

RMBL Education Program Final Paper Draft
The effects of drought on wildflower size and seed set
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Abstract

Climate change is leading to shifts in precipitation, including longer and more severe droughts. Perennial wildflowers in subalpine dry meadows are affected by current and potentially future droughts in the Rocky Mountains, and several species have shown phenotypic plasticity in response to environmental factors such as temperature, snowmelt date, and soil moisture. I compared the floral size and number of seeds between control and rainout-covered transects for the three plant species *Delphinium nuttallianum*, *Eremogone (Arenaria) congesta*, and *Erigeron flagellaris*. I found no significant difference between treatments in the flower size, nectar tube depth, or inflorescence height of any focal species. Seed set also did not vary significantly between rainout and control transects, and I did not find a correlation between floral size and seed set. These results do not indicate that the plants' reproduction is negatively impacted by increased drought stress beyond that already present in the year of study.

Introduction

Climate change is altering global temperature and precipitation patterns and leading to extreme weather, including prolonged drought events (Ripple et al., 2022; Knapp et al., 2008). The effects of these disturbances on individual species and their ecosystems vary depending on how local organisms respond (Albrich et al., 2020), and specific species' responses to changes in environmental conditions have implications for biodiversity and ecosystem functioning (Bascompte et al., 2006). For instance, models predict that 200-300 native vascular plants in New Zealand's alpine environments could become extinct in the next hundred years due to increased temperatures, causing a shift from native to nonnative species in the plant community (Halloy & Mark, 2003).

Plants are foundational species of many ecosystems. They are also especially vulnerable to extreme weather events because they are sessile and may not disperse fast enough to escape sudden changes to their environment, including water scarcity. Drought stress can harm plants' fitness in numerous ways, such as by inducing leaf loss, reducing flower size, and decreasing seed production (Vesk & Westoby, 2003; Powers et al., 2021; Rering et al., 2020). However, individual plant species have different responses to and tolerance for drought stress. For example, Kuppler & Kutowska (2021) found that drought inconsistently affected pistil length and the separation of anthers and stigmas in various plant species. Understanding how drought affects a plant community requires an understanding of how individual species respond to drought stress and how their reproductive success is impacted by that response.

Drought stress generally affects plants' reproductive abilities by causing them to produce smaller and fewer flowers and change their floral scent composition (Kuppler & Kutowska, 2021). A previous observational study found that the abundance of the subalpine perennial *Delphinium nuttallianum*, native to the Rocky Mountains in Colorado, decreased significantly after two years of drought, while the abundance of invasive *Taraxacum officinale* did not (Daly, 2022). Varied responses to environmental changes such as droughts could influence the species composition of subalpine plant communities, leading to shifts in ecosystem functions and biodiversity. However, little is known about how individual subalpine plant species' floral traits and seed set respond to drought stress, despite projections of increased drought in their habitat in the future (Udall & Overpeck, 2017).

Given this information, I investigated how drought impacts floral size and seed production as a measure of fitness for three species of subalpine wildflowers: *Delphinium nuttallianum*, *Erigeron flagellaris*, and *Eremogone (Arenaria) congesta*. I compared the flower size and seed set of plants under rainout shelters to plants receiving full precipitation. Based on the findings of previous research, I expected the plants experiencing drought stress to produce smaller flowers and fewer seeds due to their limited resources. I also examined whether flower size and seed set were correlated, testing the hypothesis that larger flowers produce more seeds (Harder & Johnson, 2009).

Methods

Study System

This experiment was conducted in a subalpine dry meadow near the Rocky Mountain Biological Laboratory in Gothic, Colorado. The area around the Rocky Mountain Biological Laboratory is well-studied, with long-term research documenting more than four decades of warming and changes in precipitation patterns (CaraDonna et al., 2014). Prior research conducted near this project's site provides valuable context for understanding the effects of continued environmental stress, such as prolonged drought, on community interactions.



