Effects of water availability on the floral traits of *Heterotheca villosa*.

Student: Rio Burk
Mentor: Janelle Bohey, Dr. Diane Campbell
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Abstract

As the climate changes, plants can change to adapt to these new conditions (Anderson & Gezon, 2015). Varied water availability, especially drought conditions, severely stresses flowers and results in smaller, shorter-lived, or aborted flowers, as flowers are an investment that drives significant water loss for the plant (Bourbia et al., 2020; Burkle & Runyon, 2016; Carroll et al., 2001; Dafni, 1996; Lankinen et al., 2017). I investigated the relationship between water availability and floral traits, including flower and disc size, flower and anther depth, inflorescence height, and floral display in the plant species *Heterotheca villosa* by experimentally adding water. I found significant differences in soil moisture and anther depth between the control and wet treatment groups, in which soil moisture was higher and anther depth was longer in the wet treatment group. These results indicate a relationship and mechanism of water allocation to specific floral traits in different water conditions and an overall resiliency to varying water availability.

Introduction

Climate change is causing an increase in the frequency and intensity of drought events (IPCC 2023). With this change in water availability, plants must find a way to adapt under these new environments. One way they can do this is through phenotypic plasticity in traits important for survival and reproduction (Dafni 1996; Lankine et al., 2017). Flowers are especially susceptible to changes in water availability since plants allocate a large portion of water resources towards reproduction (Bourbia et al., 2020). As global and regional precipitation patterns continue to change, it is becoming increasingly important to understand how reproductive traits will respond to these changes in water availability. Floral traits can respond to drought stress in several ways. A review by Kuppler and Kotowska (2021) found that under reduced water availability, plants typically showed decreases in floral size, number of flowers, and nectar volume. These decreases in visual signals and nectar rewards have implications for pollinator attraction and reproduction (Kuppler and Kotowska 2021) and can negatively affect both the pollinators and the plant itself. Therefore, drought-induced changes in floral traits have the potential to alter plant-pollinator interactions through changes in visual cues (e.g., floral display and flower size) and through food resources for pollinators (Junker and Parachnowitsch 2015).

Plants in montane environments often experience a period of drought following snowmelt and before summer monsoons begin. In Colorado, summer monsoons typically begin in July; however, over the past two years, 2024 and 2025, this important summer precipitation has become more variable (Mullane 2025). Additionally, the period of drought after the snow melts has increased as snowmelt is occurring earlier each year (Zhang et al., 2021). Because of these extremes, plants are experiencing longer periods of water stress. The reduction of the summer monsoon precipitation in recent years suggests a variability in future summer water availability that can add to and extend this drought stress (Sloat et al., 2015).

Plants that bloom later in the summer experience longer durations of drought between the date of snowmelt and the onset of summer precipitation. *Heterotheca villosa*, in particular, is an important floral resource for pollinators, as many other plants have gone to seed by the time it begins flowering, thereby offering food resources to pollinators at the end of the growing season. As summer precipitation becomes more variable, it is important to understand how flowers may respond to changes in water availability and the consequences for plant reproduction.

To understand how floral traits are impacted by variable summer precipitation, I examined floral traits in *Heterotheca villosa*, a late summer-blooming plant in the Aster family. I measured flower and disc size, anther depth, inflorescence height, and floral display (number of flowering heads) of natural populations of *Heterotheca villosa* in response to water availability. *Heterotheca villosa* serves as a floral resource for many pollinators and is important, especially because of its blooming time. Its availability in the late summer provides important food resources to pollinators as other plant species go to seed, and as water resources become more variable due to changing precipitation patterns. The effect of drought on floral morphology is well studied; studying drought effects is incredibly important as we observe global climate change. *Heterotheca sp.*, specifically, are not well profiled. By asking the question: how does water availability affect floral traits of *Heterotheca villosa*, I aimed to contribute to a greater understanding of how flowers are responding to climate change. Supported by drought experiments on floral traits, I hypothesize that if water is more available to a plant, floral traits will increase.

