

**Impacts of snowmelt timing and precipitation on the expression of
vegetative traits and floral traits in *Ipomopsis aggregata***

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Abstract

This study investigated the impact of water availability and snowmelt timing on the species *Ipomopsis aggregata*. We looked to discover if *I. aggregata*'s traits were plastic, and if that plasticity was adaptive. The two questions we aimed to answer were: How does timing of snowmelt and level of precipitation influence the expression of vegetative and floral traits in *Ipomopsis aggregata*? Are the plastic responses of vegetative traits adaptive? We hypothesized that the traits would be plastic, and that the plasticity of the vegetative traits would be adaptive. In order to analyze these questions, we measured vegetative traits including specific leaf area and trichome density, in addition to floral traits which included flower number, corolla length and width, style and stamen length, sepal width, 48-hour nectar production and nectar concentration. The experimental design included 6 10x10m plots, each with 4 2x2m plots within them. For snowmelt treatment, 3 of the 6 plots were covered with a shade cloth to cause the snow to melt about a week earlier than normal. For water treatment, the subplots within each plot were randomly assigned to water addition (50% additional precipitation), rainout (50% less precipitation), mockup (a control for the rainout structure with no prevention of precipitation), and control, which remained untouched. Corolla width, sepal width, nectar production, and nectar concentration were affected by the water treatments, while snowmelt timing had no statistically significant impacts on the traits. Although leaf trichome density affected the chance of flowering differently across the water treatments, none of the vegetative traits were plastic. Thus none of the observed traits demonstrated adaptive plasticity. This means that while some plant traits did react to the water treatments, we can make no conclusion as to whether adaptive plasticity may be a means for *I. aggregata* populations to persist in the varying conditions presented by climate change.

Introduction

Climate change is a real and constant threat to species across the world. One of the major impacts of climate change in areas such as the Rocky Mountains is decreased snowpack and earlier snowmelt (Sherwood 2013). Snowmelt timing may have a significant impact on plants that rely on the snowmelt for moisture, and the snow itself for protection (Anderson and Gezon 2015, Inouye 2008, Sherwood 2013). Earlier snowmelt results in drier soil later in the summer, making it difficult for plants that rely on soil moisture to survive (Sherwood 2013), and those effects can be exacerbated by drought conditions during the summer. The area surrounding the Rocky Mountain Biological Laboratory is a prime location for the study of the impacts of early snowmelt due to the large amount of snow that plays a significant part in the ecosystem and the clear trend toward earlier snowmelt demonstrated in the area (Inouye 2008). In addition to snowmelt, plants in the Rocky Mountains rely heavily on summer precipitation as their main water sources. A change in precipitation has the potential to significantly impact species that rely on water availability.

For a population to persist in the face of climate change, it must in some way be able to adapt to the changing environmental conditions. A population may migrate to a new location with more suitable environmental conditions that make plants in the new location more likely to survive. Additionally, a population may evolve over time as new trait values increase fitness in the new environment since plants without the altered traits fail to reproduce. The mechanism that we are focusing on is adaptive plasticity (Anderson and Gezon 2015), and how it is a possible way for populations to persist.

Adaptive plasticity is one way in which populations may be able to survive the ever-changing environment. If they are able to alter morphology appropriately to different environmental conditions in a way that improves fitness, that adaptive plasticity may help a population's chance of persistence. However, plasticity can be both beneficial and costly to plants because it allows for change according to the environment, but it may in certain circumstances hinder the plant's fitness. This may result in some traits' plasticity being adaptive, meaning that the trait's plasticity increases fitness, but others may have plasticity that is either neutral or too costly to be adaptive (Caruso et al. 2006). Plants changing in response to the environment may be essential for some plant populations to persist when the environment changes (Moritz and Agudo 2013). Moisture availability is also a key component in an environment, and altering the moisture availability can certainly cause plastic changes in traits, though the heritability of such traits is variable (Sun et al. 2020).

This study will focus on *Ipomopsis aggregata*, a native plant species that is common in the Gothic, Colorado area. *Ipomopsis aggregata* is a herbaceous subalpine plant. While it is often observed in dry environments, it performs worse under drier conditions than its closest congener (Campbell and Wendlandt, 2013) and has lower seedling emergence and seed production in years of early snowmelt (Campbell, 2019). Other plants have been shown to bloom significantly earlier than average due to earlier snowmelt, and *I. aggregata* may have a similar reaction (Anderson and Gezon 2015). Because we already knew that early snowmelt could cause early blooming and drought later in the summer, we investigated plastic changes in floral and vegetative traits caused by the early snowmelt. Additionally, adaptive plasticity had yet to be researched in relation to the plant's reaction to climate change, so we planned to compare the 2020 data with previous data from 2019 in order to establish which traits change in a way that increases fitness. We addressed two research questions: How do timing of snowmelt and level of precipitation influence the expression of vegetative and floral traits? Are the plastic responses of vegetative traits adaptive?