Figure 1. This research was conducted in a subalpine dry meadow at 38° 57' 46.8" N, 106° 59' 16.8" W between the Judd Falls trailhead and the Rocky Mountain Biological Laboratory. Ten paired transects were spread across the meadow.

The meadow where this research was conducted is sloped, has extremely rocky soil, and faces west. It is located at 38° 57' 46.8" N, 106° 59' 16.8" W and was used for previous research on plant-pollinator networks (CaraDonna et al., 2017). It is covered with snow for most of the year and has a 3-5 month growing season. Plants in the meadow acquire water mainly from snowmelt in the early spring and summer monsoon rains later in the summer, but snowmelt date is shifting earlier on average and monsoon rains are becoming more variable (Wadgyman et al., 2018; Zhang et al., 2021; Inouye et al., 2025, in review).

Most plants in the meadow are short herbaceous perennials. These include *Delphinium nuttallianum*, a flower in the Ranunculaceae family that blooms in the early summer, and the later-season *Erigeron flagellaris* (Asteraceae) and *Eremogone (Arenaria) congesta* (Caryophyllaceae). These species are common in the meadow and were already part of Janelle Bohey's drought research, making them convenient subjects for this project.

Experimental Design

Drought was simulated using rainout shelters designed to exclude about 50% of precipitation (Campbell & Wendlandt, 2013). The rainout shelters were made of PVC pipe and plastic roofing and drained rainwater into buckets (Figure 2). In 2025, they were up starting May 20 and still in place at the conclusion of this study. We emptied the buckets and checked that the shelters were upright whenever we visited the site.

Data were collected from five rainout-covered and five unmanipulated control transects. Each rainout transect was paired with a control transect as nearby as possible to account for variation in the meadow microclimate, and all transects were divided into six 2m x 2m plots. We measured the volumetric water content of the soil in each plot every week using a six-inch soil moisture probe to test the effect of our treatment on soil moisture. Three plants per species were tagged in each plot when possible.



Figure 2. Rainout shelters block 50% of precipitation to simulate drought.

Trait Measurements

Floral size was measured with calipers during the first two weeks of June for *D. nuttallianum*, the third and fourth weeks of June for *E. flagellaris*, and early July for *E. congesta*. Measurements from three randomly selected open flowers per plant were taken when possible and averaged for data analysis. Each flower's length, width, and nectar tube depth were measured; length and width were averaged to get a single flower size metric. We also measured inflorescence height. We took morphology measurements from 185 *D. nuttallianum*, 154 *E. flagellaris*, and 95 *E. congesta*.

When fruits began forming, tagged plants were covered with mesh pollinator exclusion bags until seeds dehisced to exclude seed predators and catch seeds. Two untagged plants of *Delphinium* per plot were also bagged for seed collection, since one flower is removed from some tagged plants for biomass measurements in Janelle Bohey's research and this could skew seed production data. (Due to time constraints and floral abundance, only three plants of the other two species were bagged per plot.) Once seeds dehisced, plants were snipped just below the bags and transferred to seed envelopes or containers. Seed weight, number of seeds, and number of either floral stalks (for *E. flagellaris*) or aborted and fully-formed seed pods (for *D. nuttallianum*) were recorded for each plant. Seeds from *E. congesta* are still being counted. We collected seeds from 246 *D. nuttallianum*, 154 *E. flagellaris*, and 124 *E. congesta*.

Statistical Analysis

Soil moisture was compared using a linear mixed effects model with soil moisture as a function of treatment and date as a random effect. Floral morphology and seed set data were compared between rainout and control transects using a linear mixed effects model, with morphology or seed set as a function of treatment and transect and plot as random effects. In addition, we calculated the correlation coefficient between floral size and number of seeds per fruit (for *D. nuttallianum*) or flower (for *E. flagellaris*) to examine that relationship both regardless of treatment and for each treatment group.

