

Alpine plants of Mt. Baldy: modeling phenology and documenting biodiversity

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Abstract

Alpine ecosystems are disassembling and reassembling due to climate change. The phenology of alpine plants has shifted, but empirical evidence for how spatial clustering patterns could impact this shift is lacking. This study investigated the phenology of spatially clustered versus isolated alpine plants in the Colorado Rocky Mountains, using linear models that considered co-variables such as plant size, snowmelt timing, and topography. A total of three focal species (*Senecio crassulus*, *Lupinus argenteus*, and *Ivesia gordonii*) with ca. 20 individuals per species were surveyed twice-weekly throughout July and August of 2025. We found that different aspects of phenology were affected by different variables. In

general, phenology shifts earlier due to snowmelt timing and shifts later due to the clustering effect. Natural history observations of ant behavior and a survey of the surrounding plant community supplement the understanding of the long-term Mt. Baldy research site.

Introduction

In high-elevation environments, temperature, nutrient availability, and moisture are highly variable and often limiting, making alpine plant communities particularly sensitive to environmental change (Guisan & Theurillat, 2000). Climate change is altering plant phenology, including the timing of first, last, and peak flowering (Diez et al., 2012). Across plant taxa, phenological events have generally shifted earlier in response to increased temperatures (Thackeray et al., 2016). Shifts in phenology timing will affect the demographic composition of a site, in both genetic and species composition (Springate and Kover, 2013). However, species vary in their sensitivity and reproductive strategies, resulting in changes of phenological patterns and relative orderings of species within a community (Cleland & Wolkovich, 2024; Theobald et al., 2017).

Alpine plant flowering phenology is, in part, triggered by temperature (Hülber et al., 2010). Earlier flowering times due to warmer temperatures may create a timing mismatch with pollinators, seed dispersers, or herbivores, resulting in decreased reproductive success (Kudo & Ida, 2013). However, not every species is affected the same way. Plants with shorter flowering times are more sensitive to the pollinator mismatch, and plants with a life history that develops sooner after snowmelt are most sensitive to shifting climates (Wang et al., 2024; Wipf, 2010). This species-dependent complexity results in a heterogeneous response to climate change, reshaping how alpine plant communities disassemble and reassemble. Climate change is not just modifying plant-pollinator interactions; changing interactions between plant species also affect population dynamics in alpine communities (Klanderud, 2005).

At fine spatial scales, environmental heterogeneity influences community structure and species interactions (Ohler et al., 2020). Alpine plants are often spatially clumped, with multiple species interacting in close proximity. Species modify their microhabitats, affecting the success of neighboring individuals (Stark et al., 2017). For example, alpine plants growing in clumps of the same species increased survival, fecundity, and recruitment (Blonder et al., 2018). In resource-poor, high-elevation environments, facilitative interactions such as nurse plant effects by cushion-forming species may become more prominent (Choler et al., 2001; Soliveres et al., 2015). Growing in a clump may confer benefits such as moisture retention or thermal buffering, which increases reproductive success for plants within the clump (Schöb et al., 2014). However, it may also induce costs, including competition for limited resources that reduces the reproductive success of the nurse plant in the clump (Schöb et al., 2014). These facilitative interactions can buffer individuals against environmental stress, promoting coexistence in alpine communities (Anthelme et al., 2014; Choler et al., 2001).

Phenology may be impacted by this facilitation, with the density of plant clumps impacting flowering time and reproductive success (Schmitt et al., 1987). Alpine ecosystems are under tremendous stress, but this stress may be heterogeneous due to the clumping growth form of alpine plants. What effect

does growing in multi-species spatial clusters vs. alone have on alpine plant phenology? To answer this question, I modeled the phenology of 45 individual alpine plants across 3 species at a long-term plant demography study site in the Colorado Rocky Mountains, considering clumping as a variable. I hypothesize the following: (H1) clumped plants will have a later first and peak flowering date, longer flowering duration, and higher flowering/fruitleting success due to the facilitative buffering effect of clumping; (H2) clumped plants will have more flowers per individual than isolated plants, due to density-dependent visitation of pollinators; (H3) benefits of spatial clumping are species dependent, due to life history and growth form.

The model also considers co-variables such as plant size, snowmelt timing, and topography. Plant size is correlated with the timing and duration of flowering, with larger plants flowering earlier and for longer (Ollerton and Lack, 1998). I hypothesize (H4) that my model will support this finding. Snowmelt timing affects phenology, with alpine-restricted species being more sensitive (Cornelius et al., 2013; Winkler et al., 2018). Snowmelt in the alpine is also a heterogeneous process, impacted by topography and wind patterns (Anderton et al., 2004). Given this sensitivity and the topographic heterogeneity of the site, I hypothesize (H5) that within the same year, at the same site, the patchiness of snowmelt timing may impact phenology.

In addition to phenology, interspecific interactions can impact the future demography of a site (Miller-Rushing et al., 2010). Concurrent with the phenology survey, I also conducted an ant visitation survey and plant survey within a 60-m radius of the site to characterize the natural history of the site. To understand how alpine systems will function in the future, it is important to understand what impacts plant phenology, broader ecological interactions with ants, and the surrounding plant community context.

Methods

1.1 Study Site

Field work was conducted at the Mt. Baldy Long Term Research in Environmental Biology (LTREB) site in the Elk Range of the Southern Rocky Mountains of Colorado, United States (38.978725°N, 107.042104°W). This site is within the Gunnison National Forest, on a southeast-facing ridge composed of shale scree on a ca. 20% grade slope above the tree line (Blonder et al., 2018). The vegetation is sparse, with spatial clustering evident. This project was conducted within 60 m of the long-term census demography plots established in 2014 (Figure 1) and took place during July and August of 2025.



Figure 1. Mt. Baldy long-term census plots relative to the locations of tagged plants (white circles) for the summer 2025 phenology study.

1.2 Phenology Field Survey

Of the plants present at the Mt. Baldy site, data were collected for a subset of species: *Senecio crassulus* A. Gray (Asteraceae; SENCRA), *Viola praemorsa* Douglas ex Lindl. (Violaceae; VIOPRA), *Ivesia gordonii* (Hook.) Torr. & A. Gray (Rosaceae; IVEGOR), *Lupinus argenteus* Pursh (Fabaceae; LUPARG), *Achnatherum lettermanii* (Vasey) Barkworth (Poaceae; ACHLET), *Poa fendleriana* (Steud.) Vasey (Poaceae; POAFEN), and *Poa cusickii* Vasey (Poaceae; POACUS). The species identity for ACHLET, POAFEN, and POACUS was not separated until later in the season, so references to these three species will be grouped as Poaceae.

20 individual plants, 10 in spatial clusters and 10 isolated, were tagged for SENCRA, IVEGOR, LUPARG, and Poaceae. VIOPRA, which finished flowering within the first week of the sampling period, had 10 individual plants chosen (5 in spatial clusters and 5 isolated). This resulted in a total of 90 tagged plants. The latitude and longitude of each tagged plant, in decimal degrees, were recorded using a Trimble DA2 GNSS receiver with ± 60 cm accuracy (Trimble).

Open flowers were counted twice weekly from July 2 to August 11, 2025. The number of open flowers was determined based on an existing phenology protocol for species at this site (Dalton, 2015). Additionally, the survey recorded the number of fruits for LUPARG and VIOPRA by counting the developed fruits still attached to the plant.

Spatial clusters were defined as a minimum of two plants of separate species, growing within one inch of each other. The species identity of neighboring plants within the cluster and position, center (C) or edge (E), was also recorded.

Plant size was approximated as an ellipsoid cylinder using the formula: πabh , where $a = 0.5 \times \text{length (cm)}$, $b = 0.5 \times \text{width (cm)}$, and $h = \text{height (cm)}$. The length was defined as the straight-line distance between the furthest vegetative parts when looking directly down. The width was defined as the straight-line distance between the furthest vegetative parts when looking directly down, perpendicular to the length. The height is defined as the straight-line distance from the substrate to the tip of the tallest vegetative part. For SENCRA, the height was defined as the average height of the flowering stalks. Additional vegetative and reproductive metrics were taken for certain species. The number of leaves was noted for IVEGOR, SENCRA, and VIOPRA. For LUPARG, the maximum inflorescence length was recorded for each individual.

Slope aspect (southness and westness), slope degree, and elevation were extracted for each plant location from a digital elevation model (DEM) of the Upper Gunnison Valley using the R package *rSDP* (Breckheimer, 2023).

