Check for updates

Earlier snowmelt and reduced summer precipitation alter floral traits important to pollination

John M. Powers*,#,1,2, Heather M. Briggs#,1,2, Rachel G. Dickson2, Xinyu Li1,2 and Diane R. Campbell1,2

*corresponding author: Phone: +1-801-606-7276; powersj1@uci.edu, ORCID: orcid.org/0000-0001-9926-4548

#John M. Powers and Heather M. Briggs should be considered joint first author

1Department of Ecology and Evolutionary Biology, University of California, Irvine, CA, 92697, USA

2Rocky Mountain Biological Laboratory, Crested Butte, CO, 81224, USA

Running head: Snowmelt timing and precipitation

Paper type: Primary research

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/GCB.15908

This article is protected by copyright. All rights reserved

Accepted Article

Abstract

Climate change can cause changes in expression of organismal traits that influence fitness. In flowering plants, floral traits can respond to drought, and that phenotypic plasticity has the potential to affect pollination and plant reproductive success. Global climate change is leading to earlier snowmelt in snow-dominated ecosystems as well as affecting precipitation during the growing season, but the effects of snowmelt timing on floral morphology and rewards remain unknown. We conducted crossed manipulations of spring snowmelt timing (early vs. control) and summer monsoon precipitation (addition, control, and reduction) that mimicked recent natural variation, and examined plastic responses in floral traits of *Ipomopsis aggregata* over three years in the Rocky Mountains. We tested whether increased summer precipitation compensated for earlier snowmelt, and if plasticity was associated with changes in soil moisture and/or leaf gas exchange. Lower summer precipitation decreased corolla length, style length, corolla width, sepal width, and nectar production, and increased nectar concentration. Earlier snowmelt (taking into account natural and experimental variation) had the same effects on those traits and decreased inflorescence height. The effect of reduced summer precipitation was stronger in earlier snowmelt years for corolla length and sepal width. Trait reductions were explained by drier soil during the flowering period, but this effect was only partially explained by how drier soils affected plant water stress, as measured by leaf gas exchange. We predicted the effects of plastic trait changes on pollinator visitation rates, pollination success, and seed production using prior studies on *I. aggregata*. The largest predicted effect of drier soil on relative fitness components via plasticity was a decrease in male fitness caused by reduced pollinator rewards (nectar production). Early snowmelt and reduced precipitation are strong drivers of phenotypic plasticity, and both should be considered when predicting effects of climate change on plant traits in snow-dominated ecosystems.

Accepted Article

This article is protected by copyright. All rights reserved.

Key words: climate change, drought, floral morphology, floral rewards, *Ipomopsis*, phenotypic plasticity, precipitation, snowmelt timing

Introduction

One way that organisms can respond to climate change is by altering expression of phenotype directly in response to the new environment (Franks et al. 2014; Merilä and Hendry 2014). Such phenotypic plasticity may or may not be adaptive (Caruso et al. 2006). Plants show plastic changes to climatic factors, such as water, in a wide variety of phenotypic traits, including leaf and physiological traits (Anderson and Gezon 2015; Campbell and Wendlandt 2013), timing of flowering (Anderson et al. 2012; CaraDonna et al. 2014; Hegland et al. 2009; Inouye 2008), floral morphology and rewards (Gallagher and Campbell 2017; Waser and Price 2016), and floral scent (Glenny et al. 2018). Such plastic changes have the potential not only to influence persistence of plant populations, but also to alter interactions with animal pollinators and herbivores. Although how water availability influences floral traits has been studied in several systems (reviewed in Descamps et al. 2021; Kuppler and Kotowska 2021), most studies have utilized potted plants in greenhouses or growth chambers (Burkle and Runyon 2016; Campbell et al. 2019; Carroll et al. 2001; Caruso 2006; Descamps et al. 2018; Suni et al. 2020). Only a small number of experiments have manipulated summer precipitation or soil moisture in the field (e.g., Campbell and Wendlandt 2013; Galen 2000; Gallagher and Campbell 2017; Gallagher and Campbell 2021; Walter 2020), simulating more realistic environmental scenarios.

To connect changes in water availability to expression of floral traits, we not only need field studies that simulate realistic environmental scenarios, we also need studies that consider a wider range of mechanisms through which climate can influence water availability besides precipitation during the growing season. In most areas at high latitude or high elevation, water availability to plants is affected not only by summer precipitation but also by snowpack and

This article is protected by copyright. All rights reserved.

snowmelt timing (Blankinship et al. 2014). In such areas around the globe, warming winter and spring temperatures are causing snow to melt earlier compared to preindustrial times (Clow 2010; Pederson et al. 2011; Stewart et al. 2005), which also reduces soil moisture during the early parts of summer (Blankinship et al. 2014; Seager et al. 2013). Although it is well-known that flowering time is advanced by early snowmelt (CaraDonna et al. 2014), the impact of snowmelt timing on phenotypic expression of floral traits is unknown. A few studies have investigated responses of reproductive traits such as inflorescence height, flower number, or number of flowering stalks to snowmelt date (Bemmels and Anderson 2019; Iler et al. 2019), but not, to our knowledge, traits of the flowers themselves. Depending on their life history strategy, plants can source water from either winter precipitation (directly as winter rainfall or as snowmelt in the spring), summer precipitation, or both, as revealed by stable isotope studies of xylem water (Alstad et al. 1999; Ebbs 2016; Ehleringer et al. 1991; Gierke et al. 2016; Hu et al. 2010). Therefore, it is unclear if enhanced precipitation during the summer can compensate for the negative effects of early snowmelt on plant traits, or if a late-melting snowpack can compensate for summer drought. Anticipating when such compensation might occur is made more difficult because most field studies of water-mediated changes in floral traits do not simultaneously measure any physiological indicator of water stress to the plant (Descamps et al. 2021), but see Campbell and Wendlandt (2013). A recent meta-analysis of drought effects on floral traits has called for more studies that simultaneously address water stress (Kuppler and Kotowska 2021) through mechanisms such as reduced stomatal conductance (Cowan 1978).