Results

Over the summer, soil moisture in rainout plots was significantly lower than the controls (ANOVA, $p < 0.001$; Figure 3). We quantified the magnitude of the difference in volumetric water content (VWC) between rainout and control plots using Cohen's d . Rainout plots had lower soil moisture than control plots, with a moderate effect size ($d = 0.47$, 95% CI [0.30, 0.65]).

Average flower size, nectar tube depth, and inflorescence height did not vary significantly between treatments for any focal species (linear mixed-effects model; Table 1; Figure 2). There was no effect of treatment on total seed weight, seeds per fruit, mature fruit number, aborted fruit number, or total seed count per plant of *D. nuttallianum* (Figure 5), or on flower number, seeds per flower, or total seed count per plant of *E. flagellaris* (Figure 5).

D. nuttallianum showed no significant correlation between average flower size and seeds per fruit in rainout (Spearman's rank correlation, $p = 0.523$) or control transects (Spearman's rank correlation, $p = 0.162$). *E. flagellaris* also showed no significant correlation between average flower size and seeds per flower for rainout (Spearman's rank correlation, $p = 0.441$) or control transects (Spearman's rank correlation, $p = 0.608$). When treatments were combined, average flower size again showed no significant correlation with seeds per fruit (for *D. nuttallianum*; Spearman's rank correlation, $p = 0.104$) or per flower (for *E. flagellaris*; Spearman's rank correlation, $p = 0.989$).

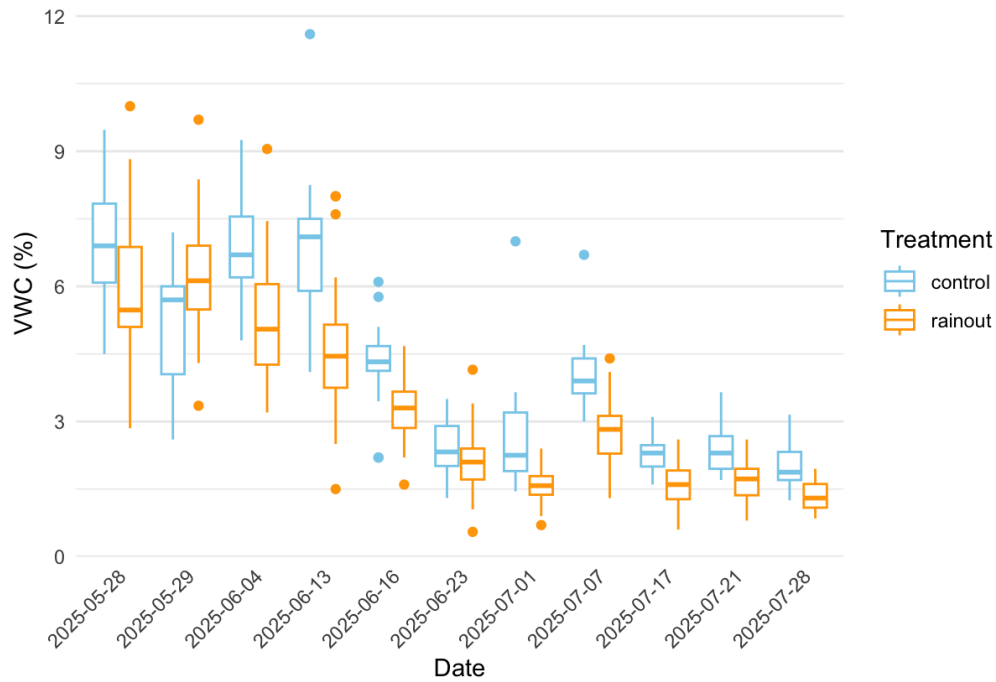


Figure 3. Soil moisture (percent volumetric water content) in rainout and control plots over the course of the experiment.

