hr. daytime, at  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$  light, and 12-hr. nighttime, at  $0 \mu\text{mol m}^{-2} \text{s}^{-1}$  light, cycle. Due to limitation of chamber space, germination treatments across all species were not run concurrently (i.e., trials were run in two batches with three species at a time). Temperature trials for *Boechea californica*, *Calyptidium parryi*, and *Eriophyllum lanatum* var. *obovatum* were grouped together and trials for *Hulsea vestita* var. *parryi*, *Phacelia mohavensis* and *Monardella breweri* ssp. *lanceolata* were grouped together. Seeds were examined every 3 days over the course of the 6 weeks. Germinated seeds were counted, recorded, and removed after each check. Germination of a seed was determined based on the appearance of a radicle. Moldy seeds were removed from the petri dish upon discovery and noted in the records. Moldy seeds were still included in the total number of seeds but were counted as not germinated. Total germination was recorded for each replicate, as well as the corresponding time duration required to reach maximum germination. Despite the attempt to maintain the temperatures listed in the Experimental Design, there appeared to be an issue with Chamber 2. This problem became evident towards the end of the germination experiments based on lower-than-expected germination rates from multiple species for that specific chamber. However, it is unclear if this impacted the overall trend of results.

### **Data Analysis**

Total percent germination was calculated for each replicate. One-way ANOVA analyses were performed for each species individually to determine if the temperature treatments had a significant impact on mean germination rates. Simple regression models were used to evaluate which temperature treatment groups, if any, were statistically different from the baseline temperature ( $17.0/0.1^\circ\text{C}$ ). The critical threshold value for determining significant differences among treatment means was  $< 0.05$ .

### **Results**

There were three possible outcomes of observable patterns from the germination trials. The possible outcomes were no observable difference in germination as temperatures increased, increased germination rates with or without statistical significance as temperatures increased, and decreased

germination rates with or without statistical significance as temperatures increased. In this study, we observed the former two.

The germination trials run with *Boechera californica* did not produce statistically significant results for any of the tested temperatures (Table 3). Average percent germination for the four temperatures ranged between 52% and 68% with no identifiable patterns. The germination trials run with *Calyptridium parryi* depicted statistically significant results for temperature treatments and germination rate with a p-value of  $< 0.0001$  (Table 4). In this case, the observed pattern suggests that germination rates increased as temperature increased considering average percent germination more than doubled between the germination trial run at 17° C (20%) and the germination trials run at 20° C and 21.5° C (44% and 47%). The germination trials for *Eriophyllum lanatum* var. *obovatum* also did not produce statistically significant results for any of the tested temperatures (Table 5). Average percent germination for the four temperatures ranged between 13% and 24% with no identifiable patterns. The germination trials that were run with *Hulsea vestita* ssp. *parryi* also did not depict statistically significant results for germination rate and temperature treatment (Table 6). However, this species seemed to follow a similar pattern as observed with *C. parryi* considering average percent germination nearly doubled between the lowest temperature treatment (~14%) and the highest temperature treatment (26%). Trials run with *Phacelia mohavensis* were most like those observed with *C. parryi*. The germination rates were statistically significant with a p-value of 0.0009 (Table 7). Average percent germination more than doubled once again between the lowest temperature treatment (~25%) and the two higher temperature treatments (~ 59% and ~52%). Lastly, trials run with *Monardella breweri* ssp. *lanceolata* produced results that were statistically significant with a p-value of .0010 (Table 8). However, the results for this species raised concerns regarding the functionality of Chamber 2, the chamber used for the 18.5° C treatment, considering that germination rates were nearly 100% for the temperature treatments run at 17° C, 20° C, and 21.5° C and were only lower for that particular chamber (~71%). Upon closer examination, it appeared that germination trials for some of the other species also depicted slightly lower

germination rates than expected for the temperature treatment set at 18.5° C, which further supported the possibility of a functionality issue with the growth chamber used to run those specific trials. This will be explored in more detail below.

Table 4. One-way ANOVA Analysis on Germination Rate (*Boechera californica*)

| Temperature Treatment | Mean Germination* | Standard Error | <i>p</i> -Value |
|-----------------------|-------------------|----------------|-----------------|
| 17.0° C               | 0.65              | 0.09           | ns              |
| 18.5° C               | 0.53              | 0.01           |                 |
| 20.0° C               | 0.60              | 0.05           |                 |
| 21.5° C               | 0.68              | 0.06           |                 |

Table 5. One-way ANOVA Analysis on Germination Rate (*Calyptridium parryi*)

| Temperature Treatment | Mean Germination* | Standard Error | <i>p</i> -value |
|-----------------------|-------------------|----------------|-----------------|
| 17.0° C               | 0.20 <sup>a</sup> | 0.06           | < 0.0001        |
| 18.5° C               | 0.02 <sup>a</sup> | 0.01           |                 |
| 20.0° C               | 0.44 <sup>b</sup> | 0.06           |                 |
| 21.5° C               | 0.47 <sup>b</sup> | 0.06           |                 |

\*Different lowercase letters indicate significant differences of germination between temperature treatments at  $p < 0.05$ .

Table 6. One-way ANOVA Analysis on Germination Rate (*Eriophyllum lanatum* var. *obovatum*)

| Temperature Treatment | Mean Germination | Standard Error | <i>p</i> -value |
|-----------------------|------------------|----------------|-----------------|
| 17.0° C               | 0.17             | 0.04           | ns              |
| 18.5° C               | 0.13             | 0.03           |                 |
| 20.0° C               | 0.24             | 0.06           |                 |
| 21.5° C               | 0.22             | 0.04           |                 |

Table 7. One-way ANOVA Analysis on Germination Rate (*Hulsea vestita* ssp. *parryi*)

| Temperature Treatment | Mean Germination | Standard Error | <i>p</i> -value |
|-----------------------|------------------|----------------|-----------------|
| 17.0° C               | 0.11             | 0.04           | ns              |
| 18.5° C               | 0.21             | 0.05           |                 |
| 20.0° C               | 0.28             | 0.06           |                 |
| 21.5° C               | 0.26             | 0.02           |                 |

Table 8. One-way ANOVA Analysis on Germination Rate (*Phacelia mohavensis*)

| Temperature Treatment | Mean Germination*  | Standard Error | <i>p</i> -value |
|-----------------------|--------------------|----------------|-----------------|
| 17.0° C               | 0.25 <sup>a</sup>  | 0.04           | 0.0009          |
| 18.5° C               | 0.34 <sup>ab</sup> | 0.04           |                 |
| 20° C                 | 0.59 <sup>c</sup>  | 0.05           |                 |
| 21.5° C               | 0.52 <sup>bc</sup> | 0.07           |                 |

\*Different lowercase letters indicate significant differences of germination between temperature treatments at  $p < 0.05$ .

Table 9. One-way ANOVA Analysis on Germination Rate (*Monardella breweri* var. *lanceolata*)

| Temperature Treatment | Mean Germination* | Standard Error | <i>p</i> -value |
|-----------------------|-------------------|----------------|-----------------|
| 17° C                 | 0.93 <sup>a</sup> | 0.03           | 0.0010          |
| 18.5° C               | 0.71 <sup>b</sup> | 0.08           |                 |
| 20° C                 | 0.99 <sup>a</sup> | 0.01           |                 |
| 21.5° C               | 1.00 <sup>a</sup> | 0              |                 |

\*Different lowercase letters indicate significant differences of germination between temperature treatments at  $p < 0.05$ .

## Discussion

Based on the results, we see two common patterns emerging. Germination rates for the six representative species were either seemingly unaffected by increasing temperature, or germination rates improved with increasing temperature.

The species that did not have different germination rates across the temperature treatments were *Boechera californica*, *Eriophyllum lanatum* var. *obovatum*, and *Hulsea vestita* ssp. *parryi*. These results make sense for *B. californica* based on the hypothesized relationship between geographic range and distribution with potential environmental plasticity as a species. This species has an interconnected distribution going southward down the California coastal mountain ranges. Based on this distribution, the species is not as isolated as some of the other study species and appears specifically adapted to tolerate warmer temperatures already considering temperatures become warmer as you travel south towards the equator. These results were more surprising for *E. lanatum* var. *obovatum*. This species occurs in the SBMTs and can also be found towards the southern end of the Sierra Nevada. Populations of this species appear isolated from one another and presumably would be more accustomed to colder temperatures based on the localities where the species is found presently. However, it is important to note that the germination rates we saw in these trials were significantly lower than those achieved by the California Botanic Garden during their viability tests. This species did not undergo any pretreatment but was sterilized in the same manner as all other species. Unfortunately, this species was the most afflicted by mold early on in the trials and occurred evenly across the temperature treatments. Moldy seeds were immediately removed upon discovery to avoid contamination of the entire seed plate and were counted as ungerminated seeds. It is possible that the standard sterilization methods used were inadequate for this species since it was one of the larger-seeded species and had more pubescence than any of the others. No response to temperature was also observed for *H. vestita* ssp. *parryi* which was surprising based on its extremely limited geographic range. The species is only found within the SBMTs and has a few

historical records in the Little San Bernardino Mountains within Joshua Tree National Park. Therefore, I assumed that the species would experience a decrease in germination rates as temperature increased.