To determine if climate-induced plasticity in floral traits is neutral, maladaptive, or adaptive (Caruso et al. 2006), a first step is to determine if a trait change influences plant fitness or fitness components, such as pollinator visitation rates, pollen receipt, or pollen export (Descamps et al. 2021). Only a handful of studies have demonstrated impacts of water-mediated changes in floral traits on pollinator visitation rates in the field (Al-Ghzawi et al. 2009; Burkle and Runyon 2016; Gallagher and Campbell 2017; Descamps et al. 2018; Glenny et al.

This article is protected by copyright. All rights reserved.

2018; Walter 2020) or in a flight cage (Kuppler et al. 2021), and all have manipulated summer precipitation only.

We studied the effects of both snowmelt timing and summer precipitation on flowers of the subalpine plant *Ipomopsis aggregata* (Polemoniaceae) through factorial manipulation of snowmelt and precipitation over three years. Our manipulations simulated realistic changes in climate in the Rocky Mountains that will likely occur over the next few decades. In our region of study in Colorado, USA, snowmelt date has advanced from 1935 - 2016 (Wadgymar et al. 2018) and has been advancing more quickly over the most recent four decades (1975 - 2018, Campbell 2019). Because summer precipitation is not common at our study site until after the onset of monsoon rains in July, earlier snowmelt creates a longer drought period in the early summer, resulting in lower soil moisture. The duration and severity of this early summer drought is predicted to increase with climate change and will cause reduced plant productivity and increased water stress in this region (Sloat et al. 2015). In the southern Rockies and Colorado Plateau, dry periods are becoming longer (Zhang et al. 2021), and the difference between precipitation and evapotranspiration is also expected to decline over the next two decades (Seager et al. 2013). In *Ipomopsis aggregata* the effects of several floral traits on pollination success are known (Campbell et al. 1996; Campbell et al. 1991; Mitchell 1993). Previous experiments have demonstrated some impacts of summer water on traits of *I. aggregata*, but not investigated the effects of snowmelt timing on traits. In a previous field experiment, increasing summer precipitation increased the number of flowers per reproductive individual and decreasing precipitation shortened corollas, but these treatments did not significantly influence corolla width or nectar production, perhaps because of the relatively small sample size (18 *I. aggregata* plants; Campbell and Wendlandt 2013). Greenhouse studies indicate that increased water can enhance pollen and nectar production (Waser and Price 2016) and alter the composition of floral volatiles in this species (Campbell et al. 2019). Although there are no previous manipulations of snowmelt timing, in a 25-year observational study, plants produced

This article is protected by copyright. All rights reserved.

fewer seeds, but not fewer flowers per reproductive individual, in years with earlier snowmelt (Campbell 2019). For several floral traits of *I. aggregata* (including all traits measured in this study with the exception of nectar concentration) we have independent evidence on how pollinator visitation, pollination success based on pollen import, pollen export, or seed production respond to trait values (Campbell 1989a). Hummingbird visitation rates increase with corolla length (Campbell et al. 1991), corolla width (Campbell et al. 1997), and nectar production (Mitchell 1993). Plants with wider corollas also export more pollen to other individuals (Campbell et al. 1996). Style length influences pollen receipt on the stigma (Campbell et al. 1994), and stamen length influences pollen exported to other flowers (Campbell et al. 1998). Narrower sepals are oviposited on less frequently by a fly (*Delia* sp.) that is a pre-dispersal seed predator (Campbell et al. 2002) and thus allow seeds to escape predation. Increased corolla length, flower number, and inflorescence height increase fruit or seed production (Campbell 1989b; Juenger and Bergelson 1997 (Campbell and Powers 2015). Therefore, plastic changes in these floral traits have the potential to influence fitness.

We asked the following questions. 1. How does an advancement in timing of snowmelt and an increase or decrease in summer precipitation influence flower number, inflorescence height, floral morphology, and nectar quantity and quality? 2. Do the effects of manipulating snowmelt timing and summer precipitation interact, and can increased summer precipitation compensate for impacts of early snowmelt on trait values? 3. To what extent are effects on floral traits driven by changes in soil moisture and consequent changes in photosynthetic rate and stomatal conductance (data from Navarro et al. 2021)? 4. What are the predicted effects of the trait changes on pollinator visitation rates, pollination success, and seed production, based on previous measures of selection on those traits?

Accepted Article

This article is protected by copyright. All rights reserved.

