

The effects of snowmelt date, soil moisture, and precipitation on nectar and floral morphology of *Ipomopsis*

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Abstract

Climate change is putting montane plant species at risk that rely on historical patterns of precipitation and snowmelt timing. Floral traits, such as nectar production and morphology can be impacted by water availability. Hybridization of plants has the potential to provide adaptation to climate change through an increase in genetic variation. This study looked at nectar production and concentration, corolla length, stamen length, and style length in response to snowmelt date, summer precipitation, and soil moisture content. The focus populations included *Ipomopsis aggregata* and hybrids of *Ipomopsis aggregata* and *Ipomopsis tenuituba*. I expected that nectar production, corolla length, stamen length, and style length would decrease as water availability in the soil decreased, while nectar concentration would increase. I also predicted that floral traits would respond less to water availability in hybrids than *I. aggregata* due to their more efficient water usage and occupation of drier, rockier soil. The response of *I. aggregata* was much more stable than the hybrid response to changes in water availability via precipitation. In 2025, average soil moisture was not found to affect average floral traits in specific plants, with all plants experiencing dry conditions. Both nectar related traits and floral morphological traits were not correlated with average soil moisture. Instead, the average nectar production decreased with Julian date as the average nectar concentration increased. Over 15 years, nectar production and concentration responded to summer precipitation, but only minimally to the date of snowmelt. Though 2025 was informative on the plants' responses to changes in water availability, the severe drought conditions may have limited this study's ability to determine the true effects of water availability on floral traits, given the narrow range of soil moisture.

Introduction

Climate change is affecting ecosystems worldwide, and montane environments are not excused from the effects. The average timing of snowmelt in spring is becoming earlier, and

precipitation patterns are changing for the worse, leading to an overall lower water availability for plant communities in some meadows in the Colorado Rocky Mountains (Powers et al., 2022). Floral trait responses of plants to warming temperatures and early snowmelt are informative of a plant species' vulnerability or resistance to extinction caused by a changing climate. Floral traits influence interactions with pollinators, who are often responsible for a plant species' reproduction by transporting pollen to a stigma. It is not entirely clear whether plant populations will be able to respond quickly enough to environmental changes, either through plastic responses or evolutionary change, or a combination thereof. Floral traits can be adaptive, but the same trait values may not be adaptive under changed environmental conditions.

A large factor in many plants' ability to produce a substantial quantity of seeds is the reward for pollinators that transfer pollen between individuals (Campbell et al., 1997; Mitchell, 1993). Nectar production is essential for the production of seeds for many self-incompatible species that require assistance from pollinators to move pollen between plants. Seed production of each year can determine the abundance of newly established individuals in the following year, so it is crucial that enough seeds are produced to maintain a healthy population size. The subalpine plant *Ipomopsis aggregata*, produces fewer seeds with early snowmelt that spring, as well as a reduced survival rate among seedlings, and fewer flowering plants the next year (Campbell, 2019). Nectar concentration can be influenced by water availability and is a factor in pollinator visitation, as are other floral morphological traits, such as corolla length (Powers et al., 2022). Without incentives for pollinators to visit an obligate outcrosser, the fitness of the plant decreases.

Montane species are especially vulnerable to changing environmental conditions, particularly plants as they cannot disperse upward as quickly as other species to remain within their climate envelope. Eventually, a species cannot disperse any higher if it reaches the peak, or runs out of materials found in higher abundance in lower elevations (Patsias & Bruelheide, 2013). Montane environments are often separated by vast stretches of lower elevation, which prevents migration amongst mountains. In the Colorado Rocky Mountains, snowmelt date is advancing and summer precipitation is becoming more variable (Powers et al., 2022), and survival of a population may depend on the ability to adapt to new climatic and environmental conditions (Campbell, 2019; Campbell & Powers, 2015).