Method

Study System

Heterotheca villosa is a common perennial aster that grows in forbs from foothills to subalpine environments (Harms, 1963). It has showy yellow inflorescences made of yellow ray petals and disc florets. *Heterotheca villosa* is a late summer-blooming plant, typically blooming from late June to August, with peak bloom previously found to be in mid-August (Forest 2010). It is pollinated by many species, serving a generalist pollinator community, including bumblebees, solitary bees, flies, and butterflies. Because of these factors, its phenology and ecosystem interactions with pollinators make it an important species to study to investigate the effects of changing summer water availability.

Study Site

This research experiment took place on the Judd Fall Trail in the Aspen forest on Rocky Mountain Biological Laboratory property. The site is rocky and has a gradual incline. This site was chosen for its accessibility to a water source for the water additions and ample *Heterotheca villosa* individuals.

Surveying and Tagging Plants

We tagged 45 individual plants and randomly assigned 15 plants per treatment group. The study site and tagged plants are visualized below (Figure 1).

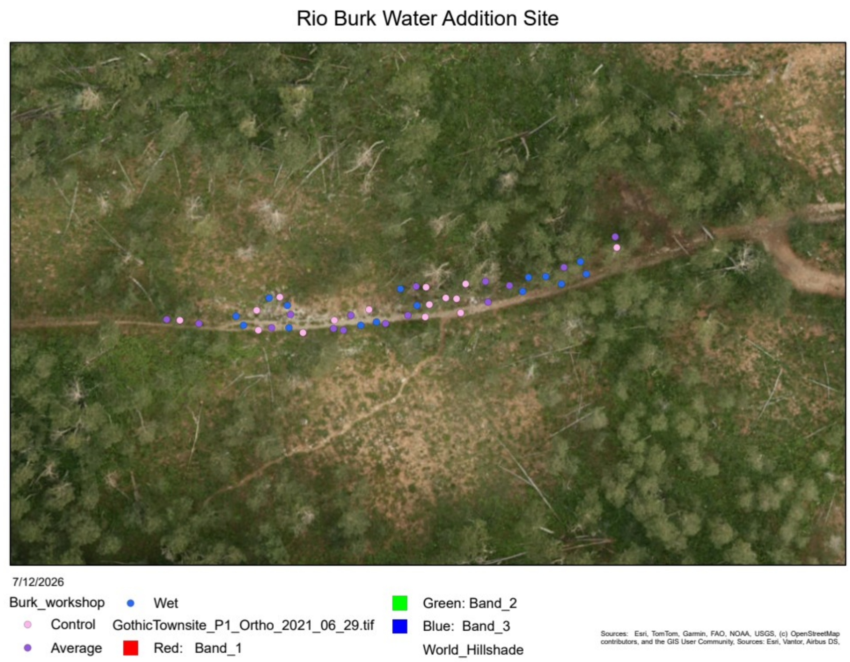

Figure 1: Study Site and Tagged Plants. Blue points are wet treatment plants, pink points are control treatment plants, and purple points are average treatment plants.

Water Addition

After tagging each plant, I assigned each plant to an experimental group: a control group, an average rainfall group, and a “wetter” rainfall group using a random group generator. Using billy barr's weather archive data, I calculated how much water each group would receive.
To calculate how much water to give for the “average rainfall” group, I added the average daily precipitation of June and July and calculated how much water that is for a square foot, determined by the average surface area of my plants. To calculate how much water to give the “wetter” rainfall group, I found the daily average rainfall of the highest rainfall records of June and July, then added them together. I doubled the amount to accommodate a more accessible every-other-day watering schedule. Average treatment group = 0.2 L * 2 days; Wet treatment group = 0.6 L * 2 days. Water was given to the average and heavy rainfall treatment plants every other day starting from June 26th until July 24th. Water was poured slowly in circles from the center of the plant to maximize water absorption by the roots and reduce runoff.