Materials and Methods

Study system

Ipomopsis aggregata ssp. *aggregata* is an herb that is widespread across montane to subalpine habitats of the western United States (Grant and Wilken 1986). Our study site was located at Maxfield Meadow, a dry open subalpine meadow 1.0 km south of the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado, USA at 38.9495°N, 106.9908°W and 2880 m above sea level in the West Elk Mountains. In this region, *I. aggregata* plants spend 2 to 10+ years as a vegetative rosette, after which they put up a flowering stalk, flower during a single season, and die, with only rare cases of iteroparity (Campbell 1997). Plants are self-incompatible and require pollinators for seed production, with 94% of pollinator visits made by hummingbirds and the remainder by insects (Price et al. 2005).

Snowmelt and precipitation manipulations

To simulate two aspects of future climate change that affect water availability and its timing throughout the growing season, we established an experimental manipulation of summer precipitation and snowmelt, and then measured floral traits over three years, 2018 - 2020. We used a replicated split-plot design with snowmelt manipulated at the plot level and precipitation manipulated at the subplot level. The treatments were applied to the same plots each year, so plants surviving to the third year experienced the longest treatment time. Six 7 m × 7 m plots were established within a 45 m × 25 m area of Maxfield Meadow (Figure 1), and three were randomly assigned an early snowmelt treatment where a black 55% woven shade cloth was applied over the entire plot in the spring to accelerate snowmelt by absorbing more heat while leaving snowmelt volume unaffected (Leonard et al. 2020). Shade cloths were set out during spring melt off when snow height reached an average of 100 cm across the study site, monitored, and removed right after bare ground became visible. In 2019, a large avalanche ran

This article is protected by copyright. All rights reserved.

through the site and deposited snow and debris, resulting in a later deployment and removal of shade cloth in two plots (dates shown in Figure S1). The date of snowmelt in each plot was established when light levels reached 82 W/m^2 (a threshold that empirically separated snow cover from direct sunlight based on visual inspection of the data) in the spring, using a light logger placed vertically in the middle of each plot in the fall (HOBO Pendant Temperature / Light Data Logger, Onset Computer Corporation, Massachusetts, USA). The 2019 avalanche added snow that prevented early snowmelt in one plot, so for analysis we recoded it as having normal snowmelt timing.

Observations and projections of earlier snowmelt with climate change are driven by both warmer spring temperatures and less winter snow accumulation (Clow 2010). In Gothic (1.5 km north and 40 m higher in elevation than the study site), spring snowpack depth has decreased from 1973 - 2016, and snowmelt timing has advanced by 1.4 ± 0.5 days per decade from 1935 - 2021 (slope ± SE, $R^2 = 0.08$, $P = 0.007$, data from Wadgymar et al. 2018 updated with latest values from billy barr, http://www.gothicwx.org/ground-cover.html, Figure S2). Depending on the year and plot, the black cloth treatments accelerated snowmelt by 3 - 11 days (mean ± SD, 6 ± 2 days) compared to the average unmanipulated plot (Figure 2). This acceleration is equivalent to 42 ± 22 y of future snowmelt advancement assuming continuation of climate change at the same rate. During the three years of the study, the combination of snowmelt treatments and interannual variation spanned the range of snowmelt dates observed over 1990 - 2017 (Figure 2).

Within each of the six snowmelt plots, four 2 m × 2 m subplots arranged in a square were randomly assigned one of four summer precipitation treatments (Figure 1), which were applied for the dates shown in Figure S1. First, a water addition treatment simulated doubled summer precipitation based on the historical average in July from 1989 - 2006 measured at the EPA CASTNET weather station GTH161, 0.9 km northeast of Maxfield Meadow (Campbell and Wendlandt 2013, https://www3.epa.gov/castnet/site_pages/GTH161.html). We added 14 L of

This article is protected by copyright. All rights reserved.

192 tap water evenly to each 4 m^2 subplot every 2 days to supplement precipitation by 1.75 mm/day.
193 Note that this treatment increased the frequency of precipitation and started before the arrival of
194 summer monsoons in each year. Second, a water reduction treatment intercepted
195 approximately 50% of incoming precipitation using a half-covered 2 m × 2 m rainout shelter. The
196 rainout shelters were constructed with a PVC pipe skeleton, with sloping clear corrugated plastic
197 greenhouse roofing slats spaced evenly on top to cover half of the plot's surface area (Yahjdian
198 and Sala 2002). Intercepted rainwater ran down these slats into an attached gutter, which then
199 fed into a bucket on the ground. Shelters were open on all four sides to allow access by
200 pollinators and small herbivores, and in a previous study did not significantly reduce light levels
201 (Campbell and Wendlandt 2013). The shelter frames were camouflaged with green and brown
202 paint to reduce deterrence or attraction of pollinators and herbivores. Third, mock rainout
203 treatments controlled for any effects of the physical PVC structures but lacked slats to intercept
204 rain. Fourth, control subplots were unmanipulated and received ambient rainfall. To assess the
205 effects of the precipitation manipulations, ambient summer precipitation, evaporation, and
206 infiltration, soil moisture was measured approximately weekly for the date ranges given in
207 Figure S1. A 12 cm soil moisture probe (HydroSense II, Campbell Scientific, Utah, USA) took
208 measurements of volumetric water content (VWC) at the four corners and center of each
209 subplot, which were averaged prior to analysis. Although there was some slope to the plots,
210 measurements of soil moisture were similar for the top and bottom of each subplot. We
211 estimated daily summer precipitation in each subplot following Methods S1. During the three
212 years of the study, the precipitation treatments spanned the range of summer precipitation totals
213 observed over 1990 - 2017 (Figure 2).
214

Accepted Article

This article is protected by copyright. All rights reserved.

