Water Availability and Selection for Vegetative Traits in *Ipomopsis*

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Abstract

Climate change is causing more extreme temperature and precipitation fluctuations in alpine and subalpine ecosystems, including more frequent periods of drought, which can place significant stress on plant populations. An understanding of how different traits can influence fitness in plant species is key to plan for the future of these ecosystems. This study focuses on vegetative traits of *Ipomopsis* (*aggregata* and hybrids with *tenuituba*) in Gunnison county. Leaf traits of trichome density, specific leaf area (SLA), and leaflet density were analyzed for their impact on plant growth over the summer. At the lower aggregata site ("agg") a negative relationship was found between trichome density and growth, and a positive relationship was found between leaflet density and growth. SLA was also analyzed for change over the past 17 years. A positive relationship was found between SLA and year, independently of the positive relationship found between SLA and melt day.

Introduction

Climate change poses a great threat to ecosystems throughout the world. In comparisons of the current rate of species loss with the background rate, even conservative estimates of species loss show loss at a rate eight to ten times faster than expected (Ceballos et al., 2015). Future climate projections, even those of lesser severity, suggest large-scale species loss is likely (Thomas et al., 2004). One of the main factors affecting persistence of a species is its ability to evolve to keep up with changing environments. While there is some evidence that species can evolve to climate-related changes (Campbell et al., 2025), whether they can keep pace with climate change is uncertain (Martin et al., 2023).

To understand the scale of biodiversity loss, efforts must be made to understand if and how species are evolving with climate change (Berteaux et al., 2004; Visser, 2008). One of the first steps in doing so is to determine if traits are under natural selection imposed by the new environmental conditions.

Alpine and subalpine ecosystems can be especially sensitive to climatic changes (Lamprecht et al., 2018). Organisms living in these environments tend to be adapted to cold temperatures, deep winter snowpack and therefore often grow slowly and live longer (Lamprecht et al., 2018). This makes alpine and subalpine organisms excellent candidates for studies of long-term changes, including those influenced by climate change (Lamprecht et al., 2018).

Within these ecosystems, plants are some of the most important organisms to study, as they are foundational components of the ecosystem with great implications for other organisms if shifts are occurring. Of plant species in Gunnison county, *Ipomopsis* is one of the most well-studied genera. *Ipomopsis aggregata* and *tenuituba* are subalpine plants that hybridize in the mountainous regions around Gunnison County, Colorado (Grant & Wilken, 1988). *Ipomopsis* is a moderately long-lived plant, and somewhat unique in that it remains as a vegetative rosette for an average of 5 years at our study sites before flowering in one year and dying (Campbell and Waser, 2007). The year 2026 has had the lowest snowpack in Rocky Mountain Biological Laboratory's (RMBL's) recorded history and follows a series of similarly near-record-low dry years (barr, n.d.). Colorado has also seen many of its highest temperatures on record within the last twenty years (barr, n.d.). These patterns align with broader global patterns of climate change, including predicted stretches of prolonged drought (Dai, 2011) and elevated global temperatures (Lindsey, R., & Dahlman, L., 2020). *Ipomopsis aggregata* has adaptive responses to changes in climate including water availability and snowmelt date (Navarro et al., 2022) and potentially

even evolutionary responses via directional selection (Campbell et al., 2022, 2024; Campbell & Powers, 2015). However, there has been limited exploration of vegetative traits other than specific leaf area (SLA = area / dry mass) and trichome density (Campbell et al., 2024; Campbell & Powers, 2015; Navarro et al., 2022). For these previously studied traits, this year presented a unique opportunity to study extreme drought.

An understanding of which traits influence the fitness components of *Ipomopsis* is the first step toward understanding how natural selection is taking place in this plant. This can inform future studies of evolution, including changes in relation to climate change. Lower SLA is selected for in years with earlier snowmelt (Campbell et al. 2024). Low SLA and high trichome density may help retain more water and regulate the leaves at cooler temperatures (Ehleringer & Mooney, 1978; Navarro et al., 2022; Poorter et al., 2009). With an understanding that these traits are beneficial in drought years, 2026 presented an opportunity to see how variation in SLA and trichome density affect growth in *Ipomopsis* in an extreme low snow year. Another trait which has not been studied which may impact drought resilience in *Ipomopsis* is leaflet density. *Ipomopsis* has compound leaves, with varying leaflet densities among leaves and individual rosettes. There is relatively little research available on the effects of leaflet density, but there is some evidence that leaflets and leaflet density can affect the microclimate in the space above and around the leaf (Parkhurst & Loucks, 1972). A basic knowledge of physics also supports this; more leaflets will generally increase the surface area of a leaf, allowing for additional cooling effects but potentially also greater space for water loss.