While *M. breweri* ssp. *lanceolata* had statistically significant results for temperature treatment and germination rate, it likely would still fall under the category of no response. Germination rates for this species were at nearly 100% for the temperature treatments run at 17° C, 20° C, and 21.5° C. However, the average percent germination for temperature treatment 18.5° C dropped to approximately 71%. A similar trend was observed in *E. lanatum* var. *obovatum*, *C. parryi*, and *B. californica* where germination rates were notably lower for the temperature trial run at 18.5° C which used the same growth chamber than what would be expected based on the pattern of average germination rates. This leads us to suspect there might have been an undetected issue with the growth chamber used for these trials. It is possible that temperatures or lighting were not being held accurately. In all other accounts, *M. breweri* ssp. *lanceolata* is the poster child for generalist plant species. Its geographic range extends from as far south as the California-Mexico border and north to Shasta County. There are minimal gaps in its distribution, and the species appears to occur in equal measures within coastal mountain ranges as well as throughout the Sierra Nevada. This species also began germinating the quickest with radicles seen within a couple of days after trials started. Therefore, despite the results from the statistical analysis, I would argue that *M. breweri* ssp. *lanceolata* belongs to the generalist group of species whose germination rates were unaffected by the rising temperatures.

The two remaining species all had statistically higher germination rates that coincided with higher temperatures. These results were surprising for *P. mohavensis* based on its current geographic range and distribution pattern. This species has isolated populations with a range that does not continue south beyond the SBMTs. *P. mohavensis* occurs predominantly in the SBMTs with other isolated populations occurring in the southern Sierra Nevada and on Mt. Pinos in Ventura County. Based on its isolation and the localities they occur in; we would have assumed that this species would have less environmental plasticity and might not respond well to the rising temperatures. However, the opposite

appears to be true based on the results. Another interesting note regarding *P. mohavensis* is that germination rates potentially plateaued after 20° C. Germination rates were significant for the species but dropped by about 7% between the temperature treatment group at 20° C and 21.5° C. It would be interesting to see how germination rates change if seeds are exposed to even higher temperatures or to have trials occur with smaller temperature intervals to try pinpointing exactly where the drop-off starts to occur.

These results were less surprising for *C. parryi* based on its current range and distribution in California. This species has occurrences as far south as San Diego County and as far north as Alpine County. However, unlike most of the other species, we see populations on the coast and in the Sierra Nevada in fairly equal measure. Based on this distribution across a variety of localities and environments, it makes sense that *C. parryi* would have more environmental plasticity and would perform well, if not better, as conditions warm.

The results from this experiment did not follow the predictions that were made based on commonly assumed differences in environmental plasticity between widespread versus narrowly distributed species. However, studies on this topic have often produced mixed results and focused on one genus rather than a mixed suite of species from the same locality. One study on ten *Acacia* species in Australia found that certain traits, such as relative growth rate, did not differ between widespread versus narrow-range species, but other traits such as photosynthetic capacity were higher in species with widespread geographic distributions (Pohlman et al., 2005). Another study done on two *Polygonum* species found that their growth responses under different water regimes followed similar trends but the magnitude of response in the more widespread species was greater than the narrowly distributed species (Bell and Sultan, 1999). However, in a different experiment, there was no evidence that a widespread *Echinacea* species was able to tolerate a wider suite of environmental conditions compared to a more narrowly distributed species from the same genus and with similar life-history traits (Baskauf and Eickmeier, 1994).

These examples begin to illustrate the complexities and mysteries that surround the relationship between plasticity in plants and their geographic distributions. It appears likely that any relationship that is to be found between these two factors is highly dependent on the species, lifeform of plants studied, habitat types where the plants are found, or even the severity of environmental conditions that the evaluated species are regularly subjected to. Perhaps broad assumptions on the environmental plasticity of a species cannot be easily assumed based on their geographic range, and species of concern will need to be individually evaluated to make any helpful determinations of what their tolerances to future climate change might look like.

## CHAPTER 3

### TESTING ECOPHYSIOLOGICAL FUNCTION IN TWO POPULATIONS OF BLUE GRAMA GRASS (*BOUTELOUA GRACILIS*)

#### Introduction

*Bouteloua gracilis* is a C4 grass species that is an important component of North American shortgrass prairies. It experiences most of its growth during the summertime and has been shown to have higher germination success at warmer temperatures while still being particularly sensitive to prolonged drought (Bokhari et al., 1975, Avendano-Gonzalez and Siqueiros-Delgado, 2021).

*B. gracilis* has a widespread distribution in the Central Plains (Figure 7), but its full range includes much of southern Canada and continues southward through parts of the eastern United States and most of the southwestern United States including Arizona, Utah, and New Mexico. *B. gracilis* also extends as far south as southern Mexico (Avendano-Gonzalez and Siqueiros-Delgado, 2021).

The species has disjunct populations within California, thus making it a good candidate for investigating local adaptation. The species is only found in a few isolated pockets within southern California, including in the San Bernardino Mountain range, the New York Mountains in the Mojave Desert, and on Clark Mountain in the Mojave Desert (Plant Range - *Bouteloua gracilis*, n.d.). The California populations have been isolated for at least 10,000 years, in a region which has a different climate and less potential for gene flow compared to populations found in other states (Avendano-Gonzalez and Siqueiros-Delgado, 2021). The mountain ranges where *B. gracilis* is found generally experience more precipitation and overall milder summer temperatures than the populations that occur in Utah (Gillies and Ramsey, 2025; Brinkerhoff and Egan, 2025). Additionally, populations from California, as well as other isolated mountainous regions, have been found to be some of the most genetically distinct from the species as a whole (Avendano-Gonzalez et al., 2019).