Trait measurements

Flower number was assessed as the total number of flowers produced during the growing season, calculated as the sum of total harvested fruits, flowers, and elongated buds by the end of the season, plus any flowers and buds destroyed for sampling. A given plant typically flowers for 4 - 5 weeks. The calyces of fruits are retained on the plant following seed dispersal or abortion, making it possible to obtain a count of total flowers produced by the plant. We also recorded the height of the tallest inflorescence of each plant weekly (Figure S1). Each year, we measured 1 - 10 flowers on each plant for floral morphology (average of 2.4 measurements per plant) or nectar (average of 1.7 flowers per plant), collected throughout the summer as they flowered (range of dates in Figure S1). Floral morphology measures were made with calipers and included corolla length and width at the opening, style length, and minimum and maximum stamen length (Campbell 1989a). Sepal width (Campbell et al. 2002) was measured in 2019 and 2020. Nectar production rate and concentration were assessed by excluding pollinators from elongated unopened flower buds for 48 hr with a bent plastic straw (Mitchell 1993). Nectar volume was measured with microcapillary tubes and sucrose concentration with a hand-held refractometer (Campbell et al. 1991). Multiplying nectar production by concentration yielded nectar sugar. Plants in all treatments were measured on a given day, so there were no systematic differences in timing of measurement across the season. The floral morphology measurements are highly repeatable for flowers on a given plant (Campbell 1992), but nectar production does respond to water stress in the related species *I. longiflora* (Villarreal and Freeman 1990). All traits except flower number were averaged across the summer for each plant.

Across the three years of the study, we measured floral morphology on 494 plants (6.9 per subplot per year), nectar concentration and production on 432 plants (6.0 per subplot per year), flower number on 610 plants (8.5 per subplot per year), and inflorescence height on 674

This article is protected by copyright. All rights reserved.

plants (9.4 per subplot per year). The numbers of unique plants are slightly lower because 4% of plants that flowered survived to flower a second year, usually from a second rosette after an inflorescence was browsed by deer (Brody et al. 2007). Minimum and maximum stamen length were strongly correlated with corolla length at the plant level ($r = 0.88$ and 0.86, $N = 494$, $P < 0.001$). We did not consider it possible to separate effects on those traits from effects on corolla length, so they were not analyzed. All remaining traits had absolute correlations < 0.7 at the plant level, with the highest correlations between style length and corolla length ($r = 0.65$), corolla width and corolla length ($r = 0.40$), and inflorescence height and flower number ($r = 0.37$). There was a weak negative correlation between nectar production and concentration ($r = -0.27$).

Statistical analyses

Questions 1 and 2: Impacts of snowmelt timing, summer precipitation, and the interaction

We analyzed the effect of snowmelt timing, summer precipitation, and their compounding effects on each trait in two ways: first as a response to the experimental manipulations and years coded as discrete levels, and second as a correlation with continuous environmental variables affected by both the treatments and natural variation among years. In the first set of models, we conducted a replicated split-plot analysis of the effects of snowmelt treatment, precipitation treatment, year, and their interactions on the trait, averaged by plant. In this split-plot design, snowmelt was applied at the level of plot, and the random effect of plot accounted for differences in conditions among individual plots. The precipitation treatment was applied at the level of each subplot within a plot, so we included a random effect of subplot nested within plot to capture the non-independence of plants within a subplot. To test if increasing summer precipitation can compensate for early snowmelt, we compared means in early snowmelt plots receiving additional water with means in control snowmelt plots receiving

This article is protected by copyright. All rights reserved.

ambient levels of water using the *glht* function of the R package *multcomp* (Hothorn et al. 2008). We used the same methods to test for differences between the precipitation addition or reduction treatments and controls. For the above split-plot analyses, we treated both the mock rainout and unmanipulated precipitation treatments as the same control treatment because no significant differences were detected in soil moisture or traits between the two treatments using the *glht* function after applying a Bonferroni correction for multiple comparisons, and combining the treatments did not greatly affect the ANOVA results.

The first set of models have the advantage of testing directly for impacts of snowmelt timing and summer precipitation, but the disadvantage that our manipulations only accelerated snowmelt by 3 - 11 days, a small range compared to the natural variation across years. We detected strong effects of year, but these could potentially be explained by interannual variation in environmental conditions other than snowmelt timing, including snowpack, spring or summer temperatures, or precipitation. Frost events that reduce flowering for some early-flowering species in some years (Inouye 2008) have little impact on *I. aggregata*, which generally form buds after frosts (D. Campbell, pers. obs.). Biotic factors such as herbivory or plant-plant interactions may also vary among years, as well as the resources that plants gained or lost in previous years due to environmental or biotic conditions. Additionally, an interaction between year and either of the two treatments could result from interannual variation in the acceleration of snowmelt by the cloth treatments or variation in the amount of precipitation intercepted by the reduction treatment. For these reasons, and to make use of the wider natural variation in snowmelt timing across the three years, we ran a second set of models that analyzed the correlations of traits with two environmental variables that change among years, treatments, and plots: snowmelt timing (the date in each plot) and summer precipitation (estimated for each precipitation treatment). This approach had the statistical power advantages of assessing a wider range of snowmelt timings as well as utilizing more precise estimates of precipitation. However, it is correlational in that both the experimental treatments and natural variation

This article is protected by copyright. All rights reserved.

influence these two variables, and they may covary across years with the other environmental variables mentioned above. To compare responses of different plant traits to the two environmental variables and their interactions, we plotted curves of the estimated marginal means for trait values (standardized by dividing by plant means) across the range of snowmelt dates and for a set of fixed summer precipitation values using the R package *emmeans* (Lenth et al. 2018). These plots allow visual interpretation of how one environmental variable can compensate and/or exacerbate the effect of the other, and standardization of the traits allows comparison of effect sizes (slopes or line spacing).