This research seeks to understand what traits have an impact on the growth and survival of vegetative *Ipomopsis* plants in an extreme low snow year. Additionally, I compare SLA in 2026 to older values dating back to 2009 in Campbell et al. (2025). I evaluated the following questions:

1. Is there a difference in growth among *Ipomopsis* at various sites based on trichome density, SLA, and leaflet density? Previous studies have used survival to the next year as a measure of fitness rather than summer growth, but those data are not yet available, so growth was used here.
2. Has SLA changed over the past 17 years in these populations of *Ipomopsis*?

My predictions were as follows:

1. *Ipomopsis* rosettes with greater leaf trichome density, lower SLA, and lower leaflet density will have higher rates of growth, because trichomes create a cooler microclimate above the leaf and slow evapotranspiration; lower SLA decreases the surface area for evaporation; and decreased leaf surface area will present less opportunities for water loss during drought.
2. Specific leaf area will show a decrease from 2009-2026 because lower values are selected for, the trait shows heritability, and it is plastic with lower values in dry years (Campbell et al., 2022, Campbell et al. 2025, Campbell et al., n.d.).

Specific Methodologies

Study Sites:

This study was conducted at three different sites around Gunnison County. Two sites are accessed from Poverty Gulch, a lower site of *Ipomopsis aggregata* at about 2900 m (hereafter *agg*) and a higher site with hybrids between *aggregata* and *tenuituba* at about 3050 m (hereafter *hyb*). The third site is the lowest, located at Vera Falls near the Gothic townsite. These sites were selected in order to gain data from a variety of plants in different elevations, locations, and conditions, as well as for continuity of long-term data with previous research by Dr. Diane Campbell and others.

Field Processes:

This study used previously tagged vegetative rosettes from years before, as well as newly tagged rosettes to keep the sample size large (as some rosettes are lost yearly and some progress to the flowering stage). Only single rosette plants were newly tagged. Plants were marked with a uniquely numbered metal disc, and flagged with a blue flag to identify the location of the vegetative rosette. The sample size for 2026 in the lower *agg* site was 50 plants, 24 in the hybrid site, and 32 at the Vera Falls site.

Two main surveys were conducted, one at the beginning of the summer (June 17-23) and one at the end of the summer (July 27-28) to determine whether the plant survived over summer and how much it grew. As effects on survival may not show up until winter, the Campbell team will also determine survival to next summer. In each survey, all living tagged vegetative plants were counted for rosette number, leaf count per rosette, and longest leaf measurement for each rosette. Soil moisture readings of volumetric water content (VWC) were also taken at each site using a Campbell Hydrosense II 6-inch probe. Leaf measurements were made using a ruler, to the nearest 0.5 millimeter. One leaf per plant was collected in each survey and taken back to the GRC lab at RMBL; leaf collections were done by hand by pinching the leaf off at the very base of the leaf.

A replicate census was also conducted at the Vera Falls site only on July 2, with an additional leaf sample and soil moisture reading for each plant in order to measure repeatability of leaf traits on the same plant. Growth was measured as the percent change in size, where size is defined as total number of leaves x length of the longest leaf (averaged across rosettes if more than one).

Post-Collection Processing

Collected leaves were taken back to the lab, scanned at 600 dpi, and measured for wet weight and dry weight to calculate SLA. Scans were done using a flatbed scanner. Weights were taken using a microbalance reading to 0.00001 g. To ready the leaves for dry weight, they were heated in a drying oven for two hours at 70 degrees Celsius.

From the scan, we looked at trichome density and leaflet density. Scans were viewed with the computer program ImageJ and using the multi-point tool, the number of trichomes per leaf were manually counted. Leaflets were also manually counted using ImageJ, and leaf length, leaflet length, and leaflet width were also taken using this program.