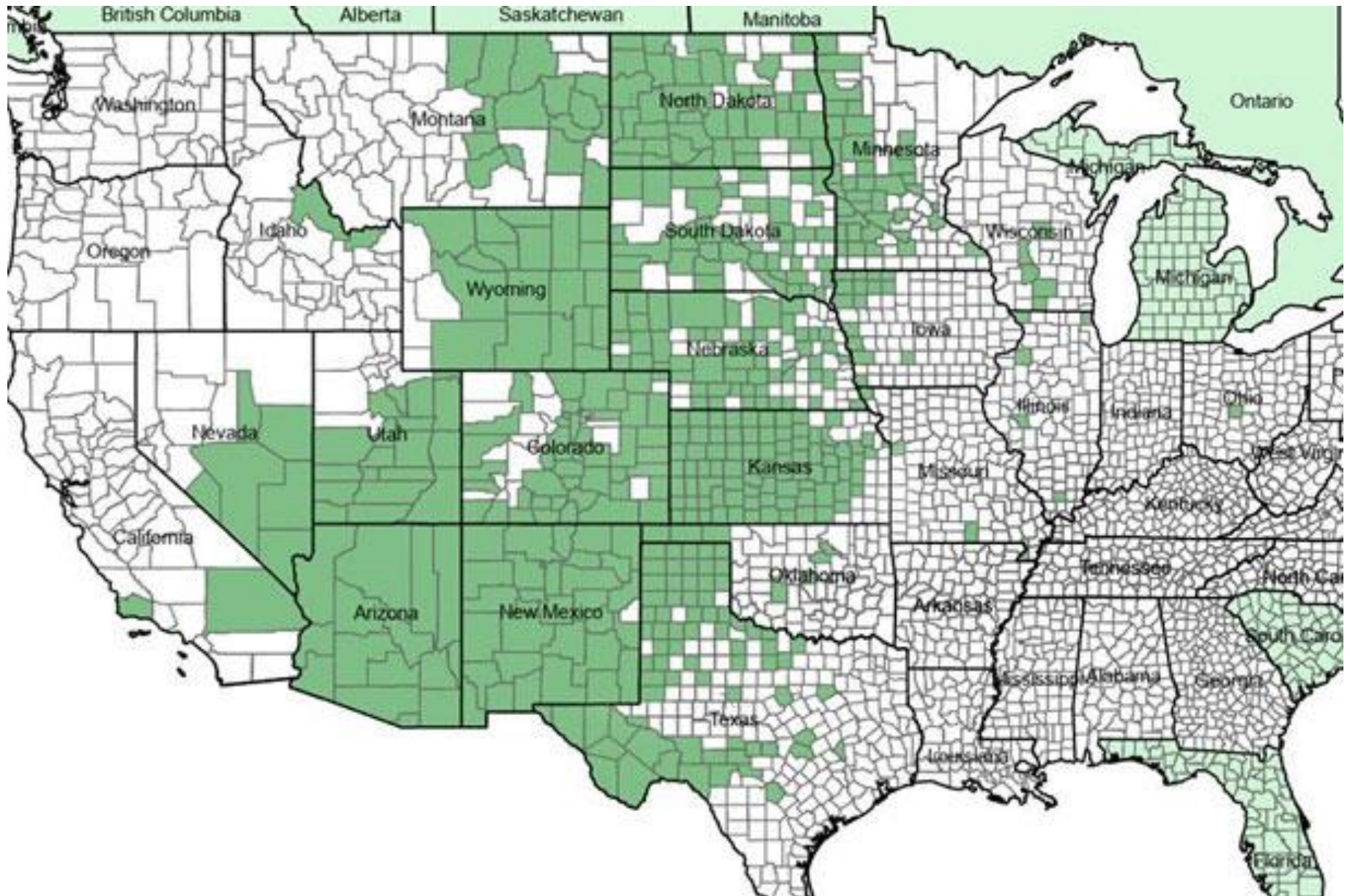


Figure 7. Current geographic distribution of *Bouteloua gracilis* within the continental United States (Gillies and Ramsey, 2025; Brinkerhoff and Egan UVU, 2025).

There are concerns regarding *B. gracilis*'s long-term persistence throughout the Central Plains due to increased drought from higher global temperatures and reduced rainfall. Over a 17-year study period which included two years of uncharacteristically severe drought, researchers saw declines in both absolute cover and frequency of *B. gracilis* (Rondeau et al., 2018). Most populations are performing well with minimal concerns about their longevity whilst some populations are facing more severe threats including competition with invasive species and habitat unsuitability due to climate change (Avendano-Gonzalez et al., 2019). *B. gracilis* is currently considered vulnerable in Nevada and imperiled in Idaho while not having any official status ranking within California (NatureServe Explorer).

Beyond the concerns of climate change impacts on the species, the isolation of the California populations of *B. gracilis* creates additional challenges. As mentioned in Chapter 1, montane plant species often face a lack of gene flow due to geographic isolation, which can limit environmental plasticity and adaptability (Atwood et al., 2011; Love et al., 2023). As such, these California populations may be more vulnerable to environmental disturbances due to the lack of gene flow with the rest of the species (Avendano-Gonzalez et al., 2019; Avendano-Gonzalez and Siqueiros-Delgado, 2021). These circumstances can also lead to genetic homogenization that could reduce the ability of the isolated California populations to bounce back after a disturbance or tolerate changing environmental conditions (Atwood et al., 2011; Hoffman and Sgro, 2011; Valencia et al., 2020; Love et al., 2023).

Due to its commercial importance, the species itself has been studied extensively regarding its genetic structure, general life history traits, and its role in desert community dynamics, to name a few examples (Blake, 1935; Collins and Xia, 2015; Avendano-Gonzalez et al., 2019). However, *B. gracilis* populations from California are not often included in broader studies and have not been well studied, particularly regarding how they might differ functionally compared to other *B. gracilis* populations, or how they will respond to rising temperatures and changing water regimes.

For this study, two populations of *B. gracilis* were used, one from the San Bernardino Mountain ranges and one from Utah. Utah populations generally occur in steppe regions throughout hot, dry

prairies or occasionally in rocky woodlands and desert scrublands. These regions experience hot, dry summers with average highs of 36.5° C, cold winters with average highs of 8.7° C, and annual precipitation ranging between 12-38 centimeters (Gillies and Ramsey, 2025; Brinkerhoff and Egan, 2025; VisitUtah, 2025). This contrasts with California populations that seemingly only occur on mountain ranges, usually between 650 to 2000 meters in elevation, and with average annual rainfall between 22-99 centimeters. The average temperature high that this species experiences during July, which is the warmest month of the year near Big Bear, CA, is 27° C and the average temperature high that is experienced in the coldest month of January is 8.1° C (National Center for Environmental Information, 2023). The species is typically found in open areas within forest or woodland habitats (Calflora, 2025).

### **Experimental Goals**

The goal for this research is to evaluate potential functional divergence of the productivity responses to increasing temperature between a southern California population of *B. gracilis* and a population from the main distribution of the species (sourced from Utah). To do so, I investigated how productivity measures of the two populations responded to warmer growing conditions beyond what is currently experienced in the San Bernardino Mountain range.

### **Hypotheses and Predictions**

*B. gracilis* is widespread in the United States and extends throughout much of Arizona, New Mexico, Utah, Colorado, Wyoming as well as other central states, but has isolated populations in the mountain ranges of southern California (Figure 7). It is found in the San Bernardino Mountain ranges and on two other mountain ranges in the Mojave Desert (Figure 8) (Calflora, 2025).

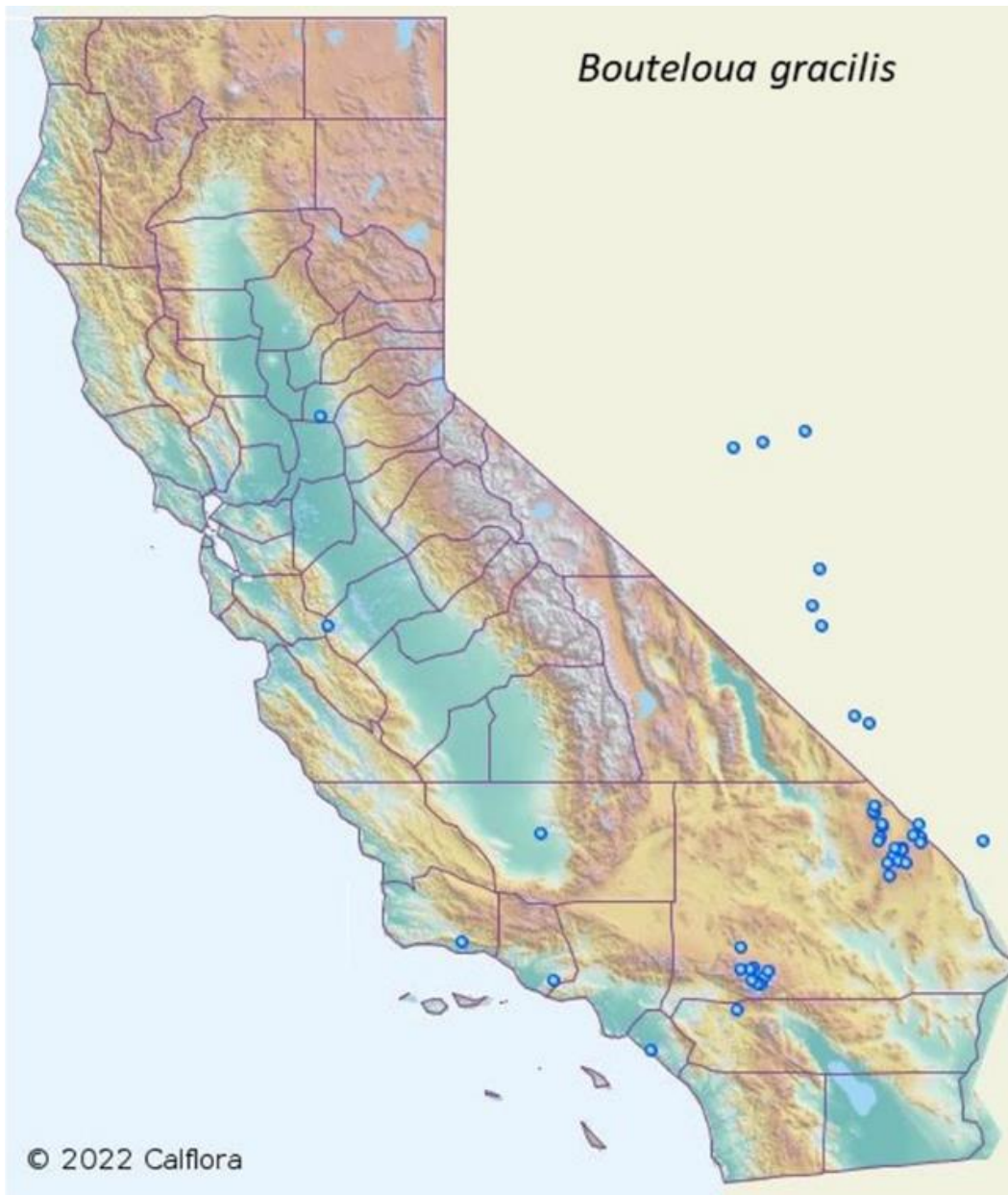


Figure 8. Observation data of *Bouteloua gracilis* within California (Calflora, 2022).