Specific leaf area (SLA) in other plants has been shown to decline in dry environments, and we expected similar results in *I. aggregata* (Poorter et al. 2009). In a previous study of this species manipulating precipitation, water treatments had an impact on flower size (Campbell and Wendlandt 2013), and we expected similar impacts in this study.

We hypothesized that the expression of vegetative and floral traits will be altered by the timing of snowmelt and level of precipitation. Therefore, the plots with the highest soil moisture

would have decreased water-conserving traits while the plots with the lowest soil moisture would have the most water-conserving traits. For example, we expected that plants in the subplots where water was added and in the plots with regular snowmelt dates would have a larger specific leaf area, since high SLA allows for greater photosynthesis when water is not limiting. Plants in the subplots that only received 50% of precipitation and are in larger plots with early snowmelt were thought likely to have much smaller specific leaf areas as thicker leaves reduce water loss through stomates. Additionally, due to the earlier snowmelt causing the ground to dry out faster, we expected that the plants might grow more trichomes, as that trait has also been associated with drought in order to save water. We also expected that plants in the drier locations would make fewer and smaller flowers. Our planned study went further than the previous one in examining effects of snowmelt timing as well as precipitation. Additionally, we expected that plants in drier conditions would produce less nectar (Table 1). We also predicted that plasticity would increase along with the amount of water that a subplot receives, and that plasticity would be adaptive. An example of adaptive plasticity for SLA is shown in Figure 1, in which a shift to higher SLA in the add water treatment increases survival while a shift to lower SLA in the rainout increases survival (Figure 1).

Methods

The focus of this study was to investigate the impacts of snowmelt and precipitation on trait expression as well as adaptive plasticity. In order to do this we collected data on vegetative and floral traits at Maxfield Meadow, a field 1km South of Gothic, Colorado on Gothic Road, and compared that data to data gathered from the summer of 2019 (see Figure 3). Western Colorado is the focal point for the fastest rates of warming in the United States, and our study site happens to be a part of these hot spots (Rangwala et al 2013).

Water Treatments

The research site has an experiment that started in 2018, and is comprised of six plots with each plot divided into four sub-plots (Figure 4, Figure 3). Of these four subplots, one acts as a mock rainout plot that just has the structure of the rainout plot, one acts as a rainout plot decreasing the amount of rain water received by 50%, one acts as a water addition plot whereby it receives 50% more rain (which is approximately 14L of extra water per subplot every other day), and the last plot acts as a control and is unmanipulated. The water treatments applied to each subplot were randomized according to plot. Each of these plots are 7x7m and each subplot is 2x2m.

Snowmelt Treatments

Additionally, three of these plots were randomly chosen to have early snowmelt, caused by covering the plots with black shade cloth in early spring. This caused the snow above these plots to melt approximately one week before the normal snowmelt ensued. The remaining three plots acted as control snowmelt plots.

Plot and Subplot Setup

Within these plots we censused a total of 434 viable plants of which 241 were in the vegetative stage and 208 flowered this year. We sampled at least 17 flowers per treatment for floral traits, 14 buds per treatment for nectar measurements and 11 leaves per treatment per plant for trichomes and specific leaf areas (Table 2). Additionally, 5 soil moisture measurements were taken per subplot per week, meaning a total of 15 measurements per treatment per week. Here treatment refers to a separation of both water and snow treatment, making eight categories as shown in Table 1. The specific plot and subplot layout is shown in Figure 2 and Figure 3.

Data Collection and Analysis

To answer our first question on the effects of snowmelt and precipitation on the expression of vegetative and floral traits, we analyzed the floral and vegetative traits in addition to the environmental conditions of this year's plants. To answer our second question focused on adaptive plasticity, we analyzed the effects of trait values on fitness components.

The vegetative traits analyzed are specific leaf area and trichome density. To do this, we sampled one leaf from four plants in each of the four subplots within the six plots and scanned them. The program ImageJ was used to determine leaf area and the number of trichomes present on each leaf from the scanned images. After the physical leaves were scanned, they were then dried by baking them at a temperature of 70 degrees celsius for two hours. The dry leaves were then weighed. Specific leaf area was calculated as leaf area/dry mass. Leaves were collected on 19/06/2020 and 28/07/2020, to separate overwinter plasticity from effects of summer precipitation. As many leaves from the same plants were collected as possible, but in cases where a plant could not be found to sample a leaf from, another plant within the same subplot was used.

We also examined floral traits including corolla length and width, style and stamen length, sepal width, maximum and minimum anther length, and 48-hour nectar production and concentration. The length and widths of the various parts of the flowers were examined by measuring these traits on one flower per flowering plant per week, totaling 402 measurements of flowers using calipers (Table 1). The 48-hour nectar production and concentration were measured by placing a straw over an elongated bud for 48 hours and using a microcapillary tube to examine the amount of nectar produced (Campbell et al. 1991). Flowers targeted for nectar measurements were buds that were predicted to open within the next 48 hours, and they were protected from pollinators using straws tied to the plant. 48 hours later, measurements were taken by removing the straw, inserting a capillary tube into the flower to determine nectar production, and placing the nectar into a refractometer to determine the concentration of sugars in the nectar.