On August 5, soil moisture (volumetric water content, % VMC) and soil temperature (°C) were measured at the base of each tagged plant using a TDR 150 Soil Moisture Meter with 3-inch probes (Spectrum Technologies). Probes were inserted as flush to the substrate as possible, with initial holes made using a hammer and nail if needed. Leading up to the sampling date, daily temperatures from billy barr's weather station ranged from 16 to 23.5 °C between August 1 and August 5 (Gothic Weather, 2025). The last significant rainfall was 0.39 inches on August 1, followed by 0.05 inches on August 2 (Gothic Weather, 2025).

The first snow-free date for each tagged plant was determined by manually reviewing near-daily images from Planet satellites between June 1 and 19, 2025, with overlaid latitude and longitude coordinates for each tagged plant. 3 m resolution orthorectified RGB imagery was downloaded for the site from the PSScene, which uses PSB.SD sensors (SuperDove) 8-Band Planet Scope (Planet Labs PBC, PlanetScope).

1.3 Ant Field Survey

Concurrent with the phenology survey, the number of ant visits on open flowers for each tagged plant was recorded on each visit date. Presence/absence of ant nest entrances at the base of each tagged plant was also recorded on each survey day. A specimen of the ants was collected for identification and deposited in the RMBL Insect Collection.

1.4 Supplemental Plant Community Survey

Voucher specimens were collected for each unique species within a 60-m radius of the long-term census plots during the survey period and deposited at the RMBL Herbarium. When possible, the plant was collected in reproductive stage to ensure accurate identification and the creation of educational herbarium specimens. Due to the sensitivity of the plant community at this site, root material was only

collected when necessary for identification. Otherwise, cuttings were made of representative features. Specimen data included the date, locality, habitat description, and associated plants. Plant features that would not be obvious from a specimen (e.g., plant height, corolla color, etc.) were sometimes included. A Garmin eTrex GPS was used to estimate latitude, longitude, elevation, and accuracy of each collection.

1.5 Data Analysis

Phenology Modeling

All analyses were done in R version 4.5.1 (R Core Team, 2025) with packages *dplyr* (Wickham et al., 2023), *stats* (R Core Team, 2025), *tidyr* (Wickham et al., 2024), *readxl* (Wickham and Bryan, 2025), *purrr* (Wickham and Henry, 2025), and *minpack.lm* (Elzhov et al., 2023). Graphs were created using *ggplot2* (Wickham, 2016) and *visreg* (Breheny and Burchett, 2017). Residual tests were done using *DHARMA* (Hartig, 2024). Coefficient estimate tables were extracted from models using *sjPlot* (Lüdecke, 2025).

Tagged plants excluded from the phenology modeling include those with strong evidence of herbivory, those that never bloomed, and those whose flowering trajectory did not follow a normal distribution. All VIOPRA were excluded from the phenology modeling due to missing the onset of flowering, and all Poaceae were excluded due to difficulty in counting open flowers and species identity confusion. This left three species (IVEGOR, LUPARG, SENCRA) for analysis.

For the remaining tagged plants, Gaussian curves were fitted over the phenology field survey data using the *nlsLM* function and the formula: $\text{total_flowers} \sim k * \exp(-0.5 * ((\text{DOY} - m)/\text{sd})^2)$, where m = the day of year (DOY) with maximum total flowers, sd = standard deviation in days, and k = the maximum value of total flowers. From the curve, the following parameters were extracted for each individual:

Summary Metric	Parameter
First flowering day	$\mu - (2 * \sigma)$
Flowering duration	standard deviation (σ)
Day of peak flowering	mean (μ)
Peak flowering amount	k

Linear models tested the independent and interactive effects of predictor variables (Table 1) on plant phenology, and an ANOVA (analysis of variance) test was run for each model. Separate models were built for each summary metric of plant phenology: first flowering day, peak flowering, flowering duration, and peak flowering amount. For peak flowering amount, a separate model was built for each species due to the scale difference (e.g., LUPARG: max ca. 150 flowers, SENCRA: max ca. 30 flowers). All model residuals passed the KS, dispersion, and outlier tests. Rank-transformed model predictions had no quantile deviations detected. Model formulas are listed in Table 2.

Table 1. Predictor variables used in linear models.

Predictor Variables	Values	Formula
Clustering	Y / N	clustering
Plant Size	πabh	plant_size
Slope Degree	0 to 90°	slope_degree
Slope Aspect (Southness)	-1 to 1	slope_aspect_S
Slope Aspect (Westness)	-1 to 1	slope_aspect_W
Elevation	Meters above sea level	elevation
Plant Species	SENCRA, IVEGOR, LUPARG	plant_species
Soil Moisture	0 to 100% VWC	soil_moisture
First Snow-Free Day	Day of Year	snowmelt_day

Table 2. Linear model formulas for each phenology summary metric.

Summary Metric	Linear Model Formula
First flowering day (FFD)	ffd ~ clustering + plant_size * plant_species + (soil_moisture * clustering) + plant_species * snowmelt_date + (elevation * slope_degree) + (log(1+slope_aspect_W)) + log(1 + slope_aspect_S)
Peak flowering day (μ)	mean ~ plant_species + clustering + (slope_degree * elevation) + log(1+slope_aspect_W) + (plant_size * plant_species) + soil_moisture + snowmelt_date
Peak flowering amount (k)	IVEGOR_k ~ (clustering * plant_size) + snowmelt_date + soil_moisture + slope_degree + slope_aspect_W SENCRA_k ~ clustering + plant_size + snowmelt_date + soil_moisture + slope_degree + slope_aspect_W LUPARG_k ~ clustering + plant_size + snowmelt_date + slope_degree + log(1+slope_aspect_W)
Flowering duration (σ)	sd ~ plant_species + clustering + (slope_aspect_S * snowmelt_date) + slope_degree + (slope_aspect_S * log(1 + slope_aspect_W)) + (soil_moisture * clustering)

Comparison to 2015 Phenology Data

Phenology data collected by Rebecca Dalton in 2015 within the long-term census plots were cleaned and reformatted to match the structure of the 2025 dataset. For 2025, the number of LUPARG inflorescences was used instead of the total number of flowers to make it comparable to the data collected in 2015. Gaussian curves were generated for each individual using the same fitting procedures applied to the 2025 data, and the same summary statistics were extracted. An ANOVA (analysis of variance) test was used to determine if there were any significant differences between these summary metrics between 2015 and 2025. Post-hoc, Tukey's HSD (honestly significant difference) test was used to determine which levels differed from one another.

Ant Visitation

Average ant visitation data from 2025 was fitted with a Gaussian curve and compared to the curve for the average number of flowers across individuals for each species. An ANOVA (analysis of variance) test was used to determine if there were any significant differences between the summary metrics (mean, sd) for the curves of the average number of ants and the average number of flowers. Post-hoc, Tukey's HSD (honestly significant difference) test was used.