Ipomopsis aggregata, a species found in high elevations, is an ideal model plant species to study due to the threat of negative population growth the species is facing, the obligate out-crossing required for seed production, and the ability of this species to hybridize with *Ipomopsis tenuituba* (Campbell et al., 1997; Meléndez-Ackerman, 1997). It is difficult for *I. aggregata* to disperse upwards, due to their seeds dispersing a short distance from the parent plant, which puts them at risk of being left behind by their habitable zone (Patsias & Bruelheide, 2013). There are hybrid populations between the two species that grow at relatively close elevations, with *I. tenuituba* growing about 400 meters higher than *I. aggregata* for the local populations of Poverty Gulch near Gothic, CO (Aldridge, 2005; Campbell et al., 1997, 2022; Meléndez-Ackerman, 1997). *Ipomopsis aggregata* is abundant in Gothic, CO, and surrounding areas. *Ipomopsis* is self-incompatible and requires pollinator visitation to produce seeds, and the local *Ipomopsis* species provide food source incentives for pollinators, most commonly hummingbirds and hawkmoths (Campbell et al., 1997; Campbell & Powers, 2015). Meanwhile, hybrids of both *Ipomopsis* species contain a wider range of genetic diversity that could potentially contain adaptations that are beneficial in a warming, drying climate (Campbell & Wendlandt, 2013). In an experimental setting, lower water availability led to lower nectar production and increased nectar concentrations in *I. aggregata*, as well as reduced corolla length, shorter styles, and shorter anthers. (Powers et al., 2022).

Though it is known that nectar production and other floral traits respond to differential water availability (Powers et al., 2025), it is worth further investigation as well as comparison between *I. aggregata* and hybrid populations to further understand the importance of water relative to other factors in phenotypic expression. Comparing this year's data on nectar with the previous 14 years at the same study sites will allow for analysis of the long term effects of earlier snowmelt and changes in water availability via precipitation and water retention of soil. Previous studies show that water availability is a factor in the phenotypic expression of floral traits (Powers et al. 2022), but they do not address how natural variation in snowmelt affects a hybrid study site in comparison with sites containing only *I. aggregata*, which is a major goal of this project. A changing environment may lead to differential selection on traits, and some traits may be correlated with one another, such as nectar production and corolla length, so a change in one may affect the function of another (Ahrens et al., 2020). Ahrens et al. (2020) found that new selective pressures or independent plastic responses to a changing environment can break

relationships between correlated vegetative traits, so it is worth investigating how floral traits are affected and what correlations may be present amongst them. Some traits may be more plastic while others may show higher heritability, such as vegetative traits and floral morphological traits, respectively (Ahrens et al., 2020; Campbell et al., 2022). On the other hand, antagonistic pleiotropy is a possibility, causing negative effects on other traits if traits are genetically correlated.

The objective of this research is to evaluate how natural variation in soil moisture due to changes in snowmelt date and precipitation influence floral morphology and nectar production. This project is part of a two-decade long project on how the expression of plant traits and natural selection on those traits are changing with the trend towards earlier snowmelt in the spring. One approach is to evaluate relationships between the plant floral traits and soil moisture during 2025. A relationship between a plant trait and soil moisture suggests phenotypic plasticity of the trait. A second approach will be to combine this year's data with data from previous years at the same sites to see if average nectar production and floral size are lower in years of earlier snowmelt or lower summer precipitation. Longer scale changes, if seen, could be due either to plasticity or to evolutionary change, indicating that earlier snowmelt and changes in precipitation have altered natural selection (Campbell & Powers, 2015).

Thus the two main questions addressed are: Are nectar production, nectar concentration, corolla length, style length, and stamen length correlated with soil moisture? Are these traits affected by snowmelt date or summer precipitation in a given year, and are the responses different for *I. aggregata* and hybrids? I hypothesized that with lower water availability, nectar production, corolla length, style length, and stamen length will decrease as nectar sugar concentration increases due to a lower water content in the nectar. I also hypothesized that hybrid populations will have a less dramatic response to water availability. Changes in these floral traits and rewards could negatively impact pollination; for example reduced nectar production could reduce hummingbird visitation (Campbell et al., 1997; Meléndez-Ackerman, 1997; Mitchell, 1993).

Methods

Study site

This research took place in 3 study sites within the Gunnison National Forest of Colorado. The first is found just outside of Gothic at Vera Falls, containing an *I. aggregata* population. The remaining two sites are located at Poverty Gulch, where one site contained *I. aggregata* at 2900 m and the other contained hybrids of *I. aggregata* and *I. tenuituba*. The latter of the two sites was at a slightly higher elevation, as *I. tenuituba* grows above *I. aggregata* at 3100 to 3250 m at this location, so the hybrids live in between the two species' elevational range (Campbell, 2019). These study sites were a part of a greater research project conducted by Dr. Diane Campbell that has lasted two decades, and the data collected in this project contributed to the growing data set.