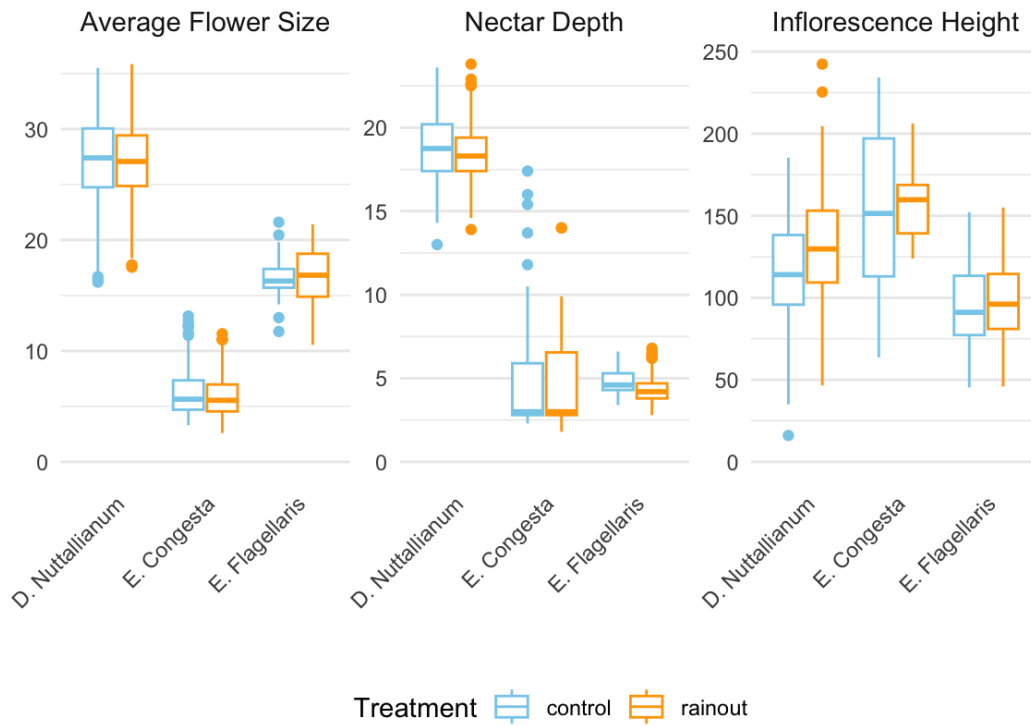


Figure 2. Average flower size, nectar tube depth, and inflorescence height (mm) per plant for *D. nuttallianum*, *E. congesta*, and *E. flagellaris* in rainout and control treatments.