Results

2.1. Phenology Modeling

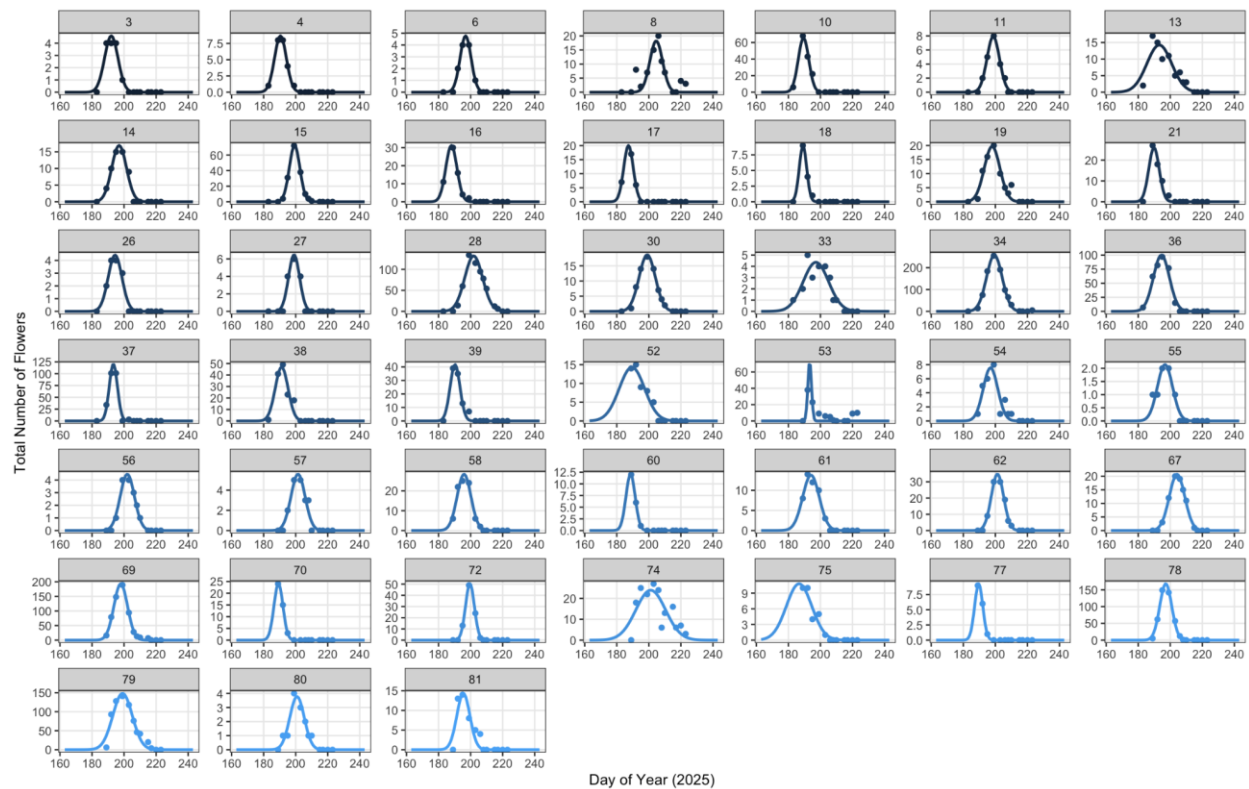


Figure 2. Fitted Gaussian curves for individual tagged plants in 2025. From the starting 90 individuals, 45 made it to the modeling.

The overall FFD model had a multiple R^2 value of 0.7638 and was significant (ANOVA, $F_{16,28} = 5.66$, $p < 0.001$). An ANOVA of the FFD model showed a significant effect of predictors plant_species, plant_size, clustering, snowmelt_date, and plant_species:snowmelt_date (Table 3).

Table 3. Significant predictors from ANOVA of FFD model, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

FFD	F	df	significance
plant_species	21.0491	2	***
plant_size	13.1071	1	**
clustering	6.8547	1	*
snowmelt_date	6.4385	1	*
plant_species:snowmelt_date	4.2697	1	*
Residuals	-	28	-

Table 4. Estimates of variables in the FFD model, where p is bolded if significant.

ffd							
Predictors	Estimates	CI	p				
(Intercept)	-4038.64	-9792.38 – 1715.11	0.162	1 + slope aspect S [log]	-6.16	-13.74 – 1.41	0.107
clustering [Y]	9.68	-1.16 – 20.52	0.078	plant size × plant species [LUPARG]	0.02	-0.00 – 0.04	0.065
plant size	-0.02	-0.04 – 0.00	0.068	plant size × plant species [SENCRA]	0.02	-0.00 – 0.04	0.063
plant species [LUPARG]	-160.37	-421.18 – 100.44	0.218	clustering [Y] × soil moisture	-2.06	-4.36 – 0.23	0.076
plant species [SENCRA]	-154.70	-330.31 – 20.91	0.082	plant species [LUPARG] × snowmelt date	1.02	-0.59 – 2.62	0.206
soil moisture	0.91	-0.57 – 2.40	0.219	plant species [SENCRA] × snowmelt date	0.97	-0.12 – 2.06	0.078
snowmelt date	-0.70	-1.66 – 0.25	0.144	elevation × slope degree	-0.10	-0.19 – 0.00	0.059
elevation	1.23	-0.39 – 2.85	0.132	Observations	45		
slope degree	336.48	-13.78 – 686.75	0.059	R^2 / R^2 adjusted	0.764 / 0.629		
1 + slope aspect W [log]	0.51	-0.88 – 1.91	0.457				

From the model estimate, clustered plants have a first flowering date ca. 9.68 days after non-clustered plants. For every cm^3 of size, larger plants have a first flowering date that is ca. 0.02 days earlier. For every day of earlier snowmelt, the first flowering date generally shifted ca. 0.70 days earlier. However, each plant species had a differential effect based on snowmelt date. This relationship was negative for IVEGOR, but could be either negative or positive (inconclusive) for LUPARG and SENCRA based on the confidence intervals (Figure 3).

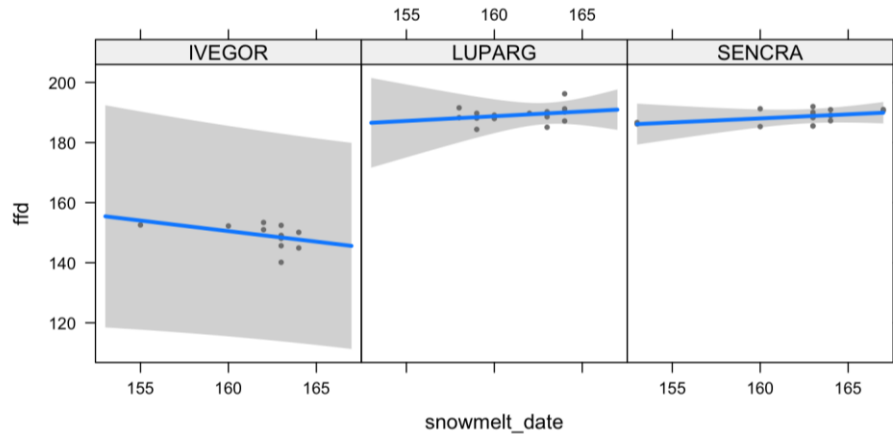


Figure 3. Visreg plot of snowmelt_date and first flowering date, based on the plant species.

The overall μ model had a multiple R^2 value of 0.7394 and was significant (ANOVA, $F_{12,32} = 7.567$, $p < 0.001$). An ANOVA of the μ model showed a significant effect of predictors plant_species, snowmelt_date, elevation, plant_size, and slope_degree:elevation (Table 5).

Table 5. Significant predictors from ANOVA of μ model, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

μ	F	df	significance
plant_species	30.1964	2	***
snowmelt_date	11.058	1	**
elevation	6.6066	1	*
plant_size	4.4184	1	*
slope_degree:elevation	4.7901	1	*
Residuals	-	32	-

Table 6. Estimates of variables in the μ model, where p is bolded if significant.

Predictors	mean						
	Estimates	CI	p				
(Intercept)	-3409.84	-7641.74 – 822.05	0.111	soil moisture	0.32	-0.57 – 1.22	0.468
plant species [LUPARG]	6.57	1.51 – 11.62	0.012	snowmelt date	0.64	0.16 – 1.11	0.010
plant species [SENCRA]	7.30	2.96 – 11.65	0.002	slope degree × elevation	-0.07	-0.14 – 0.00	0.051
clustering [Y]	0.68	-1.60 – 2.97	0.548	plant species [LUPARG] × plant size	0.00	-0.01 – 0.02	0.697
slope degree	240.39	-0.72 – 481.51	0.051	plant species [SENCRA] × plant size	0.00	-0.01 – 0.02	0.708
elevation	0.99	-0.21 – 2.19	0.103	Observations	45		
1 + slope aspect W [log]	0.23	-0.47 – 0.92	0.515	R^2 / R^2 adjusted	0.739 / 0.642		
plant size	-0.00	-0.02 – 0.01	0.714				

From the model estimate, LUPARG has a peak flowering date that is ca. 6.57 days after IVEGOR, and SENCRA has a peak flowering date that is ca. 7.30 days after IVEGOR. Snowmelt date is positively

correlated with the day of peak flowering, where for every day of later snowmelt, peak flowering is also ca. 0.64 days later. Plant size had a significant effect, but the model did not have a good estimate of this relationship direction. The elevation also impacts peak flowering, where for each meter of elevation increase, the day of peak flowering is approximately 0.99 days later; however, there is an interaction of slope degree and elevation; for steeper slopes, this relationship becomes negative (Figure 4).