Figure 1: Locations of all three sites (top left) and individual plants at Vera Falls (top right), the hybrid site (bottom left) and the Poverty Gulch *I. aggregata* site (bottom right)

Study system

Ipomopsis aggregata is an obligate out-crossing plant species that grows in a vegetative stage for five years on average in the region of Gothic, CO, before flowering, then senescences. *I. aggregata* generally does not disperse seeds further than one meter. Gene flow is limited among populations due to that limited seed dispersal and because the pollinators have small feeding territories (Campbell 1991). *I. aggregata* is known to hybridize in nature with *I. tenuituba* as well, and one hybrid population in Poverty Gulch underwent the same tests as the two *I. aggregata* populations at Vera Falls and Poverty Gulch.

Surveying and Tagging Plants

The first step of this research was to survey *Ipomopsis* plants that were previously marked, and determine how many new plants were needed to replenish the sample size. Approximately 30-50 flowering plants were selected for each study site. Plants were tagged with a specific ID, and a flag was added for ease of finding and to prevent damage to each plant.

Nectar Collection and Concentration Analysis

To measure nectar, elongated buds were covered with a small piece of plastic straw before they fully opened in the morning, and the straw was secured with a zip tie. After 48 hours, the straw was removed and the corolla tube was pulled off. Then, a standardized 32 mm long microcapillary tube that can hold 5 uL was placed into the rear end of the corolla to extract the nectar, and a ruler was used to measure the volume of nectar in the tube. Next, the nectar was blown onto a refractometer to determine the sugar percentage. If the microcapillary tube reached full capacity, it was placed back into the corolla to collect any remaining nectar and the total nectar production was recorded as millimeters for data analysis. The total nectar production over 48 hours was calculated by multiplying the millimeters achieved in the microcapillary tube by 5 ul/(2 days x 32 mm) (Campbell & Powers, 2015). Nectar was measured on the following dates: 6/19/2025, 6/25/2025, 7/2/2025, 7/9/2025, and 7/24/2025 at Vera Falls, 7/3/2025, 7/10/2025, 7/25/2025, and 7/31/2025 for the *I. aggregata* site of Poverty Gulch, and 7/18/2025, 7/25/2025, and 7/31/2025 for the hybrid site of Poverty Gulch.



Image 1, 2, and 3: Nectar Trapping, Sugar Concentration Measurement, and Refractometer

Soil Moisture Testing

A six inch soil moisture probe inserted into the soil directly adjacent to the base of each plant was used to collect the volumetric water content (VWC) when nectar and morphological traits were collected from the flowers.

Corolla Length, Style Length, and Anther Length Measurement

Calipers were used to measure the corolla length from the base of the calyx in millimeters, as well as style and the longest and shortest stamen lengths. The flower was removed for each measurement, and the corolla was split to measure the shortest stamen, and the style if it did not reach past the corolla opening.

Statistical Analysis

For the 2025 data, we first analyzed changes over the season in nectar production and concentration using a repeated measures analysis, implemented as a mixed model with site as a fixed factor, individual plant as a random factor, and Julian date as a continuous variable. Then to test for responses of individual plants to changes in soil moisture, we repeated the mixed model except using soil moisture as a continuous variable instead of Julian date. To examine microspatial variation and see if plants in wetter soil had higher nectar production or changes in other traits, we first averaged each trait for a plant. Then we ran a linear model with the fixed effect of site and the continuous variable of average soil moisture for that plant. Combining the 2025 data with that from previous years since 2010, we performed a general linear model for

year and site for the average of the trait as a function of date of snowmelt, summer precipitation, and site (*I. aggregata* versus hybrid). The date of snowmelt each year was acquired from billy barr's yearly data collection at <https://www.gothicwx.org/long-term-snow.html>, and summer precipitation was acquired as the total over June and July from the same website.

Results

When examining repeated flowers across the season to observe trends across dates, and controlling for the individual plant, the Julian date had a strong effect on both nectar production and concentration (both $P < 0.001$). Nectar production was shown to decrease by 0.03666 ul per day as the season progressed, while nectar concentration increased (Figures 2 and 3, respectively). All sites share the average decrease in nectar production per day. These seasonal changes are not, however, well-explained by soil VWC. When examining nectar production and concentration of repeated plants in specific sites in relation to VWC, there was no significant effect on nectar production ($P = 0.455$) (Figure 4). Nectar concentration was mostly unaffected by changes in VWC ($P = 0.091$) (Figure 5).