The independent variables measured were trichome density (number per area in cm^2), leaflet density (number per length in cm), and specific leaf area (area / dry mass). The response variables were growth and survival of the rosettes over the course of the summer, and for the second question, population-wide average SLA.

To answer question 1, I first found the average trait value for each plant. I also calculated repeatability of each trait at each site to ensure that the leaves collected presented a good representation of the plant as a whole. For each trait, I used a model with the fixed effect of the numeric value of date and the random effect of plant and found the percentage variance component for the plant effect. Date was included to allow for potential systematic changes in trait values across the summer. A repeatability score of zero indicates highly inconsistent traits; this would mean that a leaf from one individual is no more likely to have certain traits than another leaf from a random individual. A repeatability score of above zero (up to 100%) indicates the level of repeatability. Higher scores indicate more consistent traits by individual. Correlations between average trait values for plants were obtained as Pearson correlation coefficients. Then, I regressed growth against each trait for a plant (SLA, trichome density,

leaflet density), including population as a factor in the model, for the single-summer comparisons. Since each trait and plant growth was measured at all three sites, it is important to check if there is an interaction between trait and site on growth. The model was first run to test for an interaction with site for each trait; if significant, then the slope of trait on growth was estimated nested within the site; if non-significant, the interaction was removed and the model was run for the overall relationship between trait and growth.

To answer question 2, I first averaged SLA for each combination of population and year. Then I regressed mean SLA on year. To determine if any change over years could be explained by a trend in snowmelt, I also performed a multiple regression of mean SLA on year and snowmelt day in the spring. To obtain the snowmelt day, I used billy barr's weather data from https://www.gothicwx.org/ .

Results and Discussion

Question 1: Repeatability and trait correlations

The tests of repeatability verified that there are strong levels of repeatability within *Ipomopsis* rosettes for each trait (Table 1).

The strongest correlations found were between leaflet density and soil VWC (a positive relationship of 0.32, $p = 0.001$) and trichome density and SLA (a negative relationship of -0.27, $p = 0.005$). All other correlations between traits of individual plants or between a trait and soil VWC had an absolute value of 0.10 or less.

Table 1: Repeatability measurements for leaf traits at each site. Repeatability was obtained as the plant variance component in a model that also included the numeric value of date. All effects of plant were statistically significant ($P < 0.05$) except that for leaflet density at Vera Falls.

Site	SLA	Trichome Density	Leaflet Density
Vera Falls	60.4%	49.8%	7.1%
Lower aggregata (agg)	33.3%	48.74%	34.4%
Hybrid (hyb)	54.3%	53.4%	39.1%

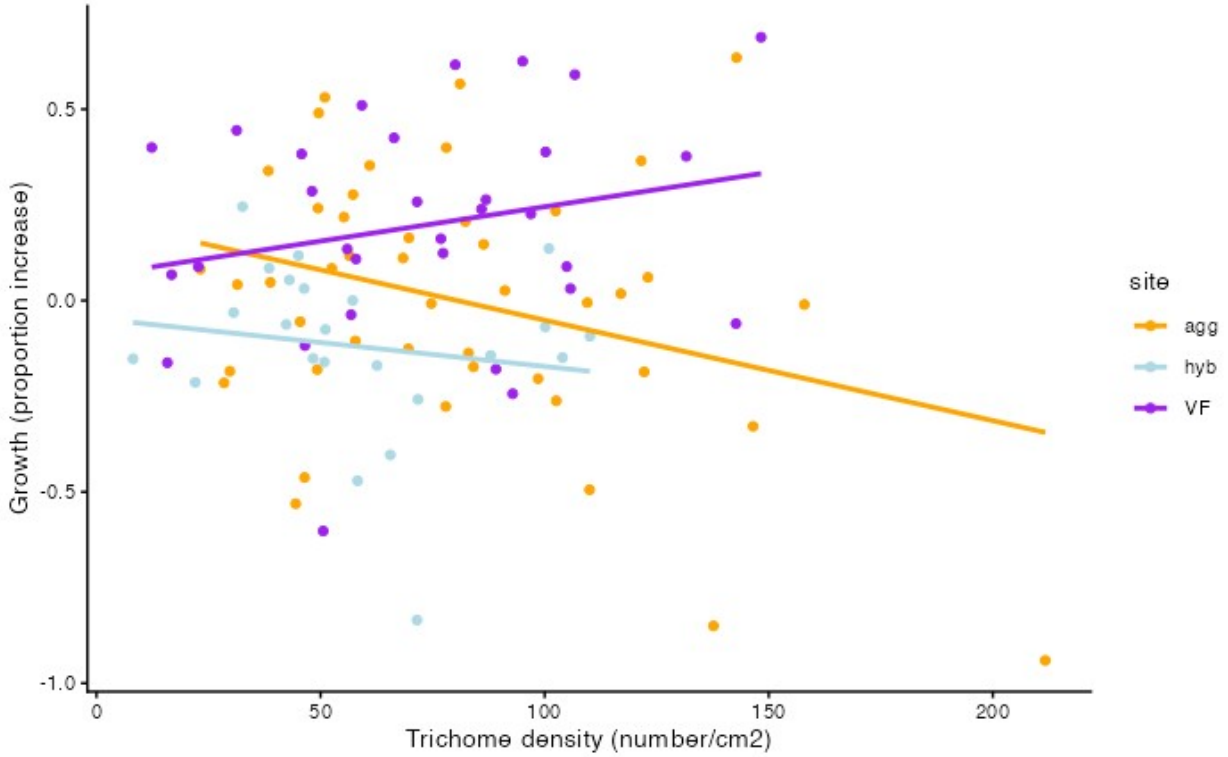
Question 1: Effects of traits on summer growth