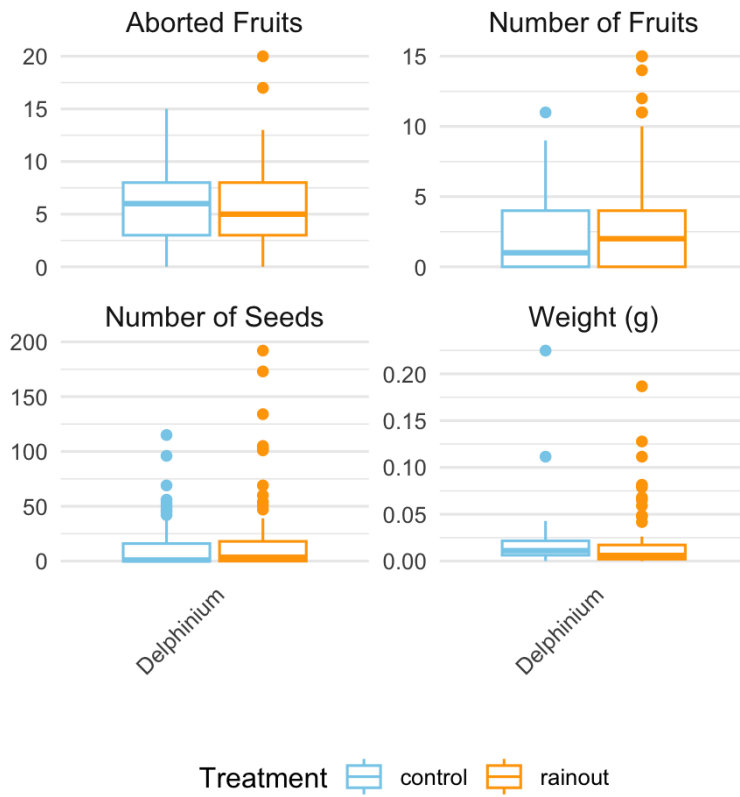


Figure 5. Aborted fruit number, mature fruit number, total seed count, and seed weight (g) for *D. nuttallianum* in rainout and control treatments.

[erigeron model table here]

Table 3. Seed set traits as a function of treatment for *E. flagellaris*.

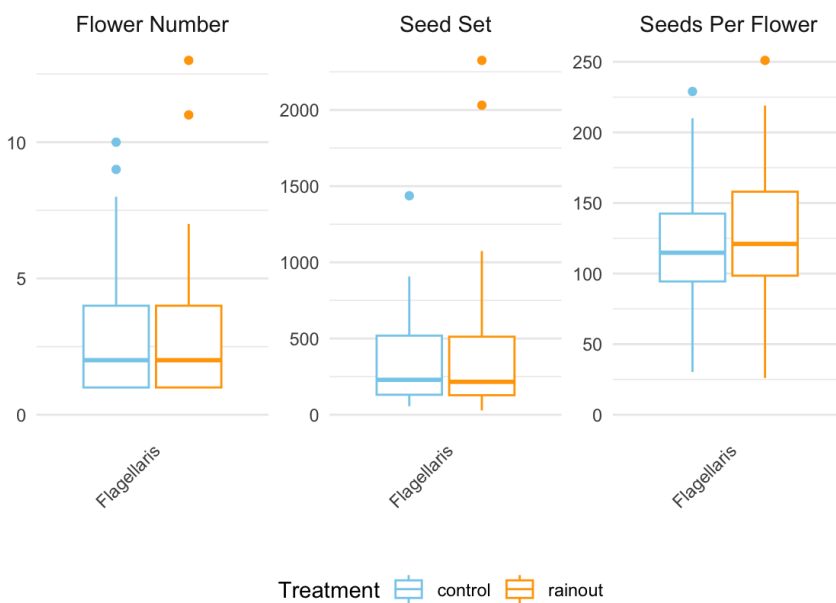


Figure 6. Flower number, total seed count, and seeds per flower for *E. flagellaris* in rainout and control treatments.