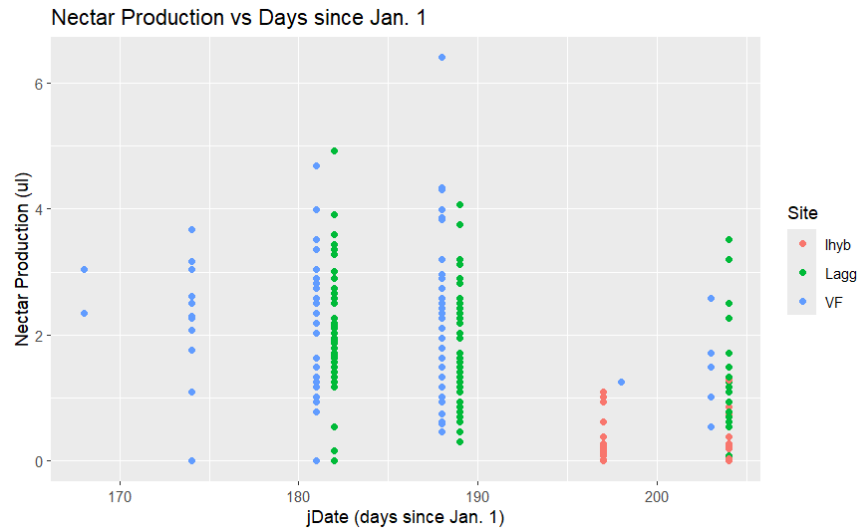


Figure 2: Nectar production versus days since Jan. 1, where each dot represents measures for an individual plant on a specific day in which the nectar production was measured. Red represents the hybrid site of Poverty Gulch, containing hybrid plants. Green represents *I. aggregata* plants within the *aggregata* site of Poverty Gulch. Blue represents *I. aggregata* plants within the Vera Falls site.

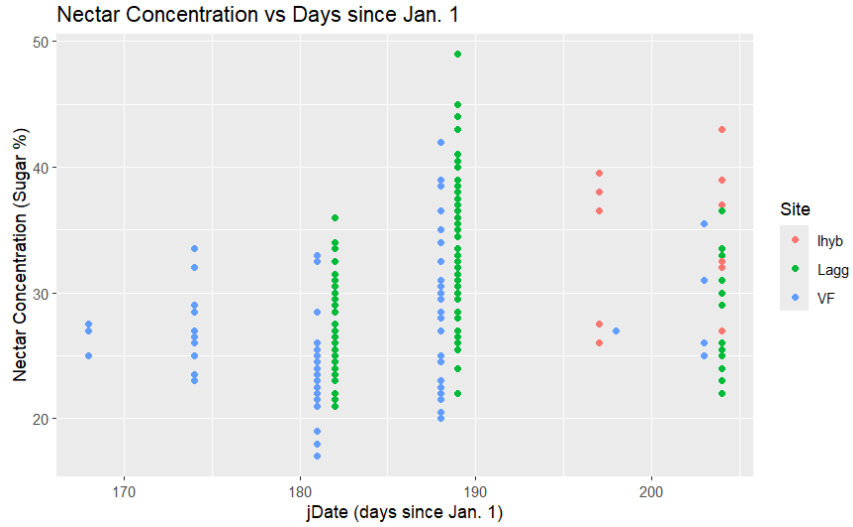


Figure 3: Nectar concentration versus days since Jan. 1, where each dot represents an individual plant on a specific day in which the nectar concentration was measured. Orange Red represents the hybrid site of Poverty Gulch, containing hybrid plants. Green represents *I. aggregata* plants within the *aggregata* site of Poverty Gulch. Blue represents *I. aggregata* plants within the Vera Falls site.