To analyze the effects of treatments on each trait, we first averaged the trait values across a subplot. Then we analyzed the 24 values using a split-plot analysis of variance. The experimental design is a split-plot, because the unit of replication for the snowmelt treatment is at the large plot level and the unit of replication for the water treatment is a subplot. Analysis employed the function lmer in the program R, with crossed fixed factors of snowmelt timing and water treatment and a random effect of plot. Here water treatment refers to one of the four

treatments: added water, reduced water, mock rainout shelter, and control. Treatments may be referenced as water addition, meaning that the subplots received 50% additional water, rainout, meaning that the subplots received 50% less water, mockup, or “mock” in some tables, meaning that the rainout structure was present but there was no prevention of precipitation, and control, meaning that the subplots were not altered by water treatment. Additionally, water_unlumped refers to the two controls being kept separate, while water combines the mockup and control into one category. Snow treatment refers to the early snowmelt caused by the shadecloth, while the remaining plots control for snowmelt. In addition we took soil moisture readings consisting of five measurements of volumetric water content (VWC) per subplot (one in each quarter and a measurement in the middle), all 12 cm deep to ensure that the depth of the moisture meter would not have an impact on the reading. These measurements were taken once a week in order to measure the amount of soil moisture present in each plot. This resulted in 105 measurements per treatment over the course of the summer, with treatment referring to both snow and water treatments.

In order to investigate our second research question regarding adaptive plasticity, we analyzed the effects of each vegetative trait measured in 2019 on survival to June 2020, separately for each treatment. The effects on survival were analyzed with logistic regression and logistic analysis of covariance since survival is a binary variable. Analysis employed the function `glm` in R, with survival assumed to have a binomial distribution.

Results

Soil Moisture

Percent volumetric water content of the soil averaged 7.4% for the water additions, 4.7% for the rainout treatment, and 5.4% and 5.5% for the two control treatments (Table 3). There is a larger difference between the water addition subplots and the other types, than between the rainout and control plots (Figure 4). Additionally, while the snowmelt treatment made a difference for the water addition and control plots, (a difference of 0.6 in VWC between early and control snowmelt for both treatments), the snowmelt had very little impact on the average soil moisture of the rainout and mockup subplots (Table 3).

Floral Morphological Traits

For all of the floral traits measured, there was no statistically significant effect caused by the snowmelt treatment (Table 4). However, the summer water treatments significantly influenced corolla width, sepal width, 24 hour nectar production, and nectar concentration. When analyzing the plasticity of corolla width, we found that the width was increased by addition of water (water treatment effect, $p = 0.0056$), although not by snowmelt ($p=0.9621$) or the snowmelt's interaction with water treatment ($p=0.3836$). This relationship is illustrated in (Figure 5) which shows that for both early snowmelt and normal, corolla width increased with the addition of water. When we were investigating the effects of these treatments on sepal width, we found that the water treatments ($p=0.0006$) were statistically significant, however, the snow

treatments ($p=0.9649$), and the interactions between the treatments ($p=0.4482$) were not statistically significant. We found that the effects of water on sepal width followed a similar trend as corolla width in which increased precipitation resulted in an increased corolla width (Figure 6).

The water treatment did influence the rate of nectar production significantly (Table 4). However, unexpectedly the water addition and reduction plot both had increased nectar production in comparison to the controls (Figure 7). When examining the nectar concentration, we found that the water treatment had a statistically significant impact with a p-value of 0.0070. Nectar concentration showed a decrease in concentration with increasing precipitation (Figure 8).

Specific Leaf Area and Trichome Density

Initially, we analyzed the plasticity of vegetative traits. What we found in analysing the plasticity of the 2019 and 2020 vegetative traits data set is that none of the traits responded detectably to the treatments either in August 2019 (Table 5) or in late July 2020 (Table 6). We decided to compare the August 2019 data set to the July 2020 data set instead of June 2020 vegetative data because by July the plants will have had more time to react to our treatments. As none of the vegetative traits had statistically significant responses, we cannot conclude that they underwent any plastic changes.

Secondly, we looked at the analysis of logistic covariance to determine adaptive plasticity. In doing so, we found detectable responses in two instances. First, the water treatment influenced the trichome density's effect on flowering (Table 7, Figure 9). Second, leaf water content decreased survival (Figure 10).