For both sets of analyses, linear mixed models were fit for each trait averaged by plant using the *lmer* function of the R package *lme4* (Bates et al. 2015) with random effects of plot and subplot, using the Kenward-Roger method to determine degrees of freedom conservatively and *lmerTest* to calculate P-values (Kuznetsova et al. 2017). The marginal R^2 goodness-of-fit for the variance explained by the fixed effects (Nakagawa and Schielzeth 2013) was calculated using the *MuMIn* R package (Bartoń 2020). Model assumptions were verified by inspecting plots of residuals for normality and homoscedasticity and plots of random effects for normality.

Question 3: Soil moisture as a mechanism

We first tested how soil moisture was affected by the snowmelt date, precipitation treatments, year, and interactions among those variables. The linear mixed model was fit to the average soil moisture in each subplot across the measurement period, with random effects of plot and subplot to match the split-plot design with repeated measures across years. The estimated marginal means were compared across levels of each treatment factor.

Then, to determine the extent to which impacts on floral traits are mediated by soil moisture, we fit linear mixed models for each trait averaged by plant, with a random effect of subplot and fixed effects of the year, the average soil volumetric water content across the measurement period (as a single plant blooms over 4 - 5 weeks), and their interaction. In this

This article is protected by copyright. All rights reserved.

case, we only included subplot as a random factor because the model is not testing for effects of the experimental treatments separately from the spatial variation among subplots that exists independent of the treatments. To compare responses of different plant traits to soil moisture, we plotted curves for each year based on estimated marginal means for the standardized trait values. Because five morphological traits were associated with flower size and had correlations with each other > 0.35 (corolla length and width, style length and minimum and maximum stamen length), we also used a redundancy analysis (RDA) to test the effect of soil moisture, year, and their interaction on these traits simultaneously. RDA is a multivariate method that shows the variation in potentially correlated traits that is explained by environmental predictors by performing a principal component analysis of the fitted values from multiple regressions of each trait on all environmental predictors (Legendre and Legendre 1998).

To examine how floral trait changes could be mediated by changes in physiological status, we combined the floral trait measurements with data from a separate study of how the same manipulations in the same experiment influenced leaf gas exchange (photosynthetic rate and stomatal conductance expressed on a per area basis) of vegetative plants (Navarro et al. 2021). Flowering plants of *I. aggregata* divert all of their resources into flowers as their leaves senesce over the summer, lowering their rates of photosynthesis gradually and complicating assessment of their physiological status from leaves (Campbell et al. 2005), so as a proxy we used the average gas exchange values of the vegetative plants measured in the same subplot and year as the flowering plants. To explore the extent to which traits respond directly to soil moisture versus indirectly through its effects on leaf gas exchange, we used structural equation modeling. All data points, including both the exogenous variable of soil moisture and all of the endogenous variables, were mean values for a subplot and thus independent units. Structural equation modeling allows specification of a causal network of paths (Grace et al. 2010) in which leaf gas exchange can potentially play a role translating effects of soil moisture into responses of floral traits. We compared three *a priori* nested models using log-likelihood ratio tests based

This article is protected by copyright. All rights reserved.

on differences in chi-square values (Mitchell 1992). First we examined a full model (Model 1) in which soil moisture (the one exogenous variable) could influence each floral trait directly or indirectly, as mediated by photosynthetic rate or stomatal conductance, with correlations allowed between the two physiological measurements, and among all floral traits. We did not include sepal width as we had measurements for that trait from only two years. We used nectar sugar rather than concentration because concentration combines the influence of water and carbohydrates. Photosynthetic rate could mediate effects on floral traits by increasing carbohydrate resources for making larger flowers or more nectar sugar. Stomatal conductance could mediate effects on nectar production (nectar volume per day) by changing water loss from the plant. Direct effects of soil moisture not mediated by leaf gas exchange could reflect changes in uptake of soil nutrients, or for nectar production simply a change in water available in the soil. Model 2 contained only the direct paths without intermediaries of photosynthetic rate or stomatal conductance. Model 3 contained only the indirect paths through photosynthetic rate or stomatal conductance. Structural equation modeling employed PROC CALIS in SAS version 9.3.