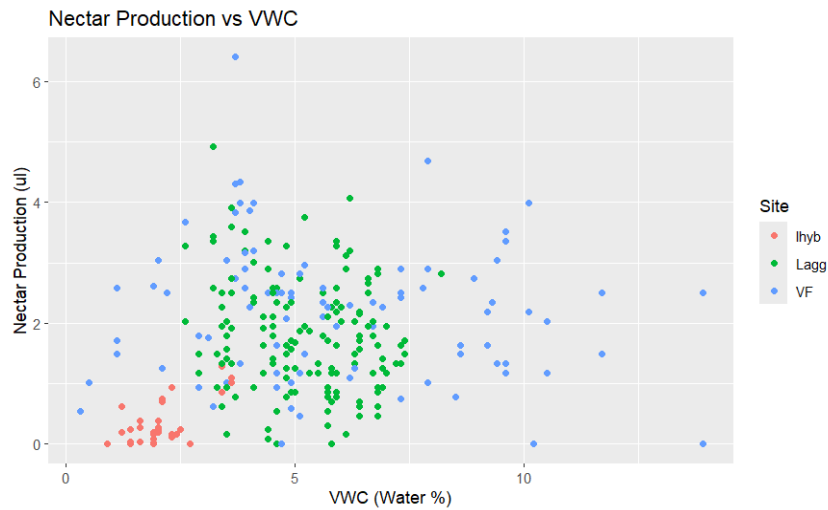


Figure 4: Nectar Production versus VWC for repeated measures on plants. Each dot represents an individual plant, and the color of the dot correlates with the site it was found in. Red represents the hybrid site of Poverty Gulch, containing hybrid plants. Green represents *I. aggregata* plants within the *aggregata* site of Poverty Gulch. Blue represents *I. aggregata* plants within the Vera Falls site.

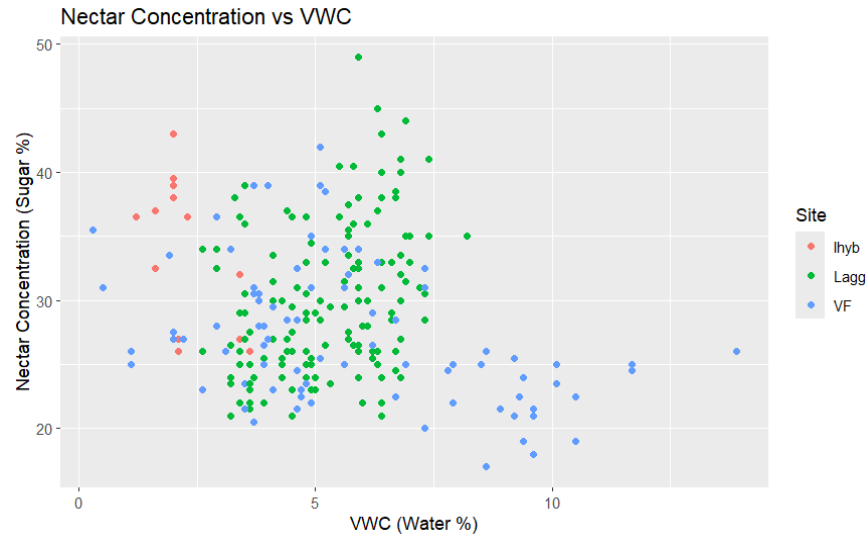


Figure 5: Nectar concentration versus VWC for repeated measures on plants. Each dot represents an individual plant, and the color of the dot correlates with the site it was found in. Red represents the hybrid site of Poverty Gulch, containing hybrid plants. Green represents *I. aggregata* plants within the *aggregata* site of Poverty Gulch. Blue represents *I. aggregata* plants within the Vera Falls site.

Soil moisture content (VWC) showed little to no effect on mean floral traits for individual plants. There was not an effect of the average VWC on the average nectar production values ($P = 0.407$). The shallow slopes in Figure 6 do not express much change with VWC, especially for *I. aggregata* plants. The same was true for nectar concentration ($P = 0.535$, Figure 7).