Discussion

Floral Traits

The large difference in soil moisture between treatments reinforced the inference that our water treatment made a significant difference in the environmental conditions between the subplots. Snowmelt treatment made less of a difference on average VWC than water treatment, but overall we saw changes in soil moisture in the direction expected. Our study found that some of the traits, including corolla width, sepal width, nectar production, and nectar concentration, had statistically significant responses to these water treatments, while other traits did not show obvious phenotypic plasticity. None of the traits had a statistically significant response to the snowmelt treatment. Snowmelt treatment in future experiments may make more of a difference if the snowmelt is induced earlier, causing a larger change in soil moisture. These results answer our first question, about the impact of snowmelt and precipitation on the expression of vegetative and floral traits. Our results do not imply that the other traits will never show statistically significant responses to water treatment or to snowmelt treatment. Combining our results with the results from 2018 and 2019 will yield larger sample sizes and hence more statistical power to detect responses, but in this 2020 study alone there was no statistically significant response for the other traits. We previously stated that we expected the flowers in general to be larger with

additional water exposure, and the trends of both corolla and sepal width head in that direction, with additional water yielding larger measurements. Previous studies of another plant species have shown that nectar production varies due to the amount of water available, but had little effect on nectar concentration (Carroll et al. 2001), while we found that both nectar concentration and production were plastic. Previous studies have shown that larger corolla width has a positive effect on the amount of pollen exchanged between flowers, so it would be a beneficial trait to have, though in this study we are unable to prove that it increases fitness (Campbell et al. 1991).

We saw larger sepal widths with more water exposure. This falls in line with our predictions, as does the trend of larger corolla width with more exposure to water. What we did not expect was that the corolla length, anther minimum, anther maximum, style length, trichome density, and specific leaf area had no statistically significant difference between treatments.

Floral traits that change with the environment can have an effect on plant fitness through pollination. In our study we found that water addition can produce wider corollas relative to other treatments. From previous studies, we know that wider corollas increase the effectiveness of pollen removal by hummingbirds (Campbell et al. 1991). Therefore flowers with wider corollas would be predicted to reproduce more than those that do not, giving them higher fitness (Campbell et al. 1991). If drier conditions persists *Ipomopsis aggregata* reproduction will decrease under these conditions.

This study will be extended in two ways by the Campbell lab, both of which depend on obtaining seed production as a measure of fitness for the flowering plants. First, those data will be used to test for the adaptive plasticity of floral traits. Second, the seed production data will be used to examine if different floral traits are favored by natural selection in the different water treatments. While we did begin the data collection and do seed collection a few times before the end of the summer, we were unable to gather an appropriate amount of data to be used for analysis in this paper. With the additional seed production data, it will be possible to test for adaptive plasticity of the changes in floral traits as well as variation in natural selection across environmental conditions.

Vegetative Traits and Adaptive Plasticity

We were able to test for adaptive plasticity of some vegetative traits, but found no evidence that any of the traits had such adaptive plasticity. One of the statistically significant trends found was that the water treatment affected how trichome density influenced the fitness component of flowering. We can see that in the water addition and reduction treatments, increased trichome density leads to more flowering, while the control plot shows that decreased trichome density leads to increased flowering (Figure 9). Trichomes provide more UV protection and conserve water by cooling the leaf, although that can slow down photosynthesis. Knowing this, the results we got did not fit our prediction as we would have expected that in the water addition treatments, plants with fewer trichomes would be more likely to flower as they can photosynthesize more, while in the reduction treatment plants with more trichomes that save water would flower more. Additionally, we would have expected that the water addition

treatment would be more likely to flower than the control or reduction treatments. The second statistically significant trend we found was the effect of water content on survival, but in this case the impact on survival was not different across water treatments (Figure 10). As none of these traits were plastic as well, we cannot conclude that any of the changes seen with these treatments was adaptive.

Overall, as there were no plastic vegetative effects and only one statistically significant effect between the treatments and fitness (Table 8, Table 7), we cannot conclude that there was any adaptive plasticity of the measured vegetative traits, as the two conditions (trait change and increase in fitness due to the trait) must both be met.

Conclusion

Our study shows that some of the traits of *Ipomopsis aggregata* are plastic, but we were unable to demonstrate that any of the plasticity was adaptive. The traits that had a statistically significant difference due to water treatments were sepal width, corolla width, nectar production, and nectar concentration. We are unable to conclude from our results if adaptive plasticity will be a way for *I. aggregata* populations to persist during the environmental changes that climate change will bring despite knowing that some of *I. aggregata*'s traits are plastic and will respond to water treatment. Further examination of trichomes and specific leaf area's responses to both water and snowmelt treatment, with larger sample sizes, would be helpful in making a more robust conclusion about the potential for adaptive plasticity of those vegetative traits. Additionally, though we concluded that there were multiple floral traits that were plastic, we did not make a conclusion about the adaptive plasticity of those floral traits, which could be discovered through the analysis of the fitness of those plants (obtained through seed production measurements that are in progress).