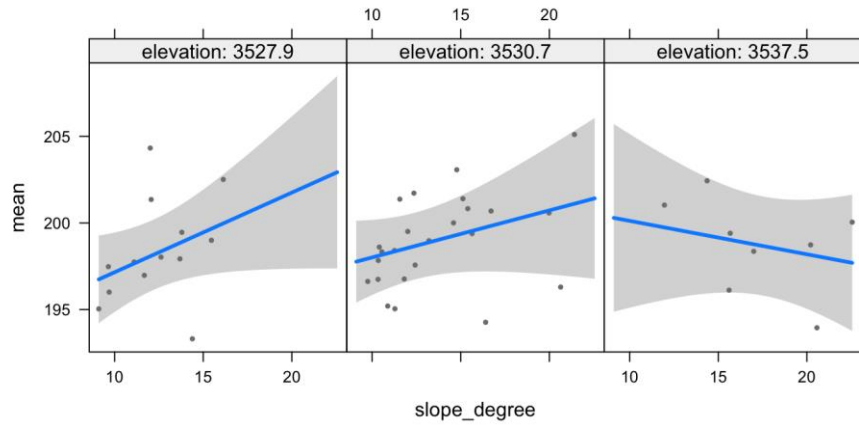


Figure 4. Visreg plot of slope degree and peak flowering date, based on the elevation (m).

The overall k_IVEGOR model had a multiple R^2 value of 0.9402 and was significant (ANOVA, $F_{7,4} = 8.977$, $p < 0.05$). An ANOVA of the k_IVEGOR model showed a significant effect of clustering:plant size and clustering (Table 7).

Table 7. Significant predictors from ANOVA of k_IVEGOR model, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

k_IVEGOR	F	df	significance
clustering:plant_size	1240.91	1	**
clustering	14.2561	1	*
Residuals	-	4	-

Table 8. Estimates of variables in the k_IVEGOR model, where p is bolded if significant.

k							
Predictors	Estimates	CI	p				
(Intercept)	-720.95	-2061.45 – 619.55	0.210	slope degree	-4.70	-9.55 – 0.15	0.055
clustering [Y]	-133.62	-195.37 – -71.86	0.004	slope aspect W	22.37	-36.54 – 81.29	0.351
plant size	-0.30	-0.46 – -0.15	0.005	clustering [Y] × plant size	0.44	0.21 – 0.67	0.006
snowmelt date	4.85	-3.97 – 13.67	0.201	Observations	12		
soil moisture	27.16	15.21 – 39.12	0.003	R^2 / R^2 adjusted	0.940 / 0.835		

From the model estimates, for every increase of 1% VMC in soil moisture, the peak flowering amount would increase by ca. 27.16 flowers. Plant size and clustering both had an effect on peak flowering amount; however, compared to smaller plants, larger plants experienced less of a peak flowering difference between clustered and non-clustered (Figure 5).

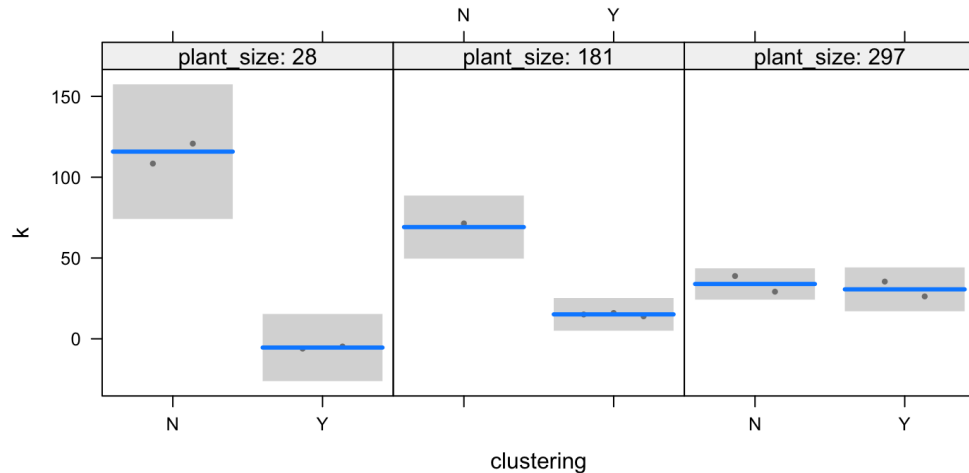


Figure 5. Visreg plot of clustering and peak flowering amount, based on plant size (cm³).

The overall k_{LUPARG} model had a multiple R^2 value of 0.9376 and was significant (ANOVA, $F_{5,9} = 27.04$, $p < 0.001$). An ANOVA of the k_{LUPARG} model showed a significant effect of predictors plant_size, clustering, snowmelt_date, and slope_aspect_W.

Table 9. Significant predictors from ANOVA of k_{LUPARG} model, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

k_{LUPARG}	F	df	significance
plant_size	79.0697	1	***
clustering	21.0573	1	**
snowmelt_date	21.4817	1	**
$\log(1 + \text{slope_aspect_W})$	11.4640	1	**
Residuals	-	9	-

Table 10. Estimates of variables in the k_{LUPARG} model, where p is bolded if significant.

Predictors	Estimates	k CI	p				
(Intercept)	3204.67	1343.74 – 5065.59	0.004	snowmelt date	-18.55	-29.37 – -7.72	0.004
clustering [Y]	-94.04	-131.59 – -56.48	<0.001	slope degree	-4.79	-12.15 – 2.58	0.175
plant size	0.01	0.00 – 0.01	0.005	1 + slope aspect W [log]	11.22	3.72 – 18.72	0.008
				Observations	15		
				R^2 / R^2 adjusted	0.938 / 0.903		

From the model estimate, clustered plants had ca. 94.04 less flowers than non-clustered plants. Larger plants produced more flowers, where for every 1 cm³ increase in size corresponded with a ca. 0.01 increase in number of peak flowers. For every day of later snowmelt, peak flowering decrease by ca. 18.55 flowers. The transformed slope aspect westness also mattered, where for every $\log(1 + 1$ degree) of westness, there was ca. 11.22 more peak flowers.

The overall k_{SENCRA} model had a multiple R^2 value of 0.6987 and was significant (ANOVA, $F_{6,11} = 4.252$, $p < 0.05$). The k_{SENCRA} model showed a significant effect of the plant size predictor.

Table 11. Significant predictors from ANOVA of k_{SENCRA} model, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

k_{SENCRA}	F	df	significance
plant_size	897.29	1	***
Residuals	-	11	-

Table 12. Estimates of variables in the k_{SENCRA} model, where p is bolded if significant.

k							
Predictors	Estimates	CI	p				
(Intercept)	-314.69	-792.41 – 163.04	0.175	soil moisture	-1.89	-5.87 – 2.09	0.318
clustering [Y]	5.50	-3.96 – 14.96	0.227	slope degree	-0.37	-2.69 – 1.96	0.734
plant size	0.00	0.00 – 0.01	0.008	slope aspect W	20.72	-9.69 – 51.12	0.162
snowmelt date	2.13	-1.08 – 5.33	0.172	Observations	18		
				R^2 / R^2 adjusted	0.699 / 0.534		

The only significant predictor for SENCRA peak flowering was plant size, but the direction of this relationship was not clear from the model estimate.

The overall σ model had a multiple R^2 value of 0.4263 and was significant (ANOVA, $F_{10,34} = 2.526$, $p < 0.05$). An ANOVA of the σ model showed a significant effect of predictors slope_aspect_S and slope_aspect_S:log(1 + slope_aspect_W) (Table 13).

Table 13. Significant predictors from ANOVA of σ model, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

σ	F	df	significance
slope_aspect_S	17.980	1	**
slope_aspect_S:log(1 + slope_aspect_W)	3.1521	1	**
Residuals	-	34	-

Table 14. Estimates of variables in the σ model, where p is bolded if significant.

<i>Predictors</i>	<i>Estimates</i>	<i>sd</i>		<i>p</i>				
		<i>CI</i>						
(Intercept)	4.88	-32.67 – 42.42	0.793		1 + slope aspect W [log]	-0.13	-0.67 – 0.41	0.628
plant species [LUPARG]	-0.60	-1.92 – 0.72	0.361		soil moisture	0.16	-0.34 – 0.65	0.524
plant species [SENCRA]	0.02	-1.13 – 1.16	0.978		clustering [Y]	-3.20	-7.23 – 0.82	0.115
snowmelt date	-0.04	-0.29 – 0.20	0.717		slope aspect S × 1 + slope aspect W [log]	-1.92	-3.25 – -0.59	0.006
slope degree	0.38	0.14 – 0.61	0.003		soil moisture × clustering [Y]	0.70	-0.15 – 1.54	0.102
slope aspect S	-0.20	-2.47 – 2.07	0.858		Observations	45		
					R ² / R ² adjusted	0.426 / 0.258		

This model was the most sensitive to the inputs, where slight changes in the model formula would drastically change the significance of variables. In this model iteration, the main significant variable explaining flowering duration is slope aspect. However, in other model iterations, the duration of flowering was significantly predicted by snowmelt timing.