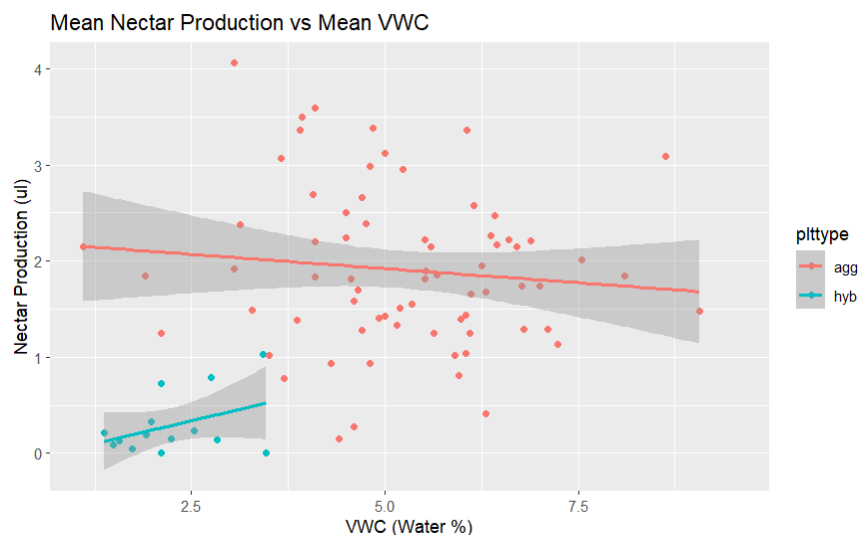


Figure 6: Mean nectar production versus mean VWC for each type of plant. The red dots represent *I. aggregata* plants' nectar production in relation to VWC, while the blue dots represent hybrid plants' equivalent values. The corresponding lines show the trend of each plant type, where the *aggregata* site of Poverty Gulch and the Vera Falls site values are joined together.

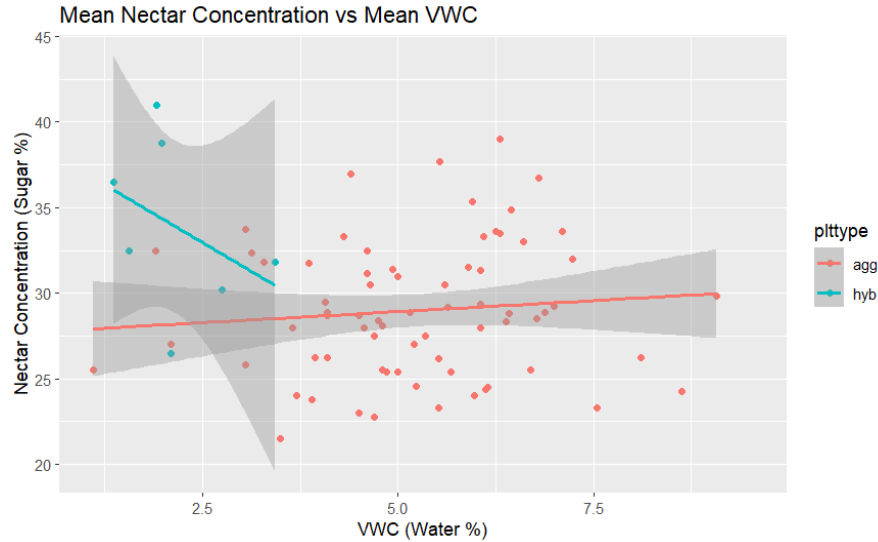


Figure 7: Mean nectar concentration versus mean VWC for each type of plant. The red dots represent *I. aggregata* plants' nectar concentration in relation to VWC, while the blue dots represent hybrid plants' equivalent values. The corresponding lines show the trend of each plant type, where the *aggregata* site of Poverty Gulch and the Vera Falls site values are joined together.

The remaining mean values of floral morphological traits showed little to no correlation with the mean VWC (all $P > 0.05$; Fig. 8). For style length, there was only a significant trend within the *I. aggregata* populations ($P = 0.087$), but the hybrid population did not show any trend ($P = 0.300$).