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Table 1: Predicted Responses of Floral Traits to Treatment, Made Prior to Data Collection

Floral Traits	Early Snowmelt or Reduced Precipitation
Style/Stamen/Anther Length	Shorter
Corolla Length/Width	Shorter/Narrower
Sepal Width	Narrower
48-Hour Nectar Production	Decreased Production
48-Hour Nectar Concentration	Higher Concentration

Table 2: Number of Plants Measured per Treatment, where treatment is separated to mean both water and snow treatments together. ES means Early Snowmelt, CS means Control Snowmelt.

	Water & ES	Control & ES	Mock & ES	Rainout & ES	Water & CS	Control & CS	Mock & CS	Rainout & CS
morphology	23	20	30	17	38	22	20	18
nectar	20	15	23	16	28	14	17	14
Trichomes and SLA	12	11	12	11	13	12	13	11

Table 3: Average Volumetric Water Content of the Soil across Treatments, Averaged from data collected weekly in the summer of 2020. These data represent the averages of 120 measurements taken per treatment, where treatment means a separation of both water and snow treatments.

Treatment	Water Addition	Rainout	Mockup	Control
Average VWC	7.4	4.9	5.6	5.5
Average VWC for early snowmelt plots	7.2	4.8	5.6	5.2
Average VWC for control snowmelt plots	7.6	4.9	5.7	5.9

Table 4: Effects of water and snow treatments on floral traits collected from plants throughout the summer of 2020. Results here are given as P-Values for split-plot analysis of effects of treatments on floral traits. Plasticity would be indicated by a significant effect of the treatment on the trait.

Traits	Water	Snow	Water:Snow
Corolla Length	0.071391	0.8776049	0.60777
Corolla Width	0.0056308	0.9621057	0.3836117
Style Length	0.2086856	0.8783692	0.2193231
Anther Max.	0.499939	0.5179088	0.4278077
Anther Min.	0.4331835	0.371467	0.2276614
Sepal Width	0.0006326	0.9649127	0.4482232
Nectar Production	0.0178524	0.9810992	0.2932613
Nectar Concentration	0.0070042	0.1522314	0.4266853

Table 5: Effects of water and snow treatments on vegetative traits collected in August 2019. Values reported are P values from the split-plot analysis of variance. Water:Snow represents an interaction between the effects of both treatments on the trait. Plasticity would be indicated by a significant effect of the treatment on the trait.

Trait	Water	Snow	Water:Snow
SLA	0.5234141	0.8288619	0.7222143
Trichome Density	0.9335659	0.9231199	0.9571413
Leaf Water Content	0.2598352	0.8841401	0.7162351

Table 6: Effects of water and snow treatments on vegetative traits collected in July 2020. Values reported are P values from the split-plot analysis of variance. Water:Snow represents the effects of both treatments together on the trait. Plasticity would be indicated by a significant effect of the treatment on the trait.

Trait	Water	Snow	Water:Snow
SLA	0.8445499	0.1295925	0.4217437
Trichome Density	0.6453195	0.989524	0.1589727
Leaf Water Content	0.3329597	0.8372607	0.2414663

Table 7: Effects of water treatment, the traits of Trichome Density, and their interaction on the fitness measurements of survival and flowering next year. Values reported are P values. Adaptive plasticity would be indicated by a significant interaction with the effect of fitness going in the same direction as the observed change in a plant trait.

Response Variable	Water	Trichome Density	Water:Trichome Density
Survival	0.263905	0.6518709	0.122526
Flowering	0.3957563	0.1812891	0.0416422

Table 8: Effects of water treatment, the traits of SLA, and their interaction on the fitness measurements of survival and flowering the next year. Values reported are P values. Adaptive plasticity would be indicated by a significant interaction with the effect on fitness going in the same direction as the observed change in a plant trait.

Response variable	Water	SLA	Water:SLA
Survival	0.7059437	0.9013564	0.7669312
Flowering	0.4842529	0.5119073	0.3077278

Figure 1: Predicted Effects of Specific Leaf Area (SLA) on Survival, made prior to data collection. We expected that the plasticity shown in the SLA trait would be adaptive, meaning that survival would increase due to the plasticity of SLA demonstrated by the change in SLA due to water availability.