Table 15. Summary of significant predictors for each model ANOVA; *p < 0.05, **p < 0.01, ***p < 0.001, blanks indicate the variable was not included in the model, and a dashed line indicates non-significance.

Variable	ffd	μ	k (IVEGOR)	k (LUPARG)	k (SENCRA)	σ
plant_species	***	***				-
snowmelt_date	*	**	-	**	-	-
clustering	*	-	*	**	-	-
plant_size	**	*		***	***	
soil moisture			-		-	-
elevation		*				
slope_aspect_S	-					**
slope_aspect_W	-	-	-	**	-	-
slope_degree			-	-	-	-
slope_degree:elevation	-	*				

plant_species:plant_size		-				
plant_species:snowmelt_date	*					
soil_moisture:clustering	-					-
clustering:plant_size			**			
slope_aspect_S:log(1 + slope_aspect_W)						**

2.2. Comparison to 2015 Phenology Data

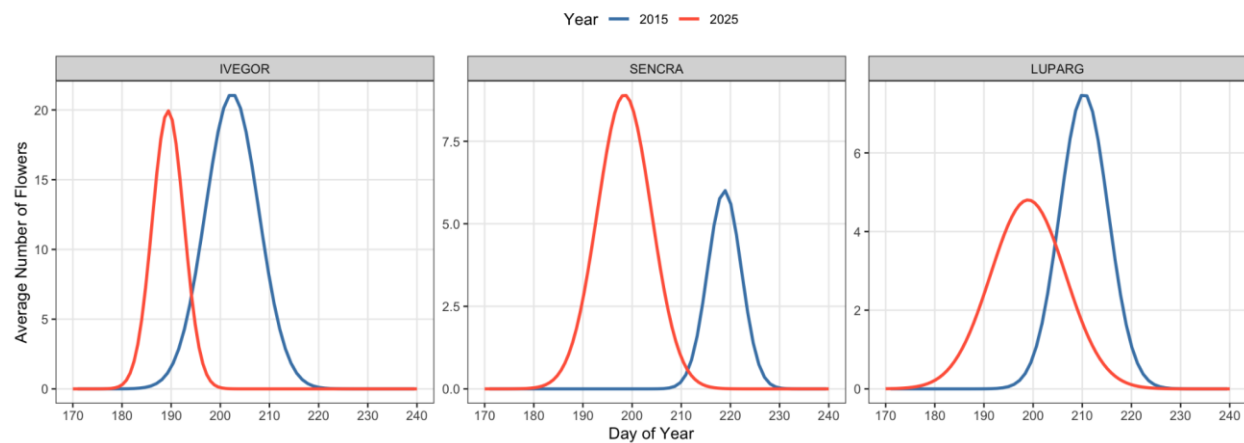


Figure 6. Summarized and curve-fitted phenology for each species, comparing 2015 and 2025.

The 2025 phenology at the site is significantly different than 2015. The first flowering day was significant by year (ANOVA, $F_{1, 158} = 249.435$, $p < 0.001$; TukeyHSD, $p < 0.001$) and by plant species (ANOVA, $F_{2, 157} = 111.181$, $p < 0.001$; TukeyHSD, $p < 0.001$). In 2025, the first flowering day was approximately 14.5 days earlier overall. IVEGOR flowered 16 days earlier in 2025 ($p < 0.001$), LUPARG 22.8 days ($p < 0.001$), and SENCRA 26 days ($p < 0.001$). Day of peak flowering (mean) also varied significantly by year (ANOVA, $F_{1, 157} = 215.50$, $p < 0.001$; TukeyHSD, $p < 0.001$) and by plant species (ANOVA, $F_{2, 157} = 85.42$, $p < 0.001$; TukeyHSD, $p < 0.001$). In 2025, peak flowering was approximately 12 days earlier overall. Duration (sd) was also longer in 2025 (ANOVA, $F_{1, 157} = 13.009$, $p < 0.001$; TukeyHSD, $p < 0.001$). This varied by plant species (ANOVA, $F_{2, 157} = 10.181$, $p < 0.001$; TukeyHSD, $p < 0.001$), but in general, flowering duration was about 1.2 days longer in 2025. Flowering duration was not significant for IVEGOR or SENCRA, but was approximately 2.4 days longer for LUPARG ($p < 0.05$).

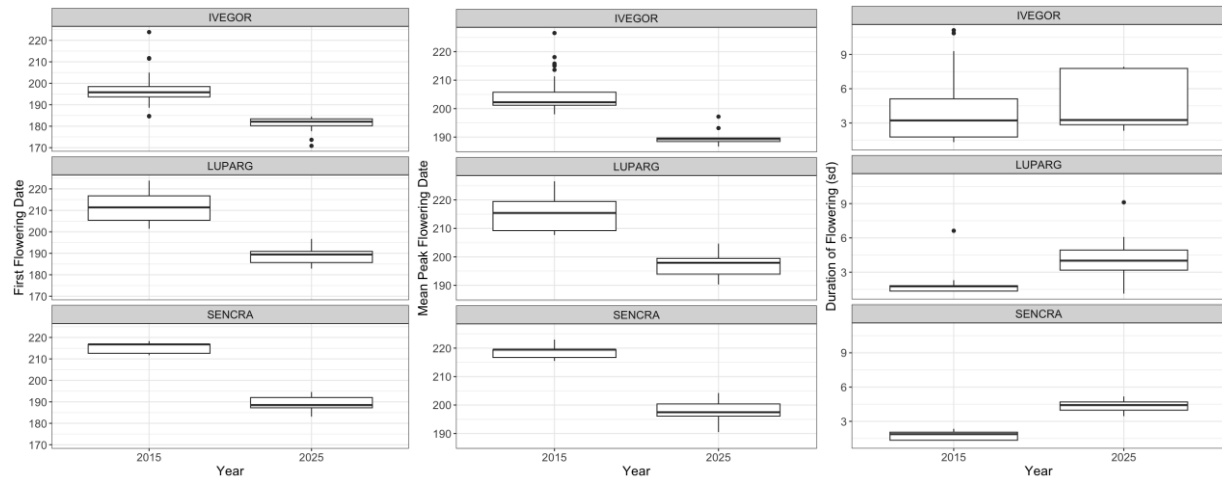


Figure 7. Boxplots of first flowering date, peak flowering day, and duration for 2015 and 2025. Each datapoint is of an individual plant, split by species.

While two years are not enough to conclude about what climatic variables are influencing this phenology, Table X summarizes metrics to contextualize. The first snow-free day in 2015 was determined using data from a weather station set up at the Mt. Baldy site, where the soil temperature first reached above 0°C. The first snow-free day in 2025 was determined using daily Planet satellite data, taking the average of the first snow-free dates for tagged plants. The July average air temperature and humidity were obtained from billy barr’s weather station (Gothic Weather, 2025). Total precipitation and snowfall were taken from September 2014/2024 to August 2015/2025 (Gothic Weather, 2025).

Table 16. Summary of different weather variables across 2015 and 2025.

Variable	2015	2025
First snow-free day of the year	177	162
July average air temperature (°C)	10.6	12.6
July average humidity (%)	75	56
Total Yearly Precipitation (cm)	41.02	27.46
Total Yearly Snowfall (cm)	852	114

2.3. Ant Visitation

The ant species dominant at the Mt. Baldy LTREB site is part of the *Formica fusca* group. Workers are ca. 4-7 mm in length, with a uniform dark body. Nest entrances are located near the base of plants, with slight mounding at the excavation site, but are otherwise inconspicuous. Entrances ranged in size (ca. <1-2 cm) and entrances per mound (ca. 1-7 entrances). The largest and most persistent nest entrances were at the base of established grasses. Nest entrances shift with the phenology of the plants.

Entrances were moved throughout the season. Earlier in the summer season (day 180), there were four ant nest entrances under *Pseudocymopterus montanus* (A. Gray) J.M. Coult. & Rose (Apiaceae; PSEMON), which has the earliest flowering phenology at the site. As the season progressed, ants seemed to have a preference for moving their nests under what was flowering, with 3 observed new nest entrances at the base of tagged SENCRA on days 189, 199, and 203. There was one new nest entrance below tagged LUPARG on day 199.