Volumetric Water Content

A six-inch Campbell Scientific Hydrosense II soil moisture probe was inserted into the soil directly adjacent to the base of each plant to measure volumetric water content (VWC). I collected soil moisture once per week on a day plants were not watered. Soil moisture was collected to confirm water absorption and the consistency of moisture near plants in the same experimental group.

Floral Trait Measuring

Flower and disc length, width, and stamen length were measured using calipers. Flower length and width were measured from the ends of rays in millimeters. Similarly, disc length and width were measured from the end of the ray, where disc florets begin, to the other end of the disc. Length and width were averaged to get a single flower and disc size metric. Flower depth was measured from the base of the bracts to the flower opening in millimeters. Anther depth was taken from the longest stamen and measured from the base of the bracts to the tip of the anthers. Inflorescence height was measured using a meter stick in cm. Three open flowers were randomly selected and measured for these traits per plant, and averaged to obtain a single plant-level measure.

Morphological trait measurements occurred after 4 weeks of watering. This timing is to ensure that the water addition has occurred long enough for it to affect the plants. The number of open flowers was measured once per week.

Statistical Analysis

I ran analysis of variance (ANOVA) on linear mixed-effects models for all traits. Linear mixed models were fit for each trait using a fixed effect of treatment and a random effect of plant using the *lmer* function of the R package lme4. Significant ANOVAS were followed by a Tukey's honest significant difference (HSD) post-hoc test to identify pairwise differences between climate treatments for each trait using the emmeans and pairwise function of the R package emmeans. Lastly, percent change was calculated between control and average, and control and wet treatments for all floral traits.

Results

Soil moisture was significant between treatments (ANOVA, $p = 0.007$; Figure 2). A post-hoc analysis showed that soil moisture was higher in the wet treatment group compared to the control group ($p = 0.009$); however, there was no difference detected between the control and average treatments ($p = 0.297$).

Anther depth was significant between treatments (ANOVA, $p = 0.03$; Figure 3). A post-hoc analysis showed that anther depth increased by 7 % in the wet treatment group compared to the control group ($p = 0.03$); however, there was no difference detected between the control and average treatments ($p = 0.25$).

We did not detect an effect of water availability on any of the other floral traits we measured (flower size, disc size, inflorescence height, and flower number; ANOVA, all p > 0.05; Figure 4). We also did not find a difference in these traits after conducting pairwise contrasts between treatment groups (Pairwise Contrast Table, p > 0.05).

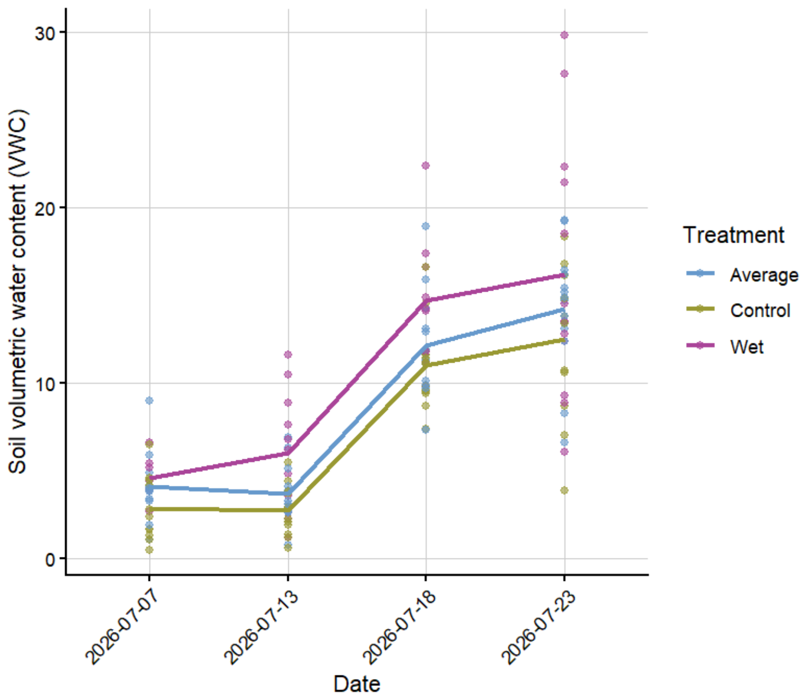

Figure 2: Soil moisture (percent volumetric water concentration) of each treatment (control, average, and wet), measured weekly with date on the x-axis.