I used parameters derived from photosynthetic temperature-response curves to evaluate the ecophysiological responses and heat tolerances of both populations when grown under variable temperature conditions. In addition, I quantified biomass increase in response to growing temperature. Due to the isolation that this species experiences in California, I hypothesized that plants from the San Bernardino Mountain range populations would have a reduced range of ecophysiological responses compared to those from the Utah population. I also predicted that plants sourced from the San

Bernardino Mountain range region would have lower tolerances for heat stress than plants sourced from the Utah populations due to the climatic differences described above (i.e., the climate of mountain ranges in California are generally milder than that of Utah).

These predictions assumed that plants grown in regions where connectivity between populations is high would have more genetic variability, giving them the means to adapt to rapidly changing climatic conditions. This information will be pertinent for predicting the long-term distribution and persistence of these plant species amidst anticipated rising temperatures in the SBMTs. The results could also provide support towards conservation efforts by helping develop a baseline of how this species functions under variable temperatures

## Methods

I investigated potential divergence between a *B. gracilis* population from the San Bernardino Mountain range of California, and a population from Utah based on temperature responses of biomass growth and two measures of photosynthetic output.

### Plant Materials

*Bouteloua gracilis* plants from Utah were sourced as seeds from a commercial seed vendor (S&S Seeds, Carpinteria, California) and raised in the California State University, Fullerton (CSUF) Greenhouse Complex. Seeds were sown in 200-count plug trays during the Fall 2022/Winter 2023 and kept growing inside the CSUF Greenhouse Complex until they reached an adequate transplant size (i.e., roots visible on the outside of the seed plugs). Experimental plants of SBMT *B. gracilis* were sourced as plugs from Greenlee & Associates (Brisbane, California), which is one of the only vendors in California that sells *B. gracilis* sourced from this target region. The trademarked name for this variety is *Bouteloua* “Angel Eyelash” grass. It can also be found under *Bouteloua gracilis* “Pestañas de Angeles”. Individual plugs were separated into three separate ramets and transplanted into 9.5-inch-tall tree pots (Stuewe & Sons, Inc TP49 – 4 x 9.5 inch “Short One” Mini-Treepot). Plants were raised to a similar size (approx. 15 cm) prior to the start of the experiment. Temperature and humidity stayed at a near constant (~ 22° C

and ~ 70 % humidity) and both Utah and SBMT plants were kept under these near same constant conditions prior to the start of the experiment. A total of 72 plants from each population were used for the experiments.

Prior to the start of the experimental treatments, plants from both populations were trimmed to the base and repotted into 9.5-inch-tall tree pots. To overcome transplant shock, plants were maintained in the greenhouse for 10 days following repotting. The aboveground biomass that was trimmed off the plants during pretreatments was collected and placed in a drying oven (70°C) for at least 72 hours, after which the material was weighed. This mass was used as a covariant for analyses of biomass growth responses to experimental temperatures.

### **Experimental Design**

Growth experiments were conducted under four 12-hour day:12-hour night temperature cycles: 27.0/8.5, 28.5/10.0, 30.0/11.5, and 31.5/13.0 ° C (day/night temperatures). Daytime light levels were 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and nighttime was 0  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . The lowest of the four temperature treatments was based on the 30-year mean July max and min temperature (~ 27° C, 9°C) for Big Bear, CA since it is one of the largest communities in the San Bernardino Mountain range and has the most reliable dataset for climate (National Center for Environmental Information 2023). July temperatures were chosen as the target month because C4 species (such as *B. gracilis*) typically grow most during summertime (Avendano-Gonzalez and Siqueiros-Delgado, 2021). Experimental temperatures increased from this baseline at intervals of 1.5° C, based on IPCC estimates for global temperature increases under the three different scenarios of low, medium, and high carbon emissions. Low emissions refer to conservative emissions below current averages that approach net zero around the year 2050 and even broach into net negative CO<sub>2</sub> emissions, medium emissions refer to emissions staying at the same rate they are present, and high emissions refer to quantities that are double what global emissions currently stand at now (IPCC, 2021).

Experimental *B. gracilis* plants from the SBMT and Utah populations were placed inside one of four Percival E36HO growth chambers (Percival Scientific; Perry, Iowa) for 150 days. Each trial consisted of 36 plants, 18 from the Utah population and 18 from the SBMTs population. Within the chambers, the plant pots were randomly arranged into a 6 x 6 matrix and placed inside plastic tubs with a shallow water level (~2-5 cm) maintained throughout the experiment to ensure that drought did not influence the condition of the plants.

### **Sampling and Measurements**

After adequate growth had occurred on all plants (~120 days), photosynthesis temperature-response curves (A-T curve) were measured on 10 randomly selected plants per treatment, 5 from each population. The A-T curves were performed using a LiCor 6400 portable gas exchange system (LiCor Inc, Lincoln NE). Three to five leaves were placed in the measurement cuvette of the LiCor 6400 gas exchange system during each measurement. Light intensity inside the cuvette during measurements was maintained at  $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ .

The system was programmed to progress through a series of cuvette temperatures during which instantaneous net photosynthesis ( $A_{\text{net}}$ ), chamber temperature ( $T_a$ ) and leaf temperature ( $T_l$ ) were recorded. The temperatures used for the A-T curves were: 27, 28.50, 30, and 31.5° C. The starting point for each curve was based on the temperature treatment in which the plant was grown, then progressed down to lower temperatures before returning to higher temperatures. A-T measurements on all 40 plants were completed within the span of one month after which point the trials ended. From the A-T curves, two parameters were derived, the maximum photosynthesis achieved,  $A_{\text{max}}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and the temperature at which maximum photosynthesis occurred,  $T_{\text{opt}}$  (°C) (Fig. 9). The former is a measure of absolute photosynthetic response to temperatures (i.e., higher or lower rates) whereas the latter is an indicator of thermal acclimation via adjustment of the response curve (i.e., peak photosynthesis occurring at higher or lower temperatures).

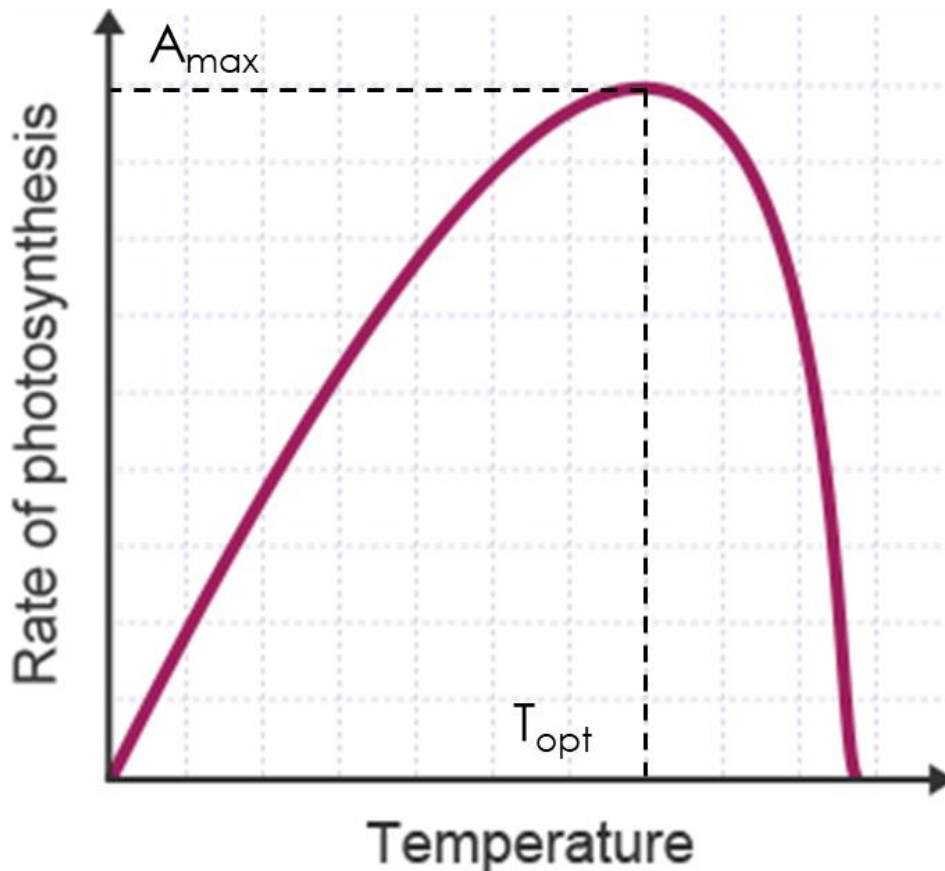


Figure 9. Example A-T Curve with Labeled  $A_{\max}$  and  $T_{\text{opt}}$  Values (BBC, 2025).