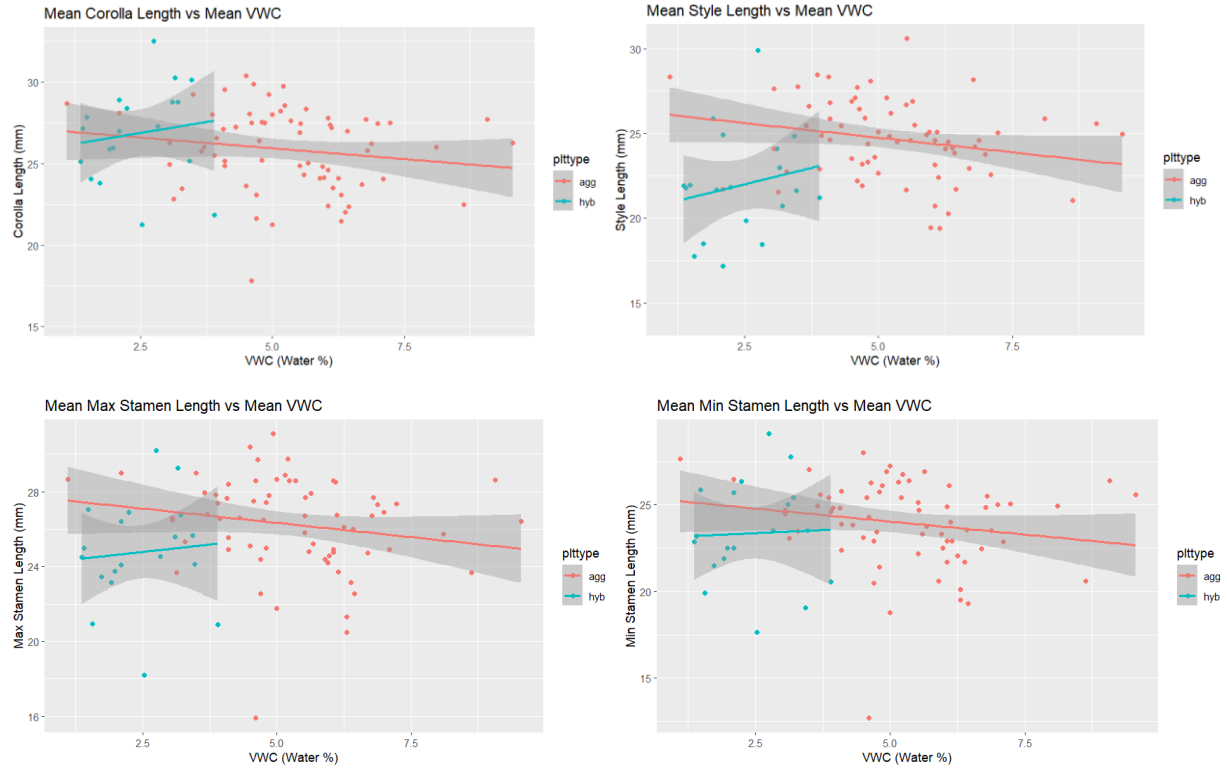


Figure 8: The average value for each floral morphological trait versus the average VWC. For each graph, the red dots represent *I. aggregata* plants in both Vera Falls and Lagg sites, and the blue dots represent hybrids of the Ihyb site. The corresponding lines indicate the relationship between the variables of each figure.

For the long-term data since 2010, summer precipitation, but not snowmelt date, strongly influenced average nectar production for a given site and year ($P < 0.001$), with the hybrid population being the most responsive (Figure 9). Snowmelt had no significant effect on nectar production ($p = 0.561$). 2015 was removed from the dataset, due to a small sample size ($N = 2$ plants) collected in that year, and there were no data for 2016.

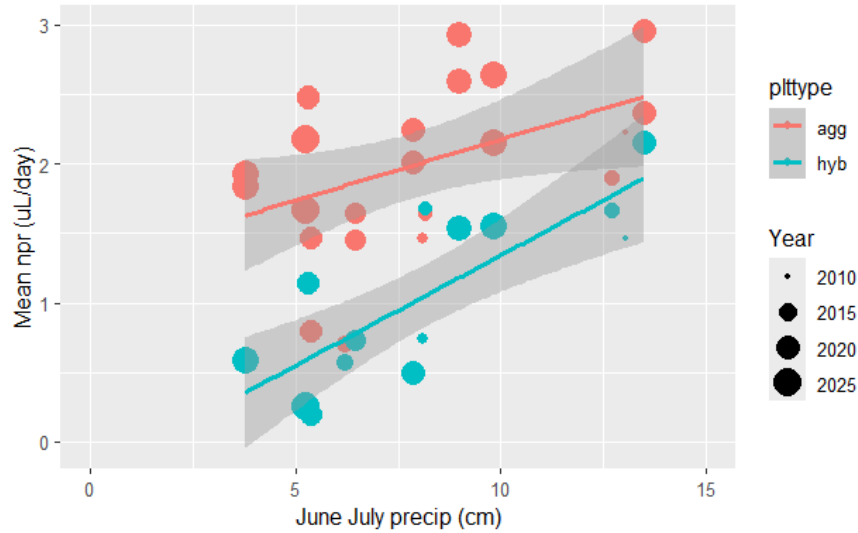


Figure 9: Nectar Production versus June-July Precipitation per year since 2010. For each year, the mean nectar production is plotted with the average precipitation between the months of June and July. Red dots represent *I. aggregata* nectar production averages, while blue represents the hybrid nectar production averages. The corresponding lines show the trends between precipitation and nectar production for the last 15 years.