There was not a significant interaction of site and SLA on growth. There was no overall effect of SLA on growth ($p = 0.94$).

The interaction between effects of site and trichome density on growth was marginally significant ($p = 0.067$), so I calculated the slope of growth on trichome density separately at each site. At the *agg* site, growth declined with higher trichome density ($p = 0.0201$; Fig. 1).

At the *hyb* site and Vera Falls site, there were no detectable effects of trichome density on growth ($p = 0.59$, $p = 0.24$ respectively).

Figure 1: The relationship between growth and trichomes per leaf area at each of the three sites. Each dot represents an individual plant. Each line represents the slope at a particular site.



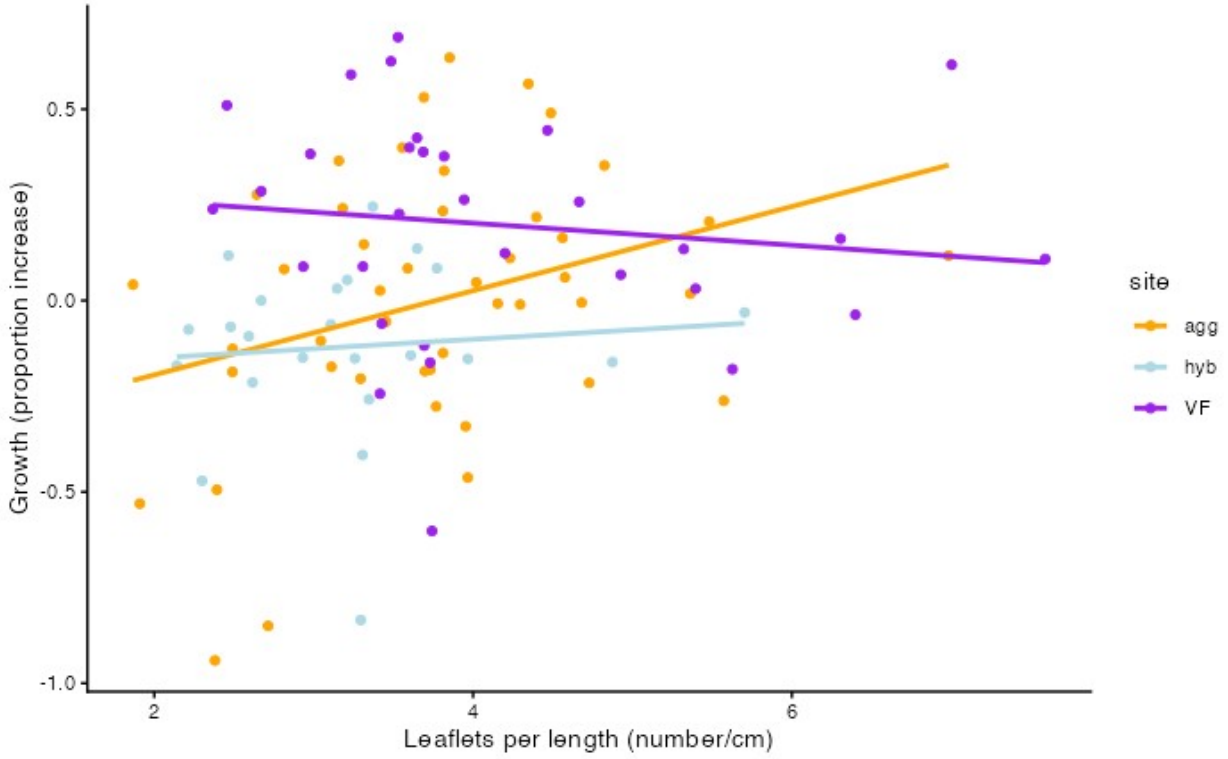
Leaflet Density

The interaction between site and leaflet density was marginally significant ($p = 0.074$), so I calculated the slopes separately at each site.

At the *agg* site, growth increased with higher leaflet density ($p = 0.014$).

At the *hyb* site and Vera Falls site, there was no detectable effect of leaflet density on growth ($p = 0.75$, $p = 0.48$ respectively).

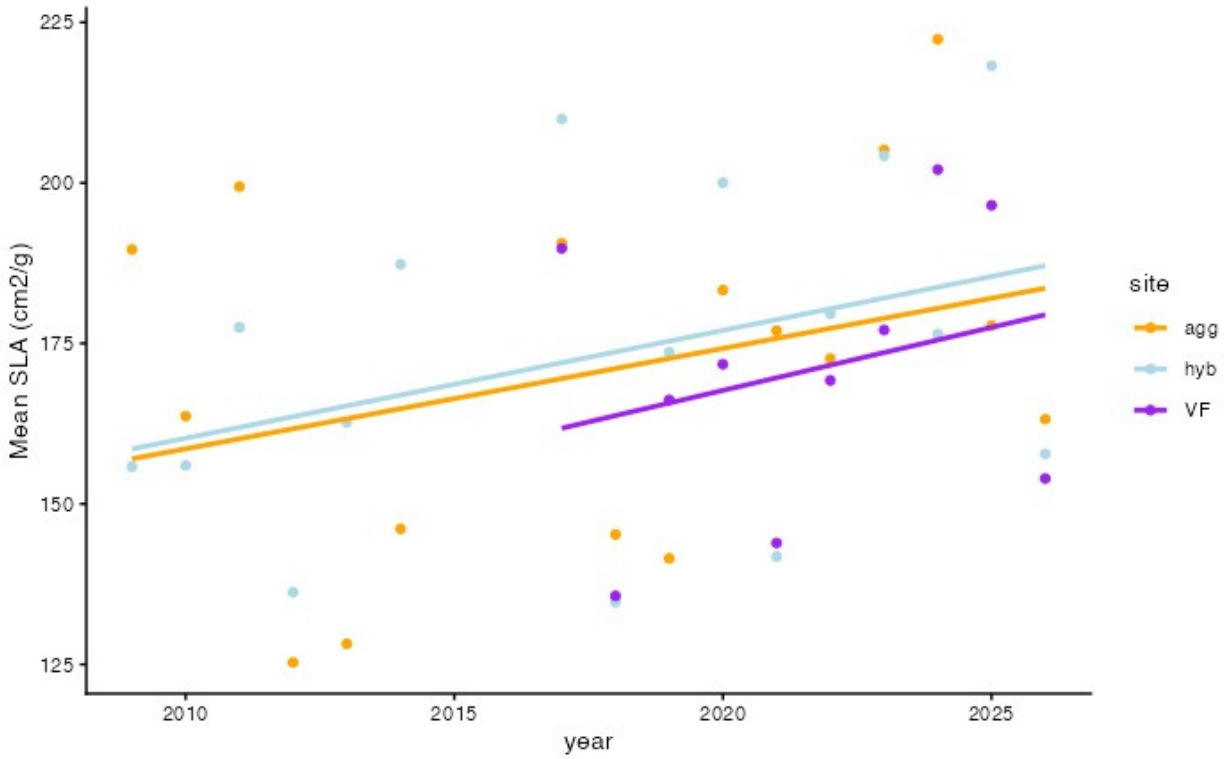
Figure 2: The relationship between growth and leaflets per length at each of the three sites. Each dot represents an individual plant. Each line represents the slope at a particular site.