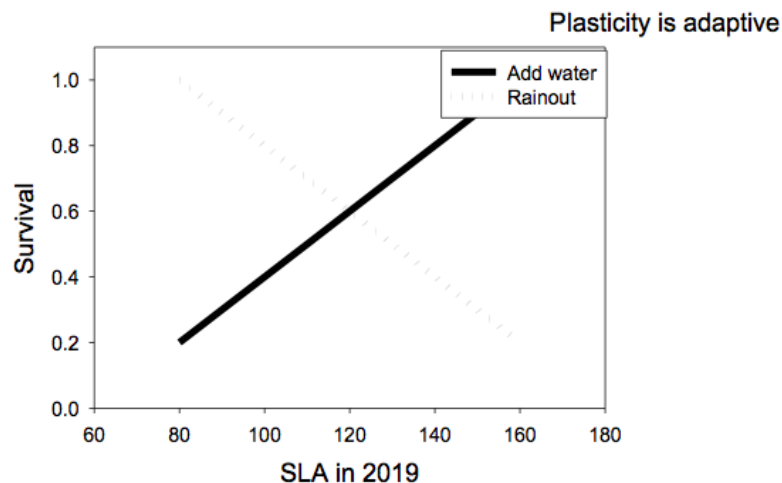


Figure 2: Diagram of Treatments (both Snowmelt and Water) at the Field Site

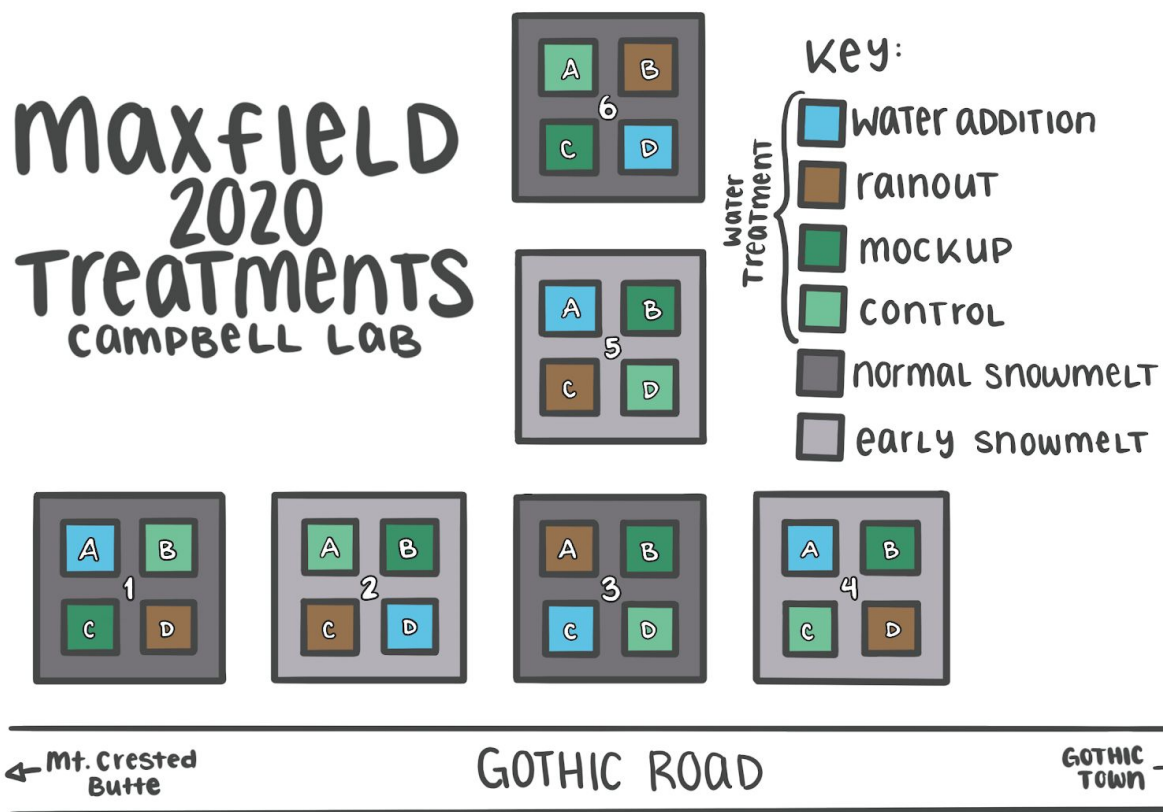


Figure 3: GIS Map of the Field Site and the Corresponding Treatments



Figure 4: Effect of Water and Snowmelt Treatments on Mean VWC (Volumetric Water Content) in the Soil