Following termination of the trials, aboveground plant material (Post-Treatment Biomass) was harvested, placed in drying ovens at 70°C for at least 72 hours, and weighed to quantify final aboveground biomass.

### Data Analysis

To examine the effect of growing temperature on plant productivity changes within populations, one-way analyses of variance (ANOVA) were conducted for the response variables  $A_{\max}$  and  $T_{\text{opt}}$  across the four temperature treatments. For comparison among treatments within each population, 95% confidence intervals were calculated for each treatment mean.

The effect of temperature on aboveground growth within populations was evaluated based on Post-Treatment Biomass (PTB) while controlling for starting biomass (Pre-PTB) using an analysis of covariance (ANCOVA) with Pre-PTB as the covariant.

## Results

The estimated mean values for  $T_{opt}$  for the SBMT population under the four temperature treatments varied between 29.47° C to 30.25° C (Table 10). The estimated mean values for  $A_{max}$  for the SBMT population varied between 4.82 to 10.43 (Table 10). The estimated mean values for  $T_{opt}$  for the UT population varied between 29.44° C to 30.71° C (Table 11). The estimated mean values for  $A_{max}$  for the UT population varied between 7.38 to 13.46 (Table 11).

Table 10. Estimated Mean Temperature Optimum and Estimated Mean Max Net Photosynthesis with 95% Confidence Intervals of SBMT *Bouteloua gracilis* Population under Experimental Temperature Treatments

| Temperature Treatment | Estimated Mean Temperature Optimum (° C) | 95% Confidence Intervals | Estimated Mean ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) | 95% Confidence Intervals |
|-----------------------|------------------------------------------|--------------------------|----------------------------------------------------------|--------------------------|
| 27.0° C               | 30.18                                    | 29.41 - 30.95            | 10.43                                                    | 7.85 - 13.02             |
| 28.5° C               | 30.25                                    | 29.48 - 31.02            | 8.04                                                     | 5.45 - 10.62             |
| 30.0° C               | 29.47                                    | 28.70 - 30.24            | 9.43                                                     | 6.85 - 12.02             |
| 31.5° C               | 30.06                                    | 29.29 - 30.83            | 4.82                                                     | 2.24 - 7.41              |

Table 11. Estimated Mean Temperature Optimum and Estimated Mean Max Net Photosynthesis with 95% Confidence Intervals of Utah *Bouteloua gracilis* Population under Experimental Temperature Treatments

| Temperature Treatment | Estimated Mean Temperature Optimum (° C) | 95% Confidence Intervals | Estimated Mean ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) | 95% Confidence Intervals |
|-----------------------|------------------------------------------|--------------------------|----------------------------------------------------------|--------------------------|
| 27.0° C               | 30.71                                    | 30.16 - 31.26            | 7.38                                                     | 4.30 - 10.46             |
| 28.5° C               | 30.21                                    | 29.66 - 30.76            | 9.37                                                     | 6.28 - 12.45             |
| 30.0° C               | 29.44                                    | 28.90 - 29.99            | 13.46                                                    | 10.38 - 16.55            |
| 31.5° C               | 29.58                                    | 29.03 - 30.13            | 10.66                                                    | 7.58 - 13.75             |

$T_{opt}$  for the SBMT population was not significantly related to the temperature at which the plants were grown ( $p$ -value = .44; Table 12). However, mean  $A_{max}$  significantly decreased as growth

temperature increased ( $p$ -value = 0.03, Table 10 and 13). For the Utah population,  $T_{opt}$  significantly decreased as the temperature under which plants were grown increased ( $p$ -value = .01, Tables 11 and 14). In contrast,  $A_{max}$  increased moderately with increasing growth temperature (Table 11), albeit statistically significant as a slightly higher critical value ( $p$ -value = .06, Table 15).

Table 12. One-Way ANOVA Temperature Optimum ( $T_{opt}$ ) SBMT Population *Bouteloua gracilis*

|           | Df | Sum Sq | Mean Sq | F value | Pr(>F) |
|-----------|----|--------|---------|---------|--------|
| Treatment | 3  | 1.89   | 0.63    | 0.96    | 0.44   |
| Residuals | 16 | 10.53  | 0.66    |         |        |

Table 13. One-Way ANOVA Peak Photosynthesis ( $A_{max}$ ) SBMT Population *Bouteloua gracilis*

|           | Df | Sum Sq | Mean Sq | F value | Pr(>F) |
|-----------|----|--------|---------|---------|--------|
| Treatment | 3  | 89.61  | 29.87   | 4.02    | 0.03   |
| Residuals | 16 | 118.96 | 7.43    |         |        |

Table 14. One-Way ANOVA Temperature Optimum ( $T_{opt}$ ) Utah Population *Bouteloua gracilis*

|           | Df | Sum Sq | Mean Sq | F value | Pr(>F) |
|-----------|----|--------|---------|---------|--------|
| Treatment | 3  | 5.18   | 1.73    | 5.14    | 0.01   |
| Residuals | 16 | 5.37   | 0.34    |         |        |

Table 15. One-Way ANOVA Peak Photosynthesis ( $A_{max}$ ) Utah Population *Bouteloua gracilis*

|           | Df | Sum Sq | Mean Sq | F value | Pr(>F) |
|-----------|----|--------|---------|---------|--------|
| Treatment | 3  | 97.53  | 32.51   | 3.07    | 0.06   |
| Residuals | 16 | 169.16 | 10.57   |         |        |

Mean post-treatment biomass (PTB), adjusted for starting biomass (Pre-PTB), for both the SBMT and UT populations of *B. gracilis*, showed a significant response to changes in growth temperature (Tables 16 and 17). The adjusted means for the SBMT population varied from 945.18 to 2110.08 grams with values mostly increasing as growth temperature rose (Table 18). The adjusted means for the Utah population varied from 640.55 to 1334.91 grams with an overall increase as growing temperature increases, but more variation within the intermediate temperature treatments (Table 18).

Table 16. One-Way ANCOVA Living Mass SBMT Population *Bouteloua gracilis*

|             | Df | Sum Sq      | Mean Sq    | F value | Pr(>F) |
|-------------|----|-------------|------------|---------|--------|
| Living Mass | 1  | 4736709.90  | 4736709.90 | 13.67   | <.0010 |
| Treatment   | 3  | 12793717.68 | 4264572.56 | 12.31   | <.0010 |
| Residuals   | 67 | 23215410.05 | 346498.66  |         |        |

Table 17. One-Way ANCOVA Living Mass Utah Population *Bouteloua gracilis*

|             | Df | Sum Sq      | Mean Sq    | F value | Pr(>F) |
|-------------|----|-------------|------------|---------|--------|
| Living Mass | 1  | 213485.82   | 213485.82  | 1.08    | 0.30   |
| Treatment   | 3  | 6008000.00  | 2002666.66 | 10.15   | <.0010 |
| Residuals   | 67 | 13212858.67 | 197206.84  |         |        |

Table 18. *Bouteloua gracilis* Adjusted Means for Living Mass

| Temperature Treatment | SBMT Adjusted Mean (g) | Utah Adjusted Mean (g) |
|-----------------------|------------------------|------------------------|
| 27° C                 | 945.18                 | 640.55                 |
| 28.5° C               | 1480.88                | 1201.56                |
| 30° C                 | 1299.02                | 758.15                 |
| 31.5° C               | 2110.08                | 1334.91                |

## Discussion

The goal of this research was to evaluate potential functional differences in productivity measures between two populations of *B. gracilis*, one of which is isolated in the San Bernardino Mountain range of California while the other occurs within the species' greater distribution throughout the Central Plains. To address this goal, I investigated how productivity measures within both populations responded to warmer growing conditions beyond what is currently experienced in the San Bernardino Mountain range.

Current climate change models predict that temperatures may rise between 1.5 to 4.5° C over the next several decades (IPCC, 2021). This prediction fueled the experimental design of this research and with the general expectation that higher temperatures would have a detrimental impact on these montane (SBMT) and high-latitude (Utah) populations. In contrast, results for both populations indicated that growing temperatures had a significant increase in biomass growth (Tables 17 and 18).