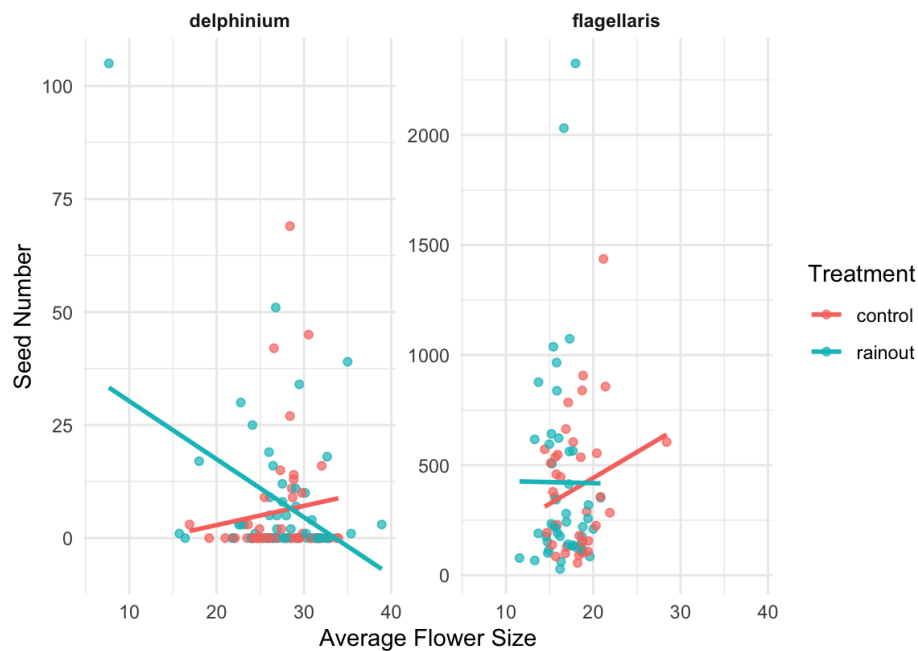


Figure 7. Average flower size vs. seeds per fruit and per flower for *D. nuttallianum* and *E. flagellaris*, respectively, in rainout and control transects.

Discussion

Soil moisture was significantly lower in rainout than control transects over the course of the experiment, so plants in the rainout transects did experience lower water availability than plants in the control transects despite extremely low rainfall in the meadow overall. However, none of the focal species demonstrated floral or seed set trait plasticity in response to this treatment. This could indicate that these traits do not respond plastically to drought stress at all, or that the difference in water availability between treatments in this experiment was not sufficient to induce a plastic response that the plants might have under other more severe drought conditions. Additionally, neither *D. nuttallianum* nor *E. flagellaris* showed a correlation between floral size and seed set, which contradicts the general trend found in a review of previous research (Harder & Johnson, 2009).

One interpretation of these results is that *D. nuttallianum*, *E. flagellaris*, and *E. congesta* do not respond to drought stress using phenotypic plasticity in their floral size or seed set traits. The subalpine meadows where these plants grow experience variable precipitation between years (Inouye et al., in review). Plants in the meadow could have adapted to this weather regime so that their reproductive success is not limited by drought stress up to a certain threshold, so that their fitness is consistent between wet and dry years. The plants in this experiment may allocate their limited water towards reproduction with a trade-off in vegetative traits, like leaf size or trichome density.

Another possibility is that these species respond plastically to drought stress, but only when water availability varies in ways that weren't examined in this study. For example, the flowers of some subalpine perennials are pre-formed underground several years before blooming (Iler & Inouye, 2013). Because all three species in the experiment are long-lived and iteroparous, they could have used prior summers' resources for this year's floral displays and seed sets, and they may show a response to this summer's drought stress sometime in the future. In addition, precipitation patterns in the area are shifting due to climate change and the plants may have been experiencing drought conditions independently of this research for years, and this summer was particularly dry. Plants may have reached the limit of their plastic response to drought stress this summer even without the rainout shelters, or maybe the plants in the population that responded strongly to drought stress were eliminated from the population by years of selective pressure before this experiment began. Comparing data on the current traits with previously collected data or data collected from old herbarium specimens could test this idea. Future research that tests incremental levels of drought stress or monitor plants over multiple years would also help confirm whether these plants' reproductive traits respond plastically to drought stress.

Previous research has often found a correlation between flower size and seed production, with larger flowers leading to more seeds (Harder & Johnson, 2009). The data collected on *D. nuttallianum* and *E. flagellaris* does not show this relationship. For *E. flagellaris*, this could be due to the morphology measurement methods used. The flower size measurement for this species was the diameter of the whole floral head, including the ray flowers, which don't produce seeds. It's possible that larger numbers or sizes of disc flowers do correlate with more seeds. However, for both species, there could also be no relationship at all between flower size and seed set, or a trade-off that cancels out the positive effect of larger flowers on seed production. Plants with large floral displays may attract more pollinators. However, if they allocate more resources towards producing large flowers, their ability to form many mature seeds may be reduced later on. This may be especially relevant to plants experiencing drought stress or other resource limitations, although I found no significant correlation between flower size and seed set for either treatment.

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