Figure 8. Ant nest entrance under PSEMON (June 25), large ant nest under POAFEN (August 11), inconspicuous entrance under ERIUMB (August 11).

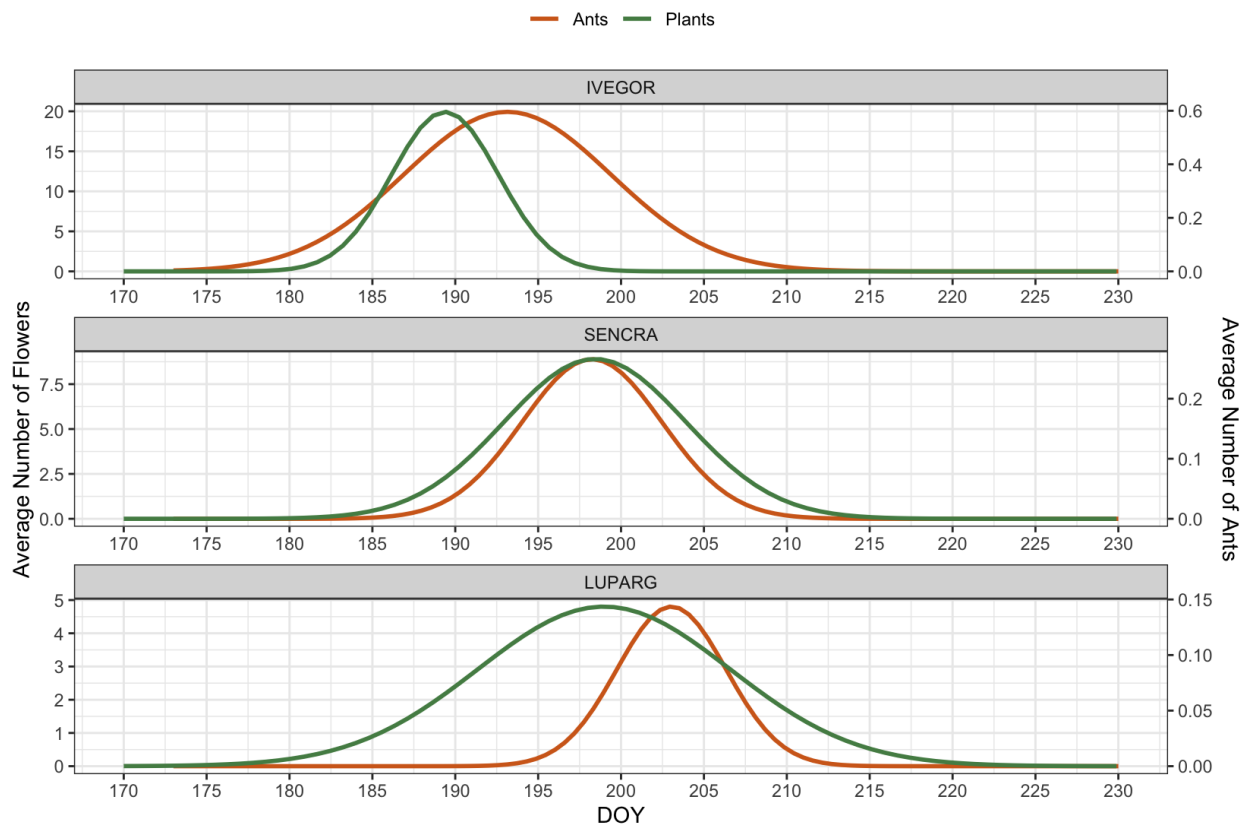


Figure 9. Gaussian curves for average ant visitation and summary plant phenology, by plant species.

Ant visitation tracks with flowering phenology through the season. There was no significant difference between the day of peak ant abundance and the day of peak flowering abundance (ANOVA, $F_{1,4} = 0.364$, $p = 0.579$), as well as no significant difference between the standard deviations of these curves (ANOVA, $F_{1,4} = 0.307$, $p = 0.609$).



Figure 10. Ants visiting IVEGOR for nectar. Photo taken July 30, 2025 below Mt. Baldy core site.

Once the bulk of the flowering season passed, the ants moved on to farming aphids (*Aphis cf. lugentis?*) on SENCRA, with the first observed aphid colony at the Mt. Baldy site on day 206. Ants were observed tending aphid colonies on tagged plants starting on day 210 and 217. The ants also scavenge for dead insects and are opportunistic predators. The first observation of alates was on August 3 (day 215).



Figure 11. Ants tending aphids on SENCRA. Photo taken August 4, 2025 east of Mt. Baldy core site.

The ant species composition experiences a shift above the site, corresponding to the change in geology from shale to finer textured quartz monzonite. A different ant species with a red abdomen dominates at this location and has not been observed at the long-term census plots.

2.4 Plant Community Survey

A full annotated species list and corresponding collection numbers for the surrounding 60-meter radius of the Mt. Baldy LTREB site can be found in Appendix A, and a map of collection points is found in Figure X. Vascular plant families are alphabetically arranged within major groups. Taxa are listed alphabetically within their respective families by genus and species epithet. Authorities are given for all taxa, and common names are also provided. The plant survey splits the surrounding 60 m radius into 4 general regions: above, below, east, and west of the core LTREB site.

Species were determined using *Sedges of Colorado* (Wingate, 2017), *Flora of Colorado* (Ackerfield, 2015), and *Grasses of Colorado* (Shaw, 2012). All identifications were verified by Dr. Rick Williams, RMBL herbarium curator. To reduce site disturbance, previously vouchered plants from 2014 were not re-collected unless a correction was needed. A correction was made for *Arnica latifolia*, which was re-identified as *Arnica rydbergii* based on achene hairs, sessile basal leaves, and exposed rocky scree habitat. Two other species, *Poa cusickii* and *Poa fendleriana*, were separated from *Achnatherum lettermanni* due to differences in their inflorescence shape and lack of awns. An updated key to the common grasses of the Mt. Baldy LTREB site is available in Appendix B.

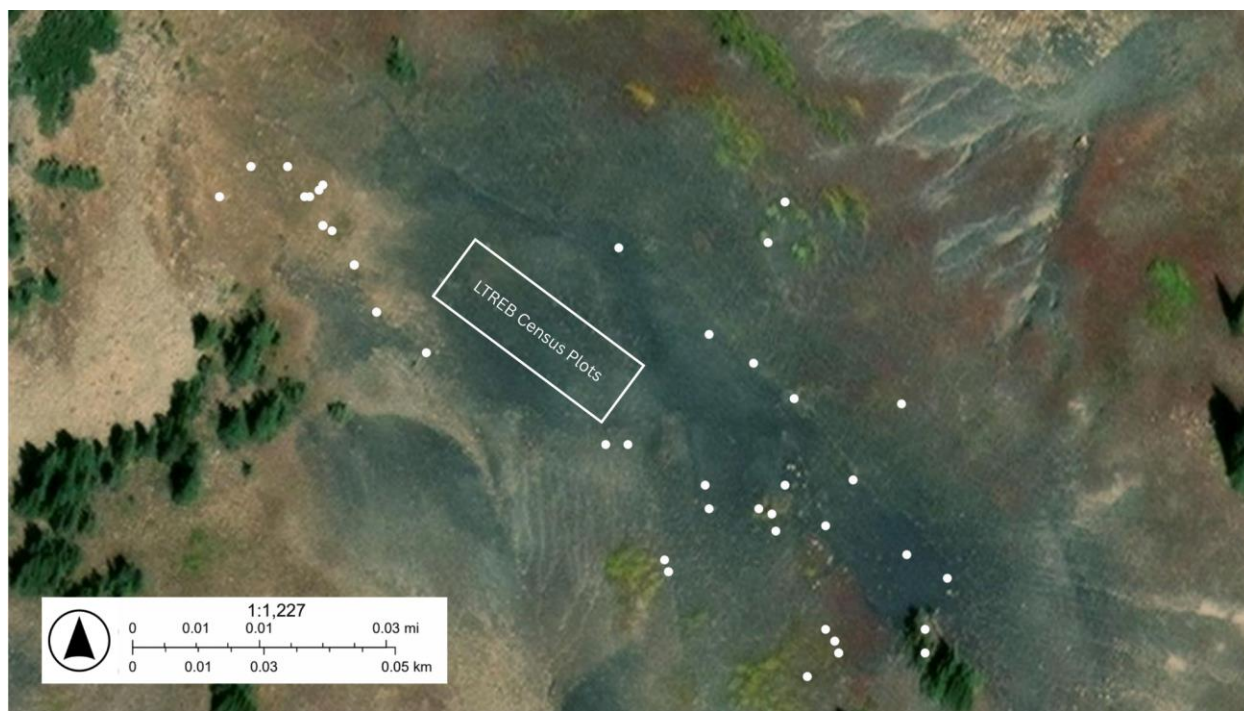


Figure 12. Map of vouchered specimens from a 60 m radius of Mt. Baldy LTREB site.