Error bars indicate standard error across the subplots

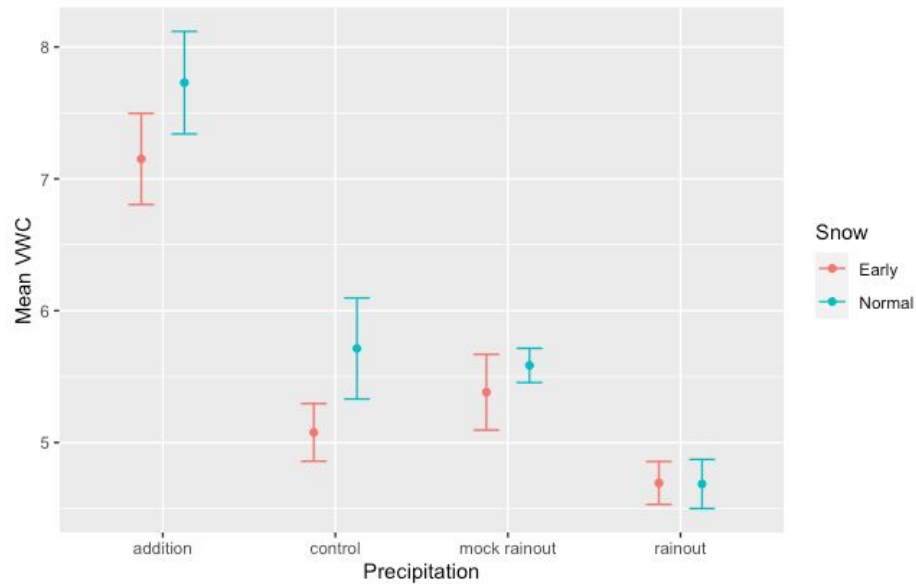


Figure 5: Effects of Water and Snowmelt Treatments on Corolla Width

Error bars indicate standard error across the subplots.

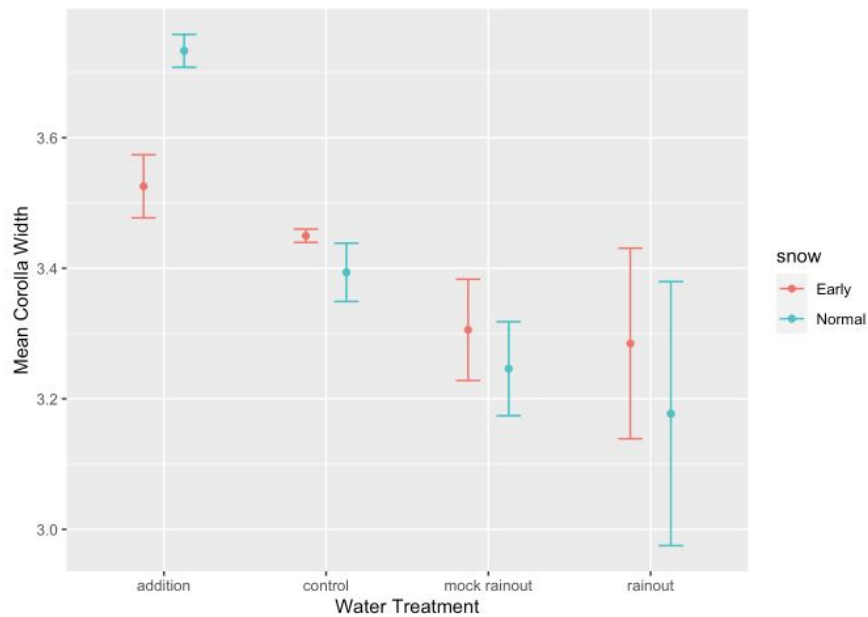


Figure 6: Effects of Water and Snowmelt Treatments on Sepal Width
Error bars indicate standard error across the subplots

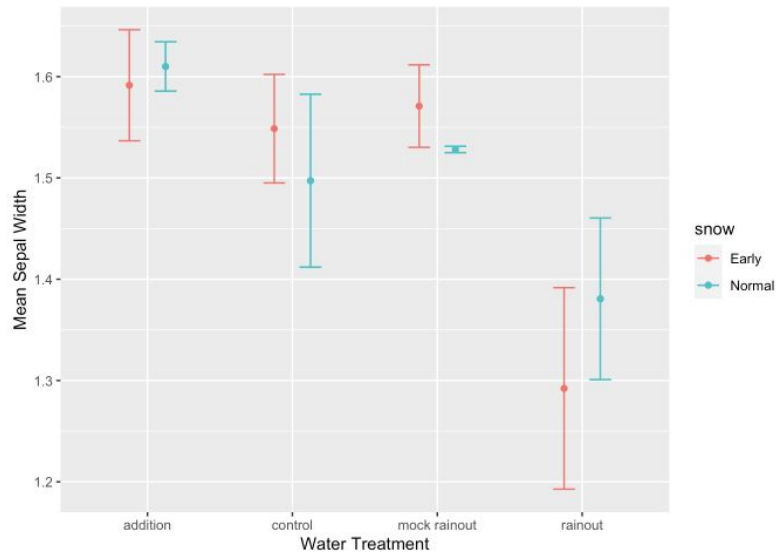


Figure 7: Effects of Water and Snowmelt Treatments on 24 Hour Nectar Production
Error bars indicate standard error across the subplots