The experimental group that had the highest values for post-treatment biomass was the SBMT population grown under 31.5° C. However, it also had the lowest values for peak photosynthesis ( $A_{\max}$ ). Therefore, although there is an increase in biomass, leaf-level processes, such as photosynthesis, potentially decreased in the plant overall. Additionally, the SBMT population had the highest biomass increase compared to the Utah population, although it remains unclear why the higher biomass values were paired with lower photosynthetic capacity in this case. One possible explanation for this observation is that warmer temperatures accelerated growth so that plants reached peak biomass earlier and transitioned to reproduction and the early stages of seasonal dormancy with a concurrent reduction of  $A_{\max}$ . Although reproductive growth was not quantified in this study, the warmer treatments of the SBMT population had visually higher frequencies of inflorescence production than the lower temperature treatments, and also higher than the Utah population overall. Furthermore, the changes in  $A_{\max}$  were not matched by physiological acclimation of  $T_{\text{opt}}$ , suggesting that the underlying biochemistry was functioning in a manner consistent with seasonal decline rather than some form of acclimation.

These findings partially parallel a study of the grass species *Avena sativa*, which found that in reproductive plants, carbon dioxide assimilation decreased at higher temperatures while PSII efficiency stayed consistent, an outcome that was previously documented in other studies (Yamasaki et al., 2002; Lopez-Palacios et al., 2022). Based on these results, it is plausible that the additional growth of *B. gracilis* plants from the SBMT population was a phenological response to growth temperatures more so than an underlying physiological adjustment. This outcome may be expected for the SBMT plants which are likely limited in their range of responses, compared to the Utah plants, due to their isolation and the reduced gene flow that the SBMT population has experienced historically.

Even though the SBMT population had greater biomass values and higher production of inflorescences, there appears to be more variation in the responses to higher growth temperatures from the Utah population compared to the SBMT population. Although we do not have information about the genetic composition of our commercially acquired seeds and seedlings, these patterns follow those expected based on the differences in population sizes and connectivity for the Utah vs SBMT locations (Avendano-Gonzalez and Siqueiros-Delgado, 2021). Generally, larger plant populations that experience regular gene flow have higher genetic diversity and exhibit broader responses to stressful environmental conditions (Bell and Sultan, 1999; Pohlman et al., 2005). However, most of these past studies looked at different species within the same genus rather than different populations from a single species. Of those that did use intraspecific comparisons, one study examined genetic diversity within and between populations of *Trollius europaeus*, a perennial herb that grows in cold meadows at variable elevations throughout Europe. The researchers found lower levels of genetic diversity in the smaller populations that occurred towards the edge of the species' geographic range compared to the larger populations that occurred more centrally within the species' range (Despres et al., 2008). This study is only one example of research that focuses on evaluating genetic variation between small, isolated populations and larger interconnected populations of a single species. However, the researchers did not examine how these differences in genetic variation might influence productivity responses, especially in the lens of

impending climate change. In our case, the isolated population exhibited higher aboveground biomass growth but reduced levels of maximum photosynthesis as temperatures increased, whereas the population with greater connectivity appeared to adjust and better tolerate the higher temperatures - exhibiting more stable values for growth, maximum photosynthesis and optimal temperatures for photosynthesis.

As climate change continues to threaten native plant communities through reductions in geographic distributions due to a lack of suitable habitat, it will become crucial to identify how our already small montane plant populations will respond and whether they have the means to adapt to a changing environment.

## CHAPTER 4

### CONCLUSIONS AND BROADER IMPLICATIONS

California is a biodiversity hotspot with over 2,000 endemic plant species (California State Parks Foundation). Endemic species, especially those from montane environments, are often limited in their distributions and can be particularly vulnerable to environmental disturbances due to their isolation, small population sizes, reduced gene flow with other populations, and specific environmental needs (Hoffman and Sgro, 2011; Valencia et al., 2020; Love et al., 2023). There are many environmental threats that native plant communities are facing due to human involvement and population expansion such as loss of habitat due to urbanization, competition from invasive species, and climate change. Higher ambient surface temperature is one component of climate change that is well understood and likely to continue based on modeling that has been conducted using variable GHG emission scenarios (IPCC, 2021).

Global average surface temperatures have already increased by 0.6 to 0.7° C since the start of the 20<sup>th</sup> century (Cayan et al., 2008). Climate change scenarios that have been modeled for California predict a 1.7° C increase by the end of the century under conservative emission scenarios and up to a 5.8° C Celsius increase under extreme emission scenarios (Cayan et al., 2008). These models attempt to predict the future conditions of California, but different localities will be affected in distinct ways. Most of the temperature increases will likely be felt during the warm summer months and research currently supports the probability that temperatures will continue to rise in the mountain ranges of California, which will have impacts on the state's vulnerable montane ecosystems through reduced snowfall leading to reductions in snowpack at moderate elevations. This reduction in snowfall and snowpack will lead to shorter periods during which a snowbed is present for species that require longer periods of cold stratification (Cayan et al., 2008; Tague and Dugger, 2010). Additionally, montane species would likely have to deal with higher-than-normal temperatures during their typical growing season. Many plant

species produce seeds that will only germinate within a set range of temperatures, which is known as the thermal germination niche (Orsenigo et al., 2015; Oliveira et al., 2019). It is unclear how the germination rates of these montane species might respond as spring temperatures get higher than normal and whether the temperatures that climate change models are predicting fall beyond the thermal germination niche for these species. Researchers across the globe are actively studying how plant communities will be impacted by these stressors and my research aimed to provide insight on how native montane plants of the San Bernardino Mountain range might respond.

In my germination experiment, I expected that germination rates would decrease as temperatures increased for species with small, restricted distributions, or that germination rates would increase for species that occupy wider ranges. The results from the germination experiments did not align with the predictions from the hypotheses considering that the average rates of germination were either unaffected by the higher temperature or increased germination rates. Approximately half of the species experienced increases in germination rates as temperatures rose while the other half experienced no change in germination rate, but these outcomes did not seem to follow a set pattern based on the species' current geographic distribution. These results imply that SBMT native montane plants might not suffer a reduction in population density or distribution range due to germination responses to predicted temperature increases. In fact, because these species are also capable of germinating under lower temperatures, this plasticity of germination could provide a competitive advantage against other species.

The lack of an obvious pattern between germination rate response and current geographic distribution suggests that species with broader distributions did not necessarily have more genetic variation or phenotypic plasticity that allowed them to better adapt to changing climatic conditions as previously thought and observed in past studies (Sultan et al., 1998; Pohlman et al., 2005). However, results from the six representative forb species used in this study may not accurately represent potential impacts across the full diversity of montane plants that inhabit the mountain ranges of California. Additionally, the design of this germination experiment was focused on how germination rates might be

impacted by conditions up to 4.5° C warmer than the current averages in the Big Bear, CA region of the San Bernardino Mountain range, which is at an approximate elevation of 2000 meters. It is imperative to also consider how other factors, including precipitation, vapor pressure deficit, and the potential for uncharacteristic hot daily extreme temperatures, might collectively influence germination or cause more harm or fatalities to seedlings. Species with physiological seed dormancy could also face reductions in population sizes and distribution based on the reduced duration of the snowbed which is necessary for cold stratification of seeds. There are many montane species that experience much lower rates of germination when they do not undergo any cold stratification (Bernareggi et al., 2016).

In the growth experiment, I predicted that the SBMT population of *Bouteloua gracilis* would have a reduced range of ecophysiological responses to rising temperatures when compared with the Utah population due to the isolation and climatic differences that the SBMT population experiences. The growth experiment had results that at first glance could suggest that there is little concern regarding how the species will fare in warmer climate conditions. Above-ground biomass was generally higher for plants from both populations when grown under warmer conditions, yet maximum net photosynthesis for the isolated population from the San Bernardino Mountain range was consistently lower as growth temperatures increased. In response to warmer temperatures, *B. gracilis* specimens from the SBMT population produced more biomass, which may have compensated for the limited plasticity of maximum net photosynthesis. Alternatively, the greater growth and lower  $A_{\max}$  might indicate an acceleration of seasonal phenological decline. It does appear that the SBMT population does not adjust temperature optimum for photosynthesis, begging the question of what might happen if temperatures rose to a point where they cannot maintain favorable photosynthesis, or increase biomass to maintain similar productivity levels. The Utah population, which is larger and more interconnected with other populations of the species, had specimens that exhibited a wider range of values for  $A_{\max}$  and were capable of adjusting their temperature optimum as growth temperatures increased.

It is possible that the California *B. gracilis* ecotype has lost genetic variability that is present in other *B. gracilis* populations – those also being from regions that experience harsher climate conditions. As a C4 grass species, *B. gracilis* plants typically perform better in warmer climates. However, the concern lies in how the isolation of the Southern California populations has impacted their genetic diversity, particularly considering that these populations experience higher precipitation during the winters and milder summer temperatures than populations from Utah. Models on this species were already suggesting that local extirpation in California could occur over the next few decades (Avendano-Gonzalez and Siqueiros-Delgado, 2021). Considering that the only populations in California occur in the SBMTs and the Little San Bernardino Mountains, it is crucial that we keep a close eye on the species to evaluate how it continues to fare over time.