The surrounding 60-meter radius of the Mt. Baldy LTREB includes 76 unique species of vascular plants (Table 17). The richest families are Asteraceae (20 species), Rosaceae (8 species), Poaceae (7 species), and Cyperaceae (5 species). The most speciose genera are *Carex* (Cyperaceae, 5 species), *Erigeron* (Asteraceae, 5 species), and *Potentilla* (Rosaceae, 3 species).

Table 17. Summary table of plant survey.

List by Taxonomic Category		List by Other Category	
Vouchered in 2025	59	Species occurring in the core LTREB site	18
Vouchered in 2014	15	Species occurring above the site	52
Families	26	Species occurring below the site	31
Genera	58	Species occurring east of the site	37
Species	72	Species occurring west of the site	41

On the SE ridge, the treeline ends 60 m below the Mt. Baldy LTREB site with *Picea engelmannii* and *Abies lasiocarpa*. Scattered trees occur above the southeast ridge, but are krummholtz and do not form forests. To the north, the geology results in a different plant community. 21 species are unique to the above site. The erosional sides of the hill are siltier and support a slightly different plant community than the exposed southeast ridge. For example, *Geum rossii*, *Fragaria virginiana*, and *Koeleria spicata* are some species that occur on both the east and west hillsides, but not the main southeast ridgeline.

Discussion

Phenology in this subset of alpine plant species was nuanced, where different aspects of phenology were affected by different variables. Plant species identity mattered for first flower date, peak flowering date, and peak flowering amount. This is most likely due to the different life histories of each species, where these phenology metrics are strongly encoded biologically. Thus, it is important to consider the shifts in these metrics for each species as well as the overall effects.

Clustering had a significant effect on first flowering date, where clustered plants flowered later than non-clustered plants. The soil temperature may have been buffered for clustered plants, potentially heating up later and thus cueing flowering to be later. Alternatively, there may be competition for resources within a cluster, causing flowering to be delayed. Clustered plants for IVEGOR and LUPARG had lower peak flowering amounts, which could also be due to competition within a cluster. However, since fruiting data has yet to be analyzed, the total reproductive success of clustered plants is not known. Perhaps clustered plants will have higher fruit success relative to the number of flowers they produce, which will mitigate the lower peak flowering amount. In terms of attracting pollinators, clustered plants may also not need to produce as much flowers as their isolated counterparts. In addition, the total lifetime reproductive success of clustered versus isolated plants may be different, where clustered plants could start reproducing earlier due to the buffering effect. Regardless, clustering seems to alter the growth and reproductive strategy of alpine plants.

Plant size had an effect on all phenology summary metrics except the peak flowering amount of IVEGOR, but we see an interaction between clustering and plant size. Smaller IVEGOR had less flowers when they

were clustered, but the largest size class of IVEGOR had no significant difference of peak flowering amount based on clustering. This may suggest that when plants reach a large enough size, the buffering effects of clustering becomes less important to their reproduction. This also suggests that this effect varies by plant species.

Topographic variables like elevation and aspect had some effects, though their impacts were likely mediated through or obscured by snowmelt timing, given strong interactions between slope, aspect, and snow cover duration. Topographic effects were the only significant predictors of the flowering duration model; however, the flowering duration model exhibited high sensitivity to minor changes in the formula, resulting in substantially different outcomes. This suggests that either key explanatory variables are missing, or the current model structure is inadequate. Additional factors that may influence phenology but were not measured in this study include previous-year resource allocation toward flowering, soil texture, and other site-specific variables.

Overall, these model findings align with previous work which showed earlier snowmelt leads to earlier flowering (Winkler et al., 2018) and clustering has different impacts for different species (Schöb et al., 2014). However, this study adds new insight by highlighting the importance of fine-scale snowmelt heterogeneity—within the same site, within the same year—on phenological variation. Snowmelt timing had significant effects for first flowering date, peak flowering date, and the peak flowering amount for LUPARG (but not IVEGOR or SENCRA). The indication of species-specific impacts may mean changes in demography. These differences in phenological responses could have meaningful consequences for plant fitness, potentially affecting reproductive success, pollinator interactions, and competition, particularly as climate change increases the variability of snowmelt patterns.

The comparison to 2015 phenology data at the site reveals that Mt. Baldy is no exception to the shifting trends in phenology over time, where plants are flowering earlier in response to warmer temperatures and earlier snowmelt (Cleland et al., 2007). The phenology of this site is already 2 to 3 weeks earlier than a decade ago: how will it be in another decade?

The supplemental ant visitation data suggests that there is a strong interaction between the ant and plant community in the alpine, potentially impacting future demographics. Ant visitation trends with the peak phenology of the various species, suggesting that ants are responding to nectar as a resource. However, when resource availability shifted (i.e. plants stop flowering), the ants moved to farming aphids. The timing of phenology is shifting, but the timing of other important ant resources, such as farming aphids, may be sensitive to other environmental cues (Mooney et al., 2023). From these observations, it is unclear how exactly ants impact the plant community, but we know they are up to something. The species identity of the ants and aphids are still under taxonomic review.

The surrounding plant community is important for understanding species diversity and abundance at the site. Because the 60 m plant survey only totaled ca. 4 hours of dedicated time, there may be more species diversity surrounding the site that I missed due to a lack of thoroughness. Early spring ephemerals and later autumn species may have also been missed, since the survey was only from July to

early August. Because this plant survey had vouchers collected for all species, the taxonomic identity of my collections can be verified in the future.

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Data availability statement

Data will be archived in accordance with the RMBL Education Program procedures, including the RMBL template metadata form and the default data repository, Environmental Data Initiative (EDI), <https://environmentaldatainitiative.org/>. All data will also be archived on the Macrosystems Ecology Laboratory Google Drive, managed by Dr. Blonder.

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Appendices

Appendix A. Annotated Plant Species List & Survey Results

#	Family	Genus	Species	Authority	Common Name	Core	West	East	Above	Below
HX402	Adoxaceae	Sambucus	racemosa	L.	Red elderberry			x		
HX370	Apiaceae	Ligusticum	porteri	Coult. & Rose	Osha		x	x		
BB10	Apiaceae	Pseudocymopterus	montanus	(A. Gray) J.M. Coult. & Rose	Alpine false spring parsley	x	x	x		x
HX366	Asteraceae	Achillea	millefolium	L.	Yarrow		x	x	x	x
BB15	Asteraceae	Agoseria	glauca	(Pursh) Raf.	Pale agoseris	x	x	x		x
HX416	Asteraceae	Antennaria	corymbosa	E. E. Nelson	Flat top pussytoes				x	
HX372	Asteraceae	Antennaria	rosea	Greene	Rosy pussytoes				x	x
HX361	Asteraceae	Arnica	parryi	A. Gray	Parry's arnica		x	x		
HX358, BB2	Asteraceae	Arnica	rydbergii	Greene	Subalpine arnica	x	x	x	x	x
BB7	Asteraceae	Chaenactis	douglasii	(Hook.) Hook. & Arn.	Douglas' dustymaiden	x	x	x	x	x
HX383	Asteraceae	Cirsium	eatonii	(A. Gray) B.L. Rob.	Mountaintop thistle				x	
HX418	Asteraceae	Erigeron	coulteri	Porter	Coulter's fleabane				x	
HX363	Asteraceae	Erigeron	elatior	(A. Gray) Greene	Tall fleabane		x			
HX417	Asteraceae	Erigeron	glacialis	(Nutt.) A. Nelson	Subalpine fleabane				x	
HX393	Asteraceae	Erigeron	leiomerus	A. Gray	Rockslide fleabane				x	
HX405	Asteraceae	Erigeron	speciosus	(Lindl.) DC.	Aspen fleabane		x	x		
HX400	Asteraceae	Helianthus	quinquenervis	(Hook.) A. Gray	Five-nerved sunflower		x			
BB5	Asteraceae	Heterotheca	villosa	(Pursh) Shinnars	Hairy goldenaster	x	x	x		x