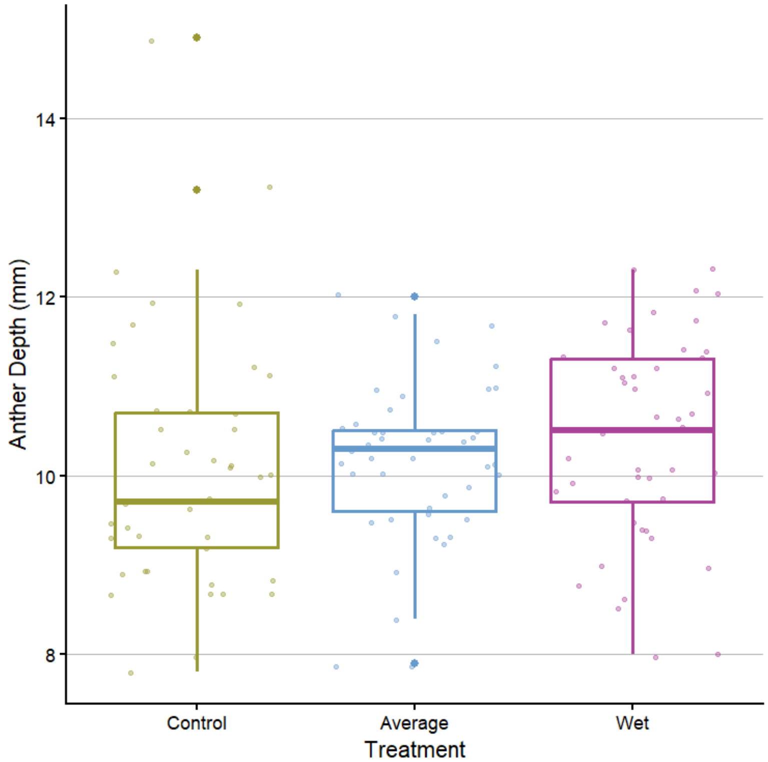

Figure 3: Anther depth in each treatment, where each color (yellow, blue, and pink) represents an individual plant.