Results from both experiments leave us with more questions to be answered. Temperature alone might not be an issue to worry about. As it stands, it seems that both seeds and adult plants of *B. gracilis* from the SBMT montane environment can manage warmer temperatures and might even prefer them. However, competition between plants could increase as conditions become warmer at these elevations. The results from this study highlight the fact that montane plants do not necessarily lack the ability to persist in warmer climates. The problem that arises when ambient temperatures get higher is that the montane species may encounter competition from species that migrate from lower elevations, representing a broader suite of plant species that may be better adapted to the warmer environmental conditions. That is, the advantage that cold-adapted montane plants once had can disappear and these montane species would then face the possibility of being outcompeted (Alexander et al., 2016; Nabe-Nielsen et al., 2025).

Another possibility to consider is how other components of climate change might collectively influence the persistence and distributions of endemic montane plant species. Rather than evaluate the impact temperature alone might have on germination or measures of plant productivity, it could be important to combine multiple climate change effects, such as simulated drought (a change of both

temperature and precipitation) to emulate future conditions. These studies could provide a more thorough picture of what changes we will see in the persistence and distribution of our native montane flora over the decades to come. Regardless of what we might find, it is crucial that scientists, land managers, consultants, and government officials continue to work together to make decisions that will protect and preserve California's biodiversity in perpetuity.

## REFERENCES

- Alexander, Jake M., Jeffrey M. Diez, Simon P. Hart, and Jonathan M. Levine. “When Climate Reshuffles Competitors: A Call for Experimental Macroecology.” *Trends in Ecology & Evolution* 31, no. 11 (2016): 831–41. <https://doi.org/10.1016/j.tree.2016.08.003>.
- Atwood, Todd C., Julie K. Young, Jon P. Beckmann, et al. “Modeling Connectivity of Black Bears in a Desert Sky Island Archipelago.” *Biological Conservation* 144, no. 12 (2011): 2851–62. <https://doi.org/10.1016/j.biocon.2011.08.002>.
- Avendaño-González, Marcela, José Francisco Morales-Domínguez, and María Elena Siqueiros-Delgado. “Genetic Structure, Phylogeography, and Migration Routes of *Bouteloua Gracilis* (Kunth) Lag. Ex Griffiths (Poaceae:Chloridoideae).” *Molecular Phylogenetics and Evolution* 134 (May 2019): 50–60. <https://doi.org/10.1016/j.ympev.2019.01.005>.
- Avendaño-González, Marcela, and María Elena Siqueiros-Delgado. “Past, Present and Future Distribution of *Bouteloua Gracilis*, a Key Species of North American Grasslands, Changes Related to Climate Change.” *Journal of Arid Environments* 186 (March 2021): 104417. <https://doi.org/10.1016/j.jaridenv.2020.104417>.
- Baskauf, Carol J, and William G Eickmeier. *Comparative Ecophysiology of a Rare and a Widespread Species of Echinacea (Asteraceae)*. n.d.
- Baskin, Carol C., and Jerry M. Baskin. 2014. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Elsevier Science.
- BBC. 2025. “Photosynthesis.” <https://www.bbc.co.uk/bitesize/guides/zcktw6f/revision/7>.
- Bell, Daniela L., and Sonia E. Sultan. “Dynamic Phenotypic Plasticity for Root Growth in *Polygonum* : A Comparative Study.” *American Journal of Botany* 86, no. 6 (1999): 807–19. <https://doi.org/10.2307/2656702>.
- Bernareggi, Giulietta, Michele Carbognani, Andrea Mondoni, and Alessandro Petraglia. “Seed Dormancy and Germination Changes of Snowbed Species under Climate Warming: The Role of Pre- and Post-Dispersal Temperatures.” *Annals of Botany* 118, no. 3 (2016): 529–39. <https://doi.org/10.1093/aob/mcw125>.
- Blake, Abigail Kincaid. “Viability and Germination of Seeds and Early Life History of Prairie Plants.” *Ecological Monographs* 5, no. 4 (1935): 405–60. <https://doi.org/10.2307/1943035>.
- Bokhari, U. G., J. S. Singh, and F. M. Smith. “Influence of Temperature Regimes and Water Stress on the Germination of Three Range Grasses and Its Possible Ecological Significance to a Shortgrass Prairie.” *The Journal of Applied Ecology* 12, no. 1 (1975): 153. <https://doi.org/10.2307/2401725>.
- Brinkerhoff, Sterling, and Ashley N. Egan. 2025. “Utah Native Plants at Capitol Reef Field Station.” <https://www.uvu.edu/crfs/native-plants/bouteoua-gracilis.html>.
- Calflora. 2025. “Information on California Plants for Education, Research and Conservation, with Data Contributed by Public and Private Institutions and Individuals.” <https://www.calflora.org/>.
- Calflora. 2025. “Plant Range - *Bouteloua gracilis*.” <https://www.calflora.org/entry/dgrid.html?crn=1131>

- California State Parks Foundation. 2025. "Protecting Wildlife and Nature."  
<https://www.calparks.org/wildlifeandnature>.
- Cayan, Daniel R., Edwin P. Maurer, Michael D. Dettinger, Mary Tyree, and Katharine Hayhoe. "Climate Change Scenarios for the California Region." *Climatic Change* 87, no. S1 (2008): 21–42. <https://doi.org/10.1007/s10584-007-9377-6>.
- Cochrane, Anne, Matthew I. Daws, and Fiona R. Hay. "Seed-Based Approach for Identifying Flora at Risk from Climate Warming: Identifying Flora at Risk from Climate Warming." *Austral Ecology* 36, no. 8 (2011): 923–35. <https://doi.org/10.1111/j.1442-9993.2010.02211.x>.
- Coffin, Debra P., and William K. Lauenroth. "Effects of Competition on Spatial Distribution of Roots of Blue Grama." *Journal of Range Management* 44, no. 1 (1991): 68. <https://doi.org/10.2307/4002642>.
- Collins, Scott L., and Yang Xia. "Long-Term Dynamics and Hotspots of Change in a Desert Grassland Plant Community." *The American Naturalist* 185, no. 2 (2015): E30–43. <https://doi.org/10.1086/679315>.
- Cui, Langjun, Jianlong Li, Yamin Fan, Sheng Xu, and Zhen Zhang. "High Temperature Effects on Photosynthesis, PSII Functionality and Antioxidant Activity of Two Festuca Arundinacea Cultivars with Different Heat Susceptibility." *Botanical Studies* 47 (2006).
- Despres, Laurence, Sandrine Lorient, and Myriam Gaudeul. "Geographic Pattern of Genetic Variation in the European Globeflower *Trollius Europaeus* L. (Ranunculaceae) Inferred from Amplified Fragment Length Polymorphism Markers." *Molecular Ecology* 11, no. 11 (2002): 2337–47. <https://doi.org/10.1046/j.1365-294X.2002.01618.x>.
- Emery, Dara E. 1988. *Seed Propagation of Native California Plants*. Santa Barbara Botanic Garden.
- Fenner, Michael. and Ken Thompson. 2011. *The Ecology of Seeds*. Cambridge University Press.
- Fernández-Pascual, Eduardo, Charlotte E. Seal, and Hugh W. Pritchard. "Simulating the Germination Response to Diurnally Alternating Temperatures under Climate Change Scenarios: Comparative Studies on Carex Diandra Seeds." *Annals of Botany* 115, no. 2 (2015): 201–9. <https://doi.org/10.1093/aob/mcu234>.
- Franco, Guido, Daniel R. Cayan, Susanne Moser, Michael Hanemann, and Myoung-Ae Jones. "Erratum to: Second California Assessment: Integrated Climate Change Impacts Assessment of Natural and Managed Systems. Guest Editorial." *Climatic Change* 113, nos. 3–4 (2012): 1099–100. <https://doi.org/10.1007/s10584-012-0520-7>.
- Gillies, Robert R., and R. Douglas Ramsey. 2025. "Climate of Utah."  
[https://extension.usu.edu/rangelands/files/RRU\\_Section\\_Five.pdf](https://extension.usu.edu/rangelands/files/RRU_Section_Five.pdf).
- Hoffmann, Ary A., and Carla M. Sgrò. "Climate Change and Evolutionary Adaptation." *Nature* 470, no. 7335 (2011): 479–85. <https://doi.org/10.1038/nature09670>.
- Hoffman, Ava M., Julie A. Bushey, Troy W. Ocheltree, and Melinda D. Smith. "Genetic and Functional Variation across Regional and Local Scales Is Associated with Climate in a Foundational Prairie Grass." *New Phytologist* 227, no. 2 (April 18, 2020): 352–64. <https://doi.org/10.1111/nph.16547>.