Discussion

The floral traits under observation varied in their response to water availability, and the hybrid and *I. aggregata* populations differed from one another as well. Soil moisture content did not explain plant to plant variation in floral traits in 2025, except for a trend for style length to decrease with soil moisture specifically in the *I. aggregata* populations (Figure 8). There was no significant effect of the mean VWC on the mean nectar production of plants. However, nectar production decreased 0.03666 ul/day and nectar concentration increased over the season. On a longer time scale, nectar production increased with summer precipitation, especially in the hybrid population. The date of snowmelt had a negligible effect on nectar production and concentration in this study.

The *I. aggregata* plants had a different response to water availability via precipitation than was predicted in the hypothesis. It was expected that hybrids would have less of a response to changes in water availability, while *I. aggregata* would be more variable. The opposite was found to be true, where the *I. aggregata* remained more stable in their nectar production than hybrids. What was even more surprising was how little they responded to changes in water

availability across 15 years. The hybrid population has genetic variation from two parent populations of *I. aggregata* and *I. tenuituba*, and if there has been selection for gene combinations that confer high survival under its normally dry conditions, it might be expected that the hybrids would be less variable in their response to changes in water availability. The *I. aggregata* populations show incredible resistance to drought conditions, which will be useful to them as climate change causes droughts to become more common.

Overall, both hypotheses were not supported by this experiment, except for precipitation over the long term analysis, but the findings were still very informative of how the *Ipomopsis* populations respond to environmental conditions in the region surrounding Gothic, CO. This year, 2025, was one of the lowest precipitation (5.2 cm across June and July) and earlier snowmelt years (Julian date = 124) within the long term analysis. It is possible that with a greater range of VWC within the soil throughout the season, the floral traits would have a noticeable response to changes in water availability in the soil, which was found to be the case in past studies conducted in the same area, and occasionally the same study sites. It is also possible that a longer term study, such as Waser et al (2016) or Powers et al (2022), is necessary to determine the true effects of soil moisture on floral traits.

In an experiment with rainouts and manipulations of snowmelt timing by Powers et al (2022), soil moisture influenced nectar production and floral morphological traits. Their study did not address how a natural population would be affected, nor how hybrid populations respond in comparison to *I. aggregata* populations. Powers et al (2022) also compared water availability via precipitation over three years, and found that corolla length, style length, and nectar production were higher in the presence of higher summer precipitation, while nectar concentration was lower. Their findings support the hypotheses of this paper, but it is worth noting that their experiment was done in a manipulated setting, while this study was conducted in a natural setting. Early snowmelt is a leading cause for lower soil moisture (Powers et al., 2022), and with a lack of summer precipitation this year, there was not much water input into the soil during the time of this study. Powers et al (2022) found that reduced soil moisture, independent of precipitation, leads to the same result as reduced precipitation, with nectar production being the most affected by soil moisture content of all floral traits. Within the three years of their study, 2018 had the lowest average VWC, while 2020 had the highest average VWC, but all three years had a higher average than 2025 for this study. Another study on the effects of soil moisture and

precipitation on *I. aggregata* by Waser et al (2016) included 6 years of soil moisture data within unmanipulated sites and found that nectar production increased with soil moisture. Their study, however, included more variability in average VWC, reaching above 12% and never below 2.7%. This year's study saw VWC values below 2.7%, sometimes reading 0%, and never near 12%. These studies did not test the effects of soil moisture on all floral traits in question in this research, so it would be worth experimenting for a longer period of time with the same traits, in hopes of collecting data during several years not experiencing a drought..

In an experiment conducted by Suni et al (2020), nectar production and concentration, among other floral traits, were examined under a treatment of dry conditions for *Phlox drummondii* from several populations. They found that nectar production was higher in arid plants adapted to dry conditions than those adapted to wetter conditions in the long-term. They also found that heritability was lower for water-limited populations than those with more access to water within the soil (Suni et al., 2020).

This study was not designed to distinguish between phenotypic plasticity and natural selection as causes for responses of nectar production to water availability or summer precipitation. A future experiment could do so by growing sibling plants under different water conditions and seeing if plants from the same sibling family tend to produce more nectar under wetter conditions than those under dry conditions. Either phenotypic plasticity or phenotypic selection may aid a population in persisting under a changing climate. Plasticity is the range in which a phenotype can be expressed in response to environmental conditions, and this can be beneficial in a changing environment if an advantageous phenotype is within the range of expression. Selection also has the potential to rescue a population, because advantageous alleles will increase in frequency. Both selection and plasticity are present to varying degrees with floral traits (Harder & Johnson, 2009; Powers et al., 2022, 2025).

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