Question 4: Predicted effects of floral trait changes on pollination success

We examined the predicted effects of floral trait changes on fitness components for traits that met two criteria: soil moisture had a significant effect on the trait, and previous studies had measured how much a relative fitness component changes with a change in mean value for the trait. Traits that met both criteria were corolla length, corolla width, style length, and nectar production. Pollinator visitation rates can increase with longer corollas, wider corollas, and nectar production (Campbell et al. 1991; Mitchell 1993; Campbell et al. 1997). Pollen receipt on stigmas increases with longer styles, and pollen exported to flowers on other plants of this self-incompatible species increases with wider corollas and higher nectar production (Campbell 1989a; Mitchell 1993). These studies had ranges for trait values similar to those in the current

This article is protected by copyright. All rights reserved.

study. Although one nectar study (Mitchell 1993) was a manipulative study, the nectar addition of 5 µL was within the natural range produced per day in our study (range = 0 - 12 µL with one outlier of 18 µL). Seed production also increases with corolla length and corolla width in a hybrid zone with a wider range of trait values, although the intensity of this selection varies greatly across years with stronger selection associated with later snowmelt (Campbell and Powers 2015). We used standardized selection differentials from these studies, which provide the change in relative fitness for each change of one standard deviation across plants in the trait, i.e. a standardized trait. We multiplied the slopes of the standardized traits on soil moisture determined under Question 3 (averaged across the three years) with these standardized selection differentials to predict the change in a relative fitness component per change in soil moisture, recognizing that there is considerable uncertainty around the quantitative estimates of selection.

Results

Questions 1 and 2: Impacts of snowmelt timing, summer precipitation, and the interaction

We first examined the effects of the year, the summer precipitation and snowmelt treatments, and their interactions on floral traits using the replicated split-plot models (Table 1, Figure 3). Whereas the snowmelt treatment elicited no main effects on floral traits in these models (all $P > 0.08$), it did influence nectar production and flower number in ways that depended on the year (Table 1; interaction $P < 0.01$). Compared to controls, precipitation reduction reduced corolla length, style length, and sepal width, and precipitation addition increased corolla length, corolla width, and nectar production, and decreased nectar concentration (post-hoc tests in Table 1). The effects of the precipitation treatments only varied across years for sepal width (interaction $P < 0.01$), which showed a stronger effect of precipitation in an early snowmelt year (2020), than in a late snowmelt year (2019). There were differences among years for all floral traits except

This article is protected by copyright. All rights reserved.

flower number. Compared to 2019 and 2020, flowers were smaller in 2018, and produced less nectar that was more concentrated. Inflorescences were taller in a late snowmelt year (2019). There were no detected interactions between the snowmelt and precipitation treatments on any trait (all $P > 0.31$). The summer precipitation addition treatment compensated for the effect of the early snowmelt treatment in years where it occurred; generalized linear hypothesis tests found no differences between subplots with early snowmelt and precipitation addition versus normal snowmelt with control precipitation (all $P > 0.09$), except for corolla width, where added precipitation overcompensated for earlier snowmelt, leading to wider corollas than in the control plots ($P = 0.03$).

We examined the responses of floral traits to the actual snowmelt dates and the total summer precipitation experienced by the flowering plants using our second set of models that incorporated both experimental effects and natural variation in those climatic variables (Table S2, Figure 4). For snowmelt date, these models detected effects that were not significant in the first models, because of low replication of the snowmelt manipulation and the greater statistical power achieved with incorporating the full range of snowmelt dates over a period of 46 days rather than an average manipulation of 6 days. Earlier snowmelt date reduced corolla length, style length, corolla width, sepal width, nectar production, and inflorescence height, and increased nectar concentration (all $P < 0.02$), but had no detected effect on flower number ($P = 0.60$). The standardized effects of snowmelt timing varied by trait, with inflorescence height and nectar concentration responding most strongly. Lower total summer precipitation (calculated based on the treatments applied to each subplot) reduced corolla length, style length, corolla width, and sepal width ($P < 0.05$), but did not have detected effects on other floral traits ($P > 0.05$). The negative effect of reduced precipitation on corolla length and sepal width strengthened with earlier snowmelt (interaction $P < 0.01$), but no other traits showed this interaction between the two climate variables ($P > 0.06$). For the traits that showed effects of the two climate variables but not an interaction, we estimated the amount of additional total summer

This article is protected by copyright. All rights reserved.

precipitation required to compensate for each day that snowmelt occurs earlier: 2.6 ± 0.5 mm for corolla width and 5.4 ± 1.6 mm for style length (mean ± SE), or 3 - 6% of the average total summer precipitation in this area (86 mm, 1990 - 2020). At the current rate of snowmelt advancement in this area (1.4 days / decade, Figure S2), this corresponds to a 4 - 7% increase in summer precipitation required per decade to maintain similar corolla widths or style lengths.

Question 3: Soil moisture as a mechanism

Soil moisture varied among years in both the overall average and in the seasonal pattern across the measurement period (Figure S3, Table S1). The early snowmelt treatment reduced average soil moisture by 0.6 ± 0.2% VWC, precipitation addition increased it by 1.8 ± 0.2% VWC, and precipitation reduction reduced it by 0.5 ± 0.2% VWC. Although the main effect of snowmelt treatment was insignificant overall ($P = 0.06$), it had a higher effect in the earlier years of 2018 and 2020 (year × snowmelt treatment interaction, $P < 0.01$). We detected no interaction between the effects of the snowmelt and precipitation treatments on soil moisture. From estimates derived from precipitation data, we infer that plants underwent a 40-day early summer drought with soil moisture < 4% VWC during 2018 (Figure S3) that is not reflected in our soil moisture measurements that occur after treatments are applied.