- IPCC. 2021. “Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.” [Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, In press, doi:10.1017/9781009157896.
- Jordan, Gilbert L., and Marshall R. Haferkamp. “Temperature Responses and Calculated Heat Units for Germination of Several Range Grasses and Shrubs.” *Journal of Range Management* 42, no. 1 (1989): 41. <https://doi.org/10.2307/3899656>.
- Kelly, Anne E., and Michael L. Goulden. “Rapid Shifts in Plant Distribution with Recent Climate Change.” *Proceedings of the National Academy of Sciences* 105, no. 33 (2008): 11823–26. <https://doi.org/10.1073/pnas.0802891105>.
- Knipe, O. D. “Influence of Temperature on the Germination of Some Range Grasses.” *Journal of Range Management* 20, no. 5 (1967): 298. <https://doi.org/10.2307/3895976>.
- Loarie, Scott R., Benjamin E. Carter, Katharine Hayhoe, Sean McMahon, Richard Moe, Charles A. Knight, and David D. Ackerly. “Climate Change and the Future of California’s Endemic Flora.” *PLoS ONE* 3, no. 6 (June 25, 2008). <https://doi.org/10.1371/journal.pone.0002502>.
- Loayza, Andrea P., Patricio García-Guzmán, Giovanni Carozzi-Figueroa, and Danny E. Carvajal. “Dormancy-Break and Germination Requirements for Seeds of the Threatened Austral Papaya (*Carica Chilensis*).” *Scientific Reports* 13, no. 1 (2023): 17358. <https://doi.org/10.1038/s41598-023-44386-y>.
- Lomolino, Mark. V. “Elevation Gradients of Species-Density: Historical and Prospective Views.” *Global Ecology and Biogeography* 10, no. 1 (January 2001): 3–13. <https://doi.org/10.1046/j.1466-822x.2001.00229.x>.
- López-Palacios, Cristian, Hugo Magdaleno Ramírez-Tobias, Joel Flores, Sandra Milena Gelviz-Gelvez, Angel Natanael Rojas-Velázquez, and Carlos Patricio Saucedo-Acosta. “Warming Due to Climate Change Alters Physiological Performance, Biomass Production and Microenvironment of *Avena Sativa*.” *Brazilian Journal of Botany* 45, no. 3 (2022): 1139–48. <https://doi.org/10.1007/s40415-022-00825-0>.
- Love, S. J., J. A. Schweitzer, and J. K. Bailey. “Climate-Driven Convergent Evolution in Riparian Ecosystems on Sky Islands.” *Scientific Reports* 13, no. 1 (2023): 2817. <https://doi.org/10.1038/s41598-023-29564-2>.
- Love, Sarah J., Jennifer A. Schweitzer, Scott A. Woolbright, and Joseph K. Bailey. “Sky Islands Are a Global Tool for Predicting the Ecological and Evolutionary Consequences of Climate Change.” *Annual Review of Ecology, Evolution, and Systematics* 54, no. 1 (2023): 219–36. <https://doi.org/10.1146/annurev-ecolsys-102221-050029>.
- Nabe-Nielsen, Jacob, Louise I. Nabe-Nielsen, and Otso Ovaskainen. “Drivers of Plant Community Composition and Diversity in Low Arctic Western Greenland.” *Ecography* 2025, no. 8 (May 9, 2025). <https://doi.org/10.1002/ecog.07816>.

- National Center for Environmental Information. 2023. "Climate Data Online."  
<https://www.ncei.noaa.gov/cdo-web/> on 03/02/2023
- NatureServe Explorer. 2025. "Bouteloua Gracilis Blue Grama."  
[https://explorer.natureserve.org/Taxon/ELEMENT\\_GLOBAL.2.145624/Bouteloua\\_gracilis](https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.145624/Bouteloua_gracilis).
- Oliveira, Túlio G. S., Alexandre A. Duarte, Isabela P. Diamantino, and Queila S. Garcia. "Thermal Niche for Seed Germination of *Xyris* Species from Brazilian Montane Vegetation: Implications for Climate Change." *Plant Species Biology* 36, no. 2 (2021): 284–94.  
<https://doi.org/10.1111/1442-1984.12312>.
- Orsenigo, Simone, Thomas Abeli, Graziano Rossi, et al. "Effects of Autumn and Spring Heat Waves on Seed Germination of High Mountain Plants." *PLOS ONE* 10, no. 7 (2015): e0133626.  
<https://doi.org/10.1371/journal.pone.0133626>.
- Pohlman, Catherine L., Adrienne B. Nicotra, and Brad R. Murray. "Geographic Range Size, Seedling Ecophysiology and Phenotypic Plasticity in Australian *Acacia* Species." *Journal of Biogeography* 32, no. 2 (2005): 341–51. <https://doi.org/10.1111/j.1365-2699.2004.01181.x>.
- Ravi, Sujith, Paolo D'Odorico, Lixin Wang, and Scott Collins. "Form and Function of Grass Ring Patterns in Arid Grasslands: The Role of Abiotic Controls." *Oecologia* 158, no. 3 (2008): 545–55. <https://doi.org/10.1007/s00442-008-1164-1>.
- Riegel, Andrew. "Life History and Habits of Blue Grama." *Transactions of the Kansas Academy of Science (1903-)* 44 (April 1941): 76. <https://doi.org/10.2307/3624869>.
- Rondeau, Renée J., Karin L. Decker, and Georgia A. Doyle. "Potential Consequences of Repeated Severe Drought for Shortgrass Steppe Species." *Rangeland Ecology & Management* 71, no. 1 (January 2018): 91–97. <https://doi.org/10.1016/j.rama.2017.07.002>.
- Sultan, S. E., A. M. Wilczek, S. D. Hann, and B. J. Brosi. "Contrasting Ecological Breadth of Co-occurring Annual *Polygonum* Species." *Journal of Ecology* 86, no. 3 (1998): 363–83.  
<https://doi.org/10.1046/j.1365-2745.1998.00265.x>.
- Tague, Christina, and Aubrey L. Dugger. "Ecohydrology and Climate Change in the Mountains of the Western USA – A Review of Research and Opportunities." *Geography Compass* 4, no. 11 (2010): 1648–63. <https://doi.org/10.1111/j.1749-8198.2010.00400.x>.
- Thomey, Michell L., Scott L. Collins, Michael T. Friggens, Renee F. Brown, and William T. Pockman. "Effects of Monsoon Precipitation Variability on the Physiological Response of Two Dominant C4 Grasses across a Semiarid Ecotone." *Oecologia* 176, no. 3 (2014): 751–62.  
<https://doi.org/10.1007/s00442-014-3052-1>.
- U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. 2023. "*Bouteloua gracilis*."  
<https://www.fs.usda.gov/database/feis/plants/graminoid/bougra/all.html>
- Valencia, Jhon B., Jeison Mesa, Juan G. León, Santiago Madriñán, and Andrés J. Cortés. "Climate Vulnerability Assessment of the Espeletia Complex on Páramo Sky Islands in the Northern Andes." *Frontiers in Ecology and Evolution* 8 (September 2020): 565708.  
<https://doi.org/10.3389/fevo.2020.565708>.

- Verrier, James T., and Kenneth Mulder. “The Distribution and Abiotic Drivers of Subtropical Plant Taxa in the Southwestern U.S. Sky Island Region: Identifying Hotspots of Conservation Significance with an Aggregation of Peripheral Species.” *Frontiers of Biogeography* 16, no. 2 (2024). <https://doi.org/10.21425/F5FBG62246>.
- VisitUtah. 2025. “Utah Weather.” <https://www.visitutah.com/plan-your-trip/weather>.
- Walck, Jeffrey L., Siti N. Hidayati, Kingsley W. Dixon, Ken Thompson, and Peter Poschlod. “Climate Change and Plant Regeneration from Seed: Climate Change and Plant Regeneration.” *Global Change Biology* 17, no. 6 (2011): 2145–61. <https://doi.org/10.1111/j.1365-2486.2010.02368.x>.
- Warshall, Peter. *The Madrean Sky Island Archipelago: A Planetary Overview*. n.d.
- Wilson, A. M., and D. D. Briske. “Seminal and Adventitious Root Growth of Blue Grama Seedlings on the Central Plains.” *Journal of Range Management* 32, no. 3 (1979): 209. <https://doi.org/10.2307/3897124>.
- Yamasaki, Takenobu, Tomokazu Yamakawa, Yoshihiro Yamane, Hiroyuki Koike, Kazuhiko Satoh, and Sakae Katoh. “Temperature Acclimation of Photosynthesis and Related Changes in Photosystem II Electron Transport in Winter Wheat.” *Plant Physiology* 128, no. 3 (2002): 1087–97. <https://doi.org/10.1104/pp.010919>.