To test whether the relationship between growth and leaflet density at the agg site was still significant when accounting for soil moisture, I ran a multiple regression with leaflet density and soil VWC. After accounting for soil moisture, the effect of leaflet density was still positive and significant (slope = 0.15 percent increase per leaflet / cm, p = 0.003). There was an independent effect of soil moisture on growth, with growth decreasing with greater soil moisture (p = 0.019). I did the same test for trichome density at the *agg* site. After accounting for soil moisture, the effect of trichome density was still negative and significant (slope = -0.003, p = 0.03). There was not an independent effect of soil moisture on growth (p = 0.14).

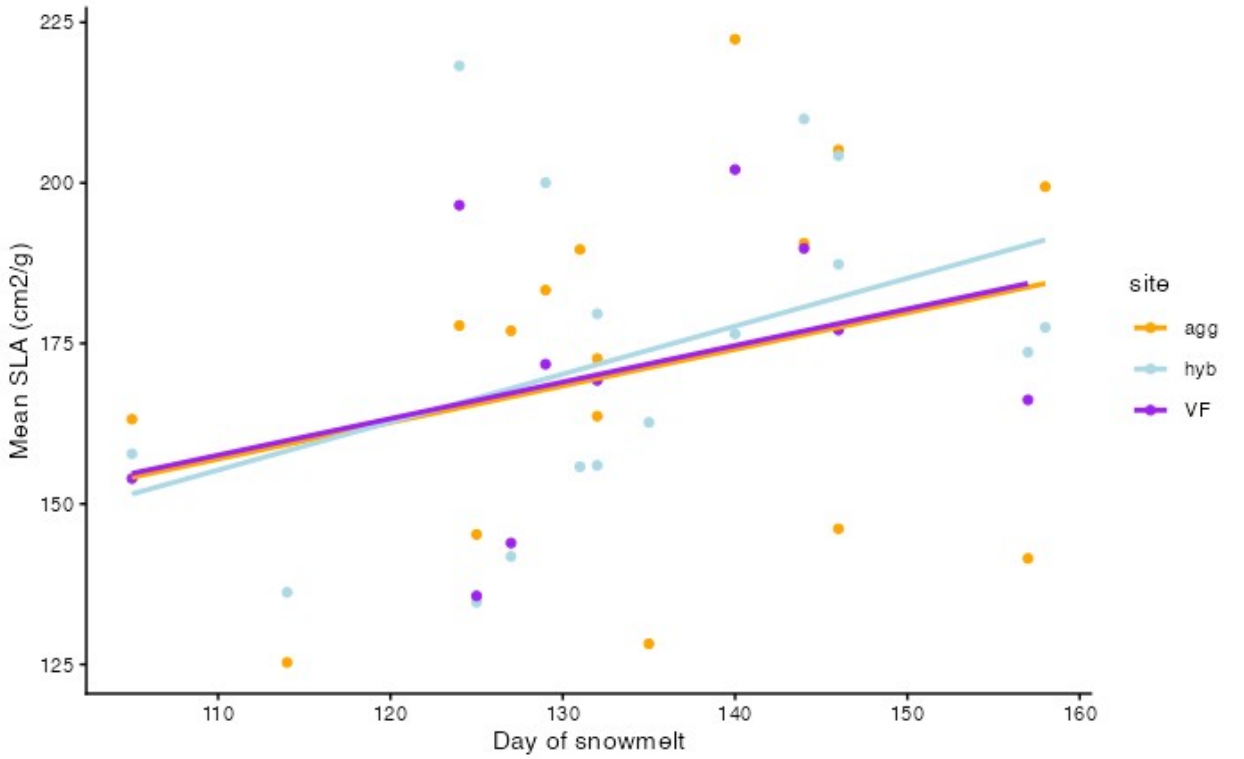
Question 2: Long Term Specific Leaf Area

Specific Leaf Area (SLA) was found to increase at an average rate of 1.450 (cm^2/g) per year, showing a marginally significant (P = 0.0501) positive relationship between SLA and year, after accounting for site, contrary to my prediction.