Decreasing soil moisture was associated with reduced corolla length, style length, corolla width, sepal width, and nectar production, and increased nectar concentration (Figure 5, Table S3). The standardized effects of soil moisture varied by trait, with the strongest effect on nectar production and the weakest on inflorescence height and flower number. The effect of soil moisture varied in magnitude across years (interaction $P < 0.05$) for two traits: there was a weaker effect on sepal width in a late snowmelt year (2019) compared to an early year (2020), and there was a slightly stronger effect on corolla width in 2020. Trait averages also varied across years ($P < 0.01$) for corolla length, corolla width, and sepal width, which were all larger in the late snowmelt year of 2019, and for nectar concentration, which was lower in 2019 (Figure

This article is protected by copyright. All rights reserved.

5). Considering floral morphology as an integrated trait, the multivariate RDA analysis also detected effects of soil moisture and year (both $P < 0.001$), but not an interaction between them (Figure S4).

The relationships of floral traits to soil moisture were partially mediated by how soil moisture altered leaf gas exchange. The full model with direct paths from soil moisture to traits as well as paths mediated through photosynthetic rate or stomatal conductance fit better than either of the nested models (difference in chi-square = 30.3, 5 df and 25.7, 5 df). All of the floral traits tested (corolla length, style length, corolla width, nectar production, and nectar sugar) responded to soil moisture through direct mechanisms that were not mediated by photosynthetic rate or stomatal conductance, while only three of the traits showed responses mediated by gas exchange (Figure 6). Subplots with higher average photosynthetic rate also had plants with wider corollas (standardized path coefficient = 0.37, $P = 0.0011$) and longer style (standardized coefficient = 0.35, $P = 0.0031$), while subplots with higher stomatal conductance and thus less water stress also had plants with higher nectar production (standardized path = 0.23, $P = 0.0012$). The strongest path detected was between soil moisture and nectar production (standardized path = 0.46, $P < 0.0001$). Although the path from soil moisture to stomatal conductance was not significant ($P > 0.05$), stomatal conductance and photosynthetic rate were highly correlated ($P < 0.0001$; Figure 6). The reduced models gave similar results, with evidence for direct paths from soil moisture to each floral trait (Figure S5A) and indirect paths mediated by gas exchange for 4 of the traits, corolla length as well as style length, corolla width, and nectar production (Figure S5B).

Question 4: Predicted effects of floral trait changes on pollination success

We combined our findings of how traits changed with soil moisture with prior estimates of selection to predict how drier soils will affect pollination success and fitness through changes in floral morphology and rewards. In previous studies, standardized selection differentials on

This article is protected by copyright. All rights reserved.

corolla length, corolla width, style length, and nectar production ranged from zero to 0.53, depending on the trait and fitness component (Table 2). Multiplying the slopes of traits on soil moisture by these estimates of selection (when significant) indicated that relative fitness components would decrease between 0 and 11.5% for every decrease of 1% VWC (Table 2). Of these four traits, the largest predicted impact on fitness was a decrease in male fitness (as estimated by pollen export) due to less frequent pollinator visitation caused by reduced nectar production of plants flowering in drier soils. Slightly weaker negative impacts on pollinator visitation and pollen export are predicted due to shorter corollas in drier soils. Female fitness as estimated by seed production is also predicted to be reduced by drought; dry soils that shorten corollas will reduce pollinator visitation and seed production, and dry soils that shorten styles are predicted to reduce pollen receipt.

Discussion

Changes in floral trait expression in response to snowmelt and precipitation

This study demonstrated that early snowmelt and reduced precipitation during the growing season can both impact the expression of floral traits important for pollination. Both environmental changes reduced soil moisture and by doing so caused a subalpine plant, *Ipomopsis aggregata*, to produce shorter corollas and styles, narrower corollas and sepals, and lower volumes of more concentrated nectar. Advancing snowmelt experimentally by just 6 days on average did not significantly affect the measured floral traits (replicated split-plot models). However, all measured aspects of floral morphology, nectar, and inflorescence height did vary detectably with the absolute snowmelt date that varied by 46 days across the 3 years of study. Early snowmelt, but not reduced summer precipitation or lower soil moisture, led to shorter inflorescences. That result suggests that inflorescence height responded to soil moisture during the early season prior to our measurements, or perhaps to frosts during that same period.

This article is protected by copyright. All rights reserved.

Whereas plants reduced flower size and the amount of water in the nectar, neither snowmelt timing nor summer precipitation affected the total number of flowers. This result is consistent with findings from a 25-year study of *I. aggregata* demonstrating a lagged association between snowmelt date and flower number for plants that flowered the year following an early snowmelt, but not plants that flowered the year of early snowmelt (Campbell 2019). For corolla length and sepal width, plants were more sensitive to changes in precipitation in years with early snowmelt, possibly because they relied more on summer precipitation than water from snowmelt for producing flowers in those years.

These results add to studies of other species that have also reported general reductions in flower size with reduced water during the growing season (Descamps et al. 2021; Gallagher and Campbell 2017; Suni et al. 2020). Responses of nectar and pollen to water availability have been mixed; for example, nectar volume was higher for dry plants in *Phlox drummondii* (Suni et al. 2020), but higher for wet plants in *Epilobium angustifolium* (Carroll et al. 2001) and *Mertensia ciliata* (Gallagher and Campbell 2017). In our analysis of the effect of soil moisture, we found that decreased water availability strongly reduced nectar production in *I. aggregata* (0.22 µL/day/%VWC), complementing other work in this species showing reductions in both pollen and nectar production with soil moisture (Waser and Price 2016; estimated effect on nectar production was 0.40 µL/day/%VWC). Our work is unusual in that we examined how traits of individual flowers respond to snowmelt timing. This research is timely because in tundra and subalpine ecosystems around the world (Pederson et al. 2011; Assmann et al. 2019; Sun et al. 2019), there are strong trends towards earlier snowmelt dates with recent and predicted climate change, while predictions for summer precipitation have high variability (IPCC 2014). For that reason, we urge other investigators of high latitude or high elevation systems to pay attention to floral plasticity in response to aspects of winter snowpack, such as snowmelt timing, as well as summer precipitation.