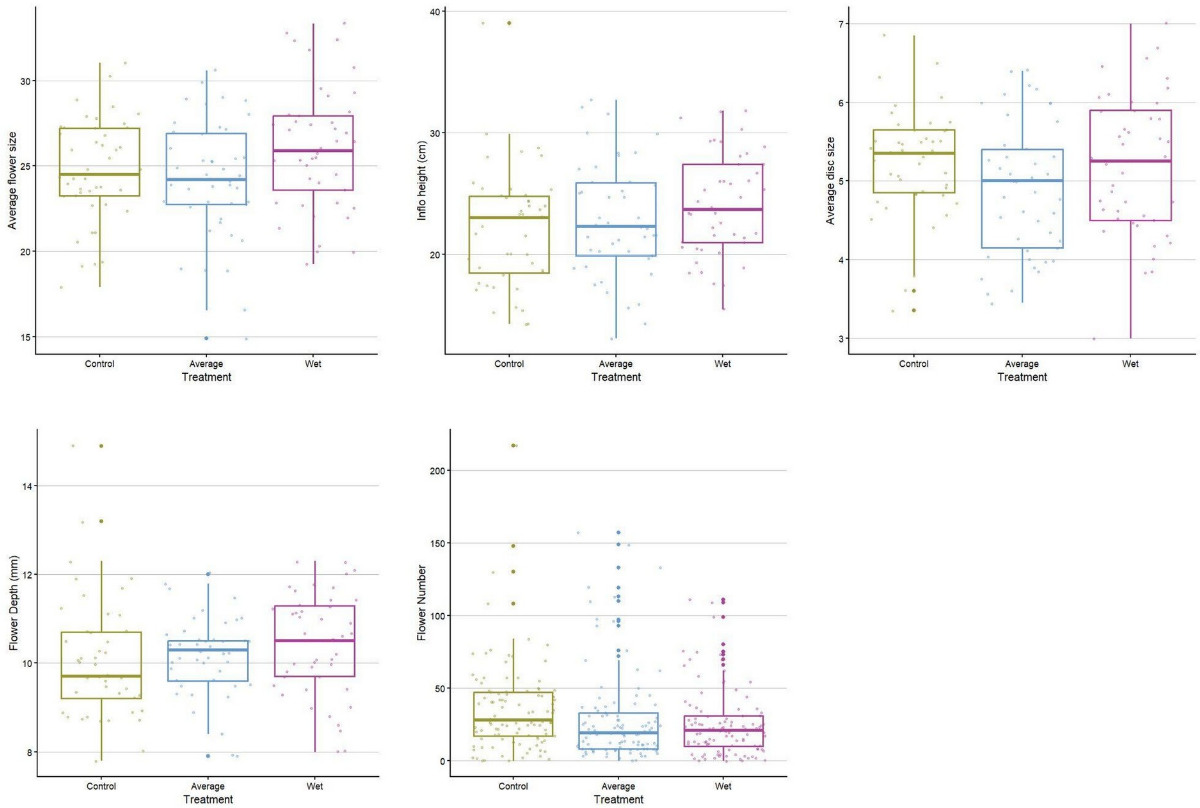

Figure 4: From Left to right, top to bottom: average flower size, inflorescence height, average disc size, flower depth, flower number per treatment, control, average, and wet.

Discussion

Soil moisture was significantly higher in the wet treatment group than in the control and average groups over the course of the experiment, so plants in the wet group had consistently higher soil moisture over the duration of the watering period compared to the other groups. This trend of greater effects in the wet compared to control and average treatment was also found in the anther depth, where anther depth of the wet and control groups differed significantly from each other. No other floral or morphological traits responded to the experimental water addition.

Overall, my hypothesis was only supported by the increase in anther depth under the wettest condition. These findings suggest that *Heterotheca villosa* may be resilient under variable water conditions.

The lack of significant difference in soil moisture between the control and average treatment groups could explain the overall lack of difference between the response variables in each treatment group. This suggests that the water addition for the average group was not enough to exceed a water threshold that traits can respond to during this short timescale. *Heterotheca villosa's* water threshold is something worth studying through a physiological or water-isotope lens.

Late summer precipitation may not be a strong predictor of floral morphology and traits. Perhaps the production of these traits is predetermined by water availability before the start of the growing season. Since *H. villosa* is a long-lived perennial species, these plants may store resources from prior years to use for reproduction; therefore, short-term watering may be less influential on floral traits in the same year. Studying *Heterotheca villosa* life cycle-history more closely, and comparing it to the availability of other sources of water, such as snowmelt, may contribute more to responses of floral traits within a single year.

In a meta-analysis of drought on floral traits, many of the studies found a change in flower size and flower number, suggesting there is a relationship between water availability and flower morphology and display (Kuppler and Kotowska 2021). However, in *H. villosa*, we did not find a change in flower size or flower number, suggesting that other environmental or life-history factors might be more influential in *H. villosa's* reproductive strategy. Glenny, Runyon, and Burkle (2018) found that in *H. villosa*, drought-treated *H. villosa* plants had reduced petal area compared to control plants. However, none of the other traits measured (plant size, mean petal area, floral display, and floral olfactory traits) responded to drought. Their findings support the overall trend reported in Kuppler and Kotowska (2021). No paper in the meta-analysis collected anther depth as a variable.

In this study, we found that anther depth responded to water availability but not the other floral morphological or display traits we measured. To understand how changes to anther depth may affect plant reproduction, plant-pollinator interactions of *Heterotheca villosa* should be studied since anther depth may alter the efficiency of pollination and overall impact reproduction.

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