HX371	Asteraceae	Hieracium	triste	Willd. ex Spreng.	Woolly hawkweed				x	
HX401	Asteraceae	Oreochrysum	parryi	Rydb.	Parry's goldenrod		x		x	
HX394	Asteraceae	Packera	werneriiifolia	(A. Gray) W.A. Weber & Á. Löve ex Trock	Alpine groundsel				x	
HX368	Asteraceae	Senecio	amplectens	A. Gray	Showy alpine ragwort			x	x	
BB3	Asteraceae	Senecio	crassulus	A. Gray	Thickleaf groundsel	x	x	x	x	x
HX355	Brassicaceae	Boechera	stricta	(Graham) Al-Shehbaz	Drummond's rockcress		x			x
HX392	Brassicaceae	Erysimum	capitatum	(Douglas) Greene	Western wallflower				x	
HX379	Brassicaceae	Noccaea	fendleri	(A.Gray) Holub	Fendler's pennycress		x	x	x	x
HX415	Campanulaceae	Campanula	parryi	A. Gray	Parry's bellflower				x	
HX391	Caprifoliaceae	Lonicera	involucrata	(Richardson) Banks ex Spreng.	Twinberry honeysuckle			x	x	
HX356	Caryophyllaceae	Androsace	septentrionales	L.	Rock jasmine		x	x		x
BB4	Caryophyllaceae	Arenaria	congesta	Nutt.	Ballhead sandwort	x	x	x	x	
HX384	Crassulaceae	Rhodiola	integrifolia	Raf.	King's crown				x	
HX382	Cyperaceae	Carex	chalciolepis	Holm	Copper-scaled sedge				x	
HX360	Cyperaceae	Carex	ebenea	Rydb.	Ebony sedge		x			
HX398	Cyperaceae	Carex	geyeri	Boott	Geyer's sedge					x
HX399	Cyperaceae	Carex	rossii	Boott	Ross's sedge					x
BB12	Cyperaceae	Carex	siccata	Dewey	Dry-land sedge	x	x	x		
HX365	Ericaceae	Vaccinium	cespitosum	Michx.	Dwarf blueberry		x		x	x
BB6	Fabaceae	Lupinus	argenteus	Pursh	Silvery lupine	x	x	x		x
HX385	Gentianaceae	Frasera	speciosa	Douglas ex Griseb.	Monument plant				x	
HX414	Gentianaceae	Gentiana	parryi	Engelm.	Parry's gentian		x		x	
HX362	Grossulariaceae	Ribes	montigenum	McClatchie	Mountain gooseberry		x			x
BB8	Hydrophyllaceae	Phacelia	hastata	Douglas ex Lehm.	Silverleaf phacelia	x	x	x	x	x

HX395	Hydrophyllaceae	Phacelia	sericea	(Graham) A. Gray	Silky phacelia			x	x	
HX374	Juncaceae	Juncus	parryi	Engelm.	Parry's rush				x	
HX413	Onagraceae	Chamerion	angustifolium	(L.) Holub	Fireweed		x	x		x
HX375	Orobanchaceae	Castilleja	occidentalis	Torr.	Western paintbrush				x	x
HX397	Orobanchaceae	Pedicularis	racemosa	Douglas ex Benth.	Sickletop lousewort					x
HX396	Pinaceae	Abies	lasiocarpa	(Hook.) Nutt.	Subalpine fir					x
HX403	Pinaceae	Picea	engelmannii	Engelm.	Engelmann spruce		x	x	x	x
HX409, BB9	Poaceae	Achnatherum	lettermanii	(Vasey) Barkworth	Letterman's needlegrass		x	x	x	x
HX408	Poaceae	Bromus	porteri	(Coult.) Nash	Porter's brome		x			
HX406	Poaceae	Deschampsia	cespitosa	(L.) P.Beauv.	Tufted hairgrass		x	x	x	x
HX412, BB11	Poaceae	Elymus	lanceolatus	(Scribn. & J.G. Sm.) Gould	Thickspike wheatgrass	x	x	x	x	x
HX404	Poaceae	Koeleria	spicata	(L.) Barberá et al.	Spike oatgrass			x		
HX376	Poaceae	Poa	cusickii	Vasey	Cusick's bluegrass	x	x	x	x	x
HX411	Poaceae	Poa	fendleriana	(Steud.) Vasey	Fendler's bluegrass	x	x	x	x	x
BB13	Polygonaceae	Eriogonum	umbellatum	Torr.	Sulphurflower buckwheat	x	x	x	x	x
HX388	Pteridaceae	Cryptogramma	acrostichoides	R. Br.	American parsley fern				x	
HX387	Ranunculaceae	Anemone	multifida	Poir.	Cutleaf anemone				x	
HX381	Ranunculaceae	Aquilegia	coerulea	E. James	Colorado blue columbine				x	
HX407	Ranunculaceae	Delphinium	barbeyi	(Huth) Huth	Subalpine larkspur			x		
HX367	Rosaceae	Fragaria	virginiana	Duchesne	Virginia strawberry		x	x	x	
HX369	Rosaceae	Geum	rossii	(R. Br.) Ser.	Alpine avens		x	x	x	
BB14	Rosaceae	Ivesia	gordonii	(Hook.) Torr. & A. Gray	Gordon's mousetail	x	x	x	x	x
HX378	Rosaceae	Potentilla	gracilis	Hook.	Slender cinquefoil		x		x	
HX410	Rosaceae	Potentilla	hippiana	Lehm.	Woolly cinquefoil					x

HX364	Rosaceae	Potentilla	pulcherrima	Lehm.	Beautiful cinquefoil		x	x	x	
HX386	Rosaceae	Rubus	idaeus	L.	Red raspberry				x	
HX373	Rosaceae	Sibbaldia	procumbens	L.	Creeping sibbaldia		x		x	
HX380	Saxifragaceae	Heuchera	parvifolia	Nutt.	Littleleaf alumroot				x	
HX389	Saxifragaceae	Saxifraga	bronchialis	L.	Spotted saxifrage				x	
HX357	Scrophulariaceae	Penstemon	whippleanus	A. Gray	Whipple's penstemon	x	x	x	x	
HX359	Valerianaceae	Valeriana	acutiloba	Rydb.	Sharpleaf valerian	x		x	x	
HX390	Valerianaceae	Valeriana	edulis	Nutt.	Edible valerian				x	
HX377	Violaceae	Viola	adunca	Sm.	Hookedspur violet				x	
BB16	Violaceae	Viola	praemorsa	Douglas ex Lindl.	Canary violet	x	x	x	x	x

Appendix B. Updated Key to Common Mt. Baldy Grasses

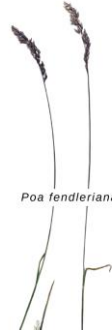
- 1a.** Awns present
- 2a.** Lemma awns longer (12-25 cm) and bent sharply twice, narrow panicles, spikelets appressed to the branches *Achnatherum lettermanii*
- 2b.** Lemma awns shorter (3–8 mm) and twisted but usually bent once, panicles more openly cylindrical and silvery-shiny, siltier soils. *Koeleria spicata*
- 1b.** Awns absent
- 3a.** Glumes flat and broadly lanceolate, each spikelet is distinct like a grain of rice, plants can turn purple/reddish in late summer *Elymus lanceolatus*
- 3b.** Not like above, glumes are small and the inflorescence is not appearing 2-dimensional
- 4a** Panicle open, purple-hued, and floppy *Deschampsia cespitosa*
- 4b.** Panicle compact, leaf tips curved like a boat genus *Poa*
- 5a.** Panicle deltoidal, 2-12 cm long. Generally shorter and denser in growth habit. Ligules 0.5-3 mm long, cobwebby hairs at base of callus. Blades up to 2 mm wide, uppermost flag leaf 0.5-5 cm long and usually closer to the inflorescence. *Poa cusickii*
- 5b.** Panicle cylindrical, 2-30 cm long. Generally taller and sparser in growth habit. Ligules usually ~1 mm long, cobwebby hairs at base of callus absent. Blades 1-4 mm wide, uppermost flag leaf < 1-2 cm long and farther from inflorescence. *Poa fendleriana*



Achnatherum lettermanii



Poa cusickii



Poa fendleriana