This article is protected by copyright. All rights reserved.

Since predictions for summer precipitation have such high variability, it is of interest to know if high summer precipitation could compensate for the predicted earlier snowmelt driven by climate change. In this study system, compensation appears possible for most floral traits, with the caveat that we measured the impacts in an experiment that did not manipulate all aspects of climate change. Effects of snowmelt timing and precipitation could be different under higher summer temperatures in the future, as high temperature can dry soils and increase evapotranspiration (Seager et al. 2013). We detected no significant differences between control plots and early snowmelt plots that received additional water, except where water addition overcompensated for early snowmelt. The observed changes in floral traits in response to early snowmelt and reduced precipitation are associated with reductions in soil moisture. Our early snowmelt treatment reduced soil moisture by less than our water additions increased it (0.5% vs 1.8%), so it is not a surprise that compensation occurred under those treatments. Our results indicate that a doubling of average summer precipitation could compensate for any changes in trait values that occurred under an earlier snowmelt of 6 ± 2 days (mean ± SD), which we estimated to be equivalent to 44 ± 22 y of further climate change. However, such a doubling of precipitation throughout the growing season is very unlikely, especially over the course of multiple seasons. Climate models downscaled for this region of North America predict reductions in precipitation during spring through June, with some predicting a potential increase of 2 - 4% in mid-summer by 2070 - 2099, as timing of the summer monsoon shifts (Seth et al. 2011). Since we estimated that a 3 - 6% increase in total summer precipitation would compensate for one day earlier snowmelt (for corolla width or style length), a 4% increase in future precipitation, even if it extended throughout the summer, could not compensate for the 11 days earlier snowmelt predicted by 2099 if snowmelt timing continues to change at its historical estimated rate of 1.4 days per decade (Figure S2). Moreover, since 1990 in Gothic, the average daily summer precipitation has decreased by 14 ± 5% per decade, and the proportion of summer days with precipitation has declined by 11 ± 5% per decade (mean ± SE, Figure S6).

This article is protected by copyright. All rights reserved.

Accepted Article

These trends are reflected broadly in the Southern Rocky Mountains and Colorado Plateau, where summer precipitation is declining and becoming more variable, and drought periods are lengthening (Zhang et al. 2021).

Potential mechanisms

The mechanisms driving responses of floral traits to soil moisture are rarely investigated at a physiological level. We observed effects of soil moisture mediated by gas exchange as well as direct effects of soil moisture. For *I. aggregata*, the changes in corolla width, style length, and nectar concentration were linked to leaf gas exchange of neighboring vegetative plants experiencing similar conditions in our structural equation model. A decrease in stomatal conductance in dry soils was associated with lower nectar production, as expected under higher water stress. A decrease in photosynthetic rate was associated with narrower corollas, potentially shorter corollas (Figure S5B), and shorter styles, which could be explained by reduced carbon availability for flower construction. Mechanisms that could have altered phenotypic expression of floral traits in ways not mediated by gas exchange include a decrease in uptake of nitrogen or other nutrients in drier soils, as floral construction can be costly in terms of nitrogen as well as carbon (Andersson 2005), and a direct effect of water availability to the roots on nectar production. Indeed nectar production appeared limited more by water than by carbohydrates, as we detected no influence of carbon assimilation through photosynthesis on that trait, in contrast to the effect of foliar photosynthesis seen on nectar in *Corydalis ambigua* (Kudo and Ida 2010). Changes in reproductive effort with leaf gas exchange can be idiosyncratic; in a nearby study of other subalpine species, one species increased its reproductive effort under warming because of reduced leaf photosynthesis and thus favored reproduction in a tradeoff with vegetative growth, while a different species increased its reproductive effort with no change in leaf gas exchange (Lambrecht et al. 2007).

This article is protected by copyright. All rights reserved.

Predicted effects on pollination

In only a few cases do we know if shifts in floral traits with drought can alter pollinator visitation or other fitness components (Al-Ghzawi et al. 2009; Burkle and Runyon 2016; Gallagher and Campbell 2017; Glenny et al. 2018; Walter 2020; reviewed in Descamps et al. 2021; Kuppler et al. 2021). Results have been mixed, with some showing negative responses of pollinator visitation rate to decreased soil moisture (Gallagher and Campbell 2017; Kuppler et al. 2021) and others finding results dependent upon the species of plant or pollinator (Burkle and Runyon 2016; Glenny et al. 2018). By combining our results with previous studies of *I. aggregata* going back as far as three decades (e.g., Campbell 1989a), we were able to predict that pollinator visitation by hummingbirds, in response to a single trait change, could decrease by 2 - 8% with a 1% decrease in soil moisture (depending on the trait), and other relative fitness components could decrease by up to 11%. Because multiple floral traits responded to soil moisture, it is likely that decreases in pollinator visitation would be greater than those estimated for any single floral trait; traits with positive associations with soil moisture have positive correlations with each other, but those correlations are only partial