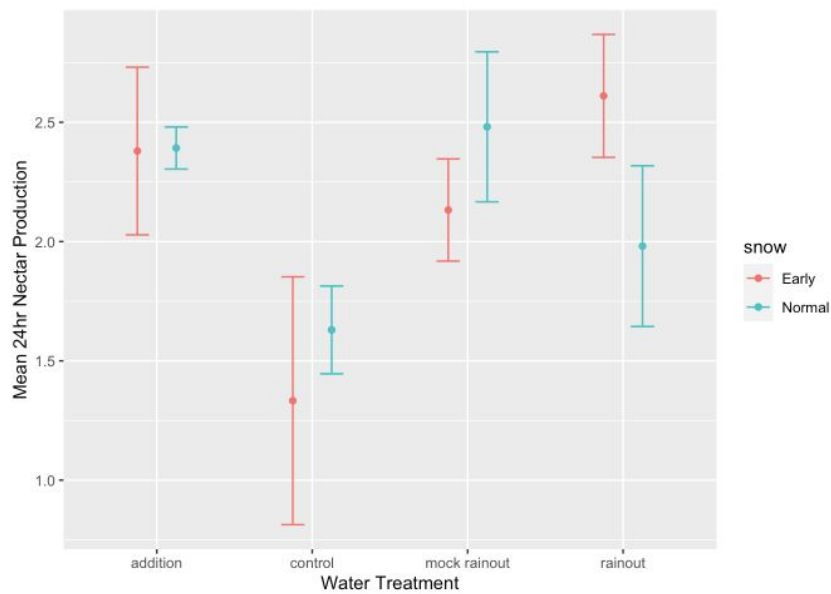


Figure 8: Effect of Water and Snowmelt Treatment on Nectar Concentration
Error bars indicate standard error across the subplots

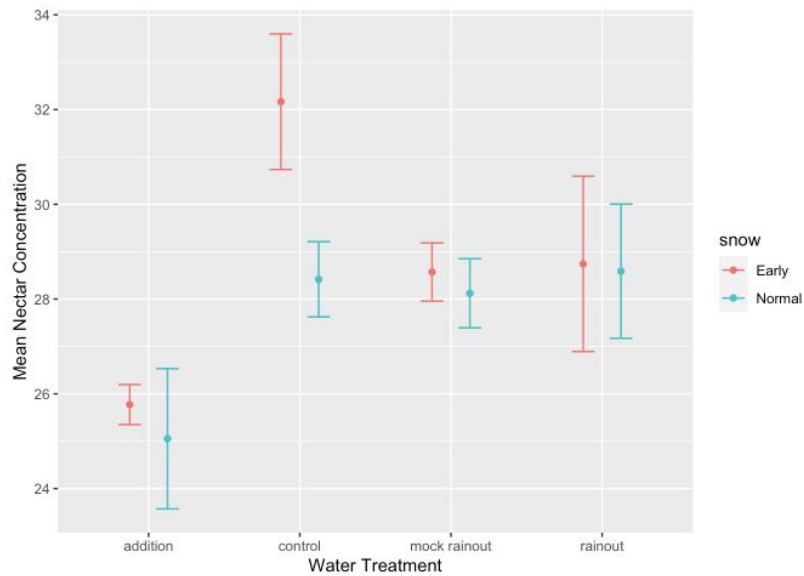


Figure 9: Effect of Trichome Density on Flowering is Dependent on Water

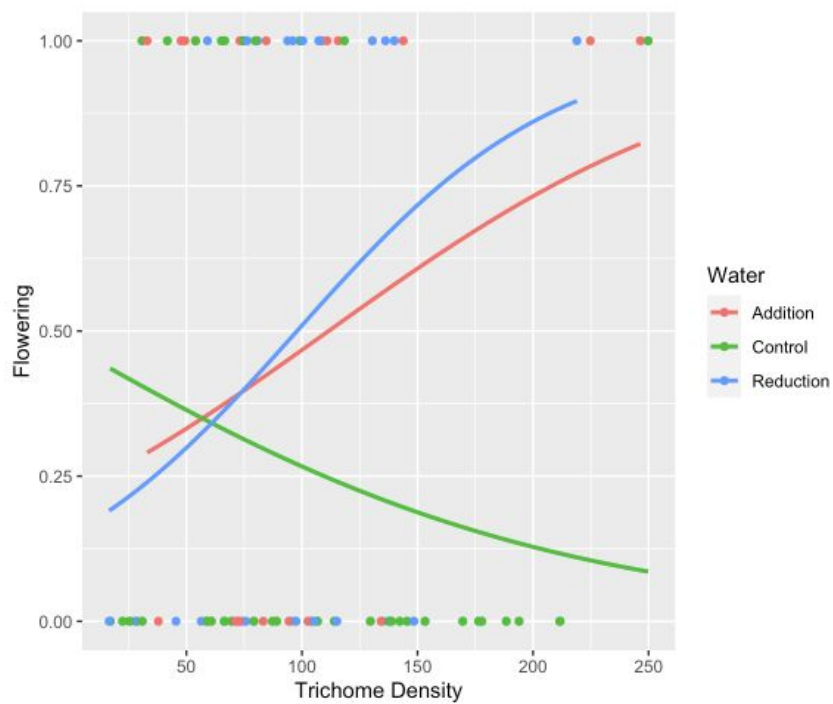


Figure 10: Effect of Water Treatments and Leaf Water Content on Survival