I had predicted that SLA would decrease by year, as average date of snowmelt (melt day) has decreased by year (with some variation) (barr, n.d.), and lower SLA is linked to earlier snowmelt date (Campbell et al. 2024). However, despite this pattern, SLA appears to be increasing over time.

In the multiple regression with both year and melt day, mean SLA increased with a later day of snowmelt ($P = 0.00184$; slope = 0.845 cm^2/g per day). This indicates that there is a significant positive relationship between melt day and SLA.



In the same multiple regression, the effect of year on SLA had a slope of 2.058 cm^2/g per year (P = 0.00386). Thus both year and melt day have significant effects on SLA, and these are independent of each other. This suggests that there is another year-dependent factor influencing SLA.

Discussion

Plants with greater leaflet density had higher growth over the summer, as did plants with lower trichome density. This result is interesting, as in a dry summer, we might expect plants with higher trichomes (and higher reflectance) to have fitness benefits, but this does not appear to be the case. Higher leaflet density does seem to benefit the plants, but why this is remains unclear. Since there is a significant effect of leaflet density on growth, future research could evaluate how leaflets may change the microclimate of the leaf or other ways that leaflet density may alter how *Ipomopsis* interacts with its environment.

These effects on growth were only detectable at the *agg* site. One reason for this may have been sample size. Around 50 plants were sampled at the *agg* site, compared to about 30 at Vera Falls and about 25 at the hybrid site. Differences among sites, such as aspect, temperature, and soil moisture may have also played a role in this difference. Further research could include more study sites that vary in aspect or soil moisture to try to understand if these environmental variables affect the relationship of traits to fitness.

One of the limitations of this study is that I was only able to look at summer aboveground growth. It is unclear how that measure relates to overall fitness, especially since most mortality occurs not during the summer but from fall to spring. A follow-up study could examine the relationship between leaflet density and survival to the next summer. Longer term studies could also evaluate whether leaf traits have any impact on the plant's fitness in its eventual flowering stage, such as corolla length, seed count, nectar volume, and more. Additionally, this study does not account for any belowground growth, which could change in different ways than

aboveground growth. Belowground growth is difficult to evaluate without killing the plants, but it is good to be aware of when evaluating plant fitness. The mechanism of how leaf traits affect growth could also be evaluated by measuring photosynthetic rates for plants with different leaf traits.

The analysis of long-term data revealed significant effects of both melt day and year on SLA, and these effects were independent of each other. These independent effects suggest that there is another year-dependent factor influencing SLA, which is valuable to know as it opens the question of what the other factor is, presenting an opportunity for future research. An initial avenue for this could include looking into a relationship between temperature and SLA. In controlled settings, higher temperatures decrease leaf mass per area (Poorter et al. 2009) thus increasing SLA, potentially countering the expected decline in SLA with early snow melt seen under climate change.

With further study, it would also be valuable to look at different ways of measuring leaflet density. Leaflet density was measured as the number of leaves divided by the leaf length. However, this does not account for the overall shape or area of the leaf, as some leaves may be longer and thinner or shorter and wider. One potential way to look at leaflets and leaf shape more wholistically could be to take a measure of leaf "cover area" - the whole area contained by the perimeter of the leaf as if it were a non-compound leaf, so including empty space, and then measure how much of that "cover area" was made up of empty space or gaps between leaflets. Leaves could be compared between their ratio of leaf-space to empty space. Factors such as temperature, elevation, and aspect may also significantly impact *Ipomopsis* fitness and have interactions with leaf traits. Future studies could include these variables to gain a broader understanding of how leaf traits and the environment interact to influence fitness. A longer term study measuring leaf shape over multiple years in different conditions would also be valuable. This would be especially useful as in this summer, some of the plants at sites such as the hybrid site were considerably stressed and did not experience any growth, while plants at Vera Falls did experience growth, perhaps due to the higher average soil moisture (8.8 VWC at Vera Falls versus 3.2 VWC at the hybrid site). Highly drought stressed plants may respond differently to environmental variables, including the way that leaf traits affect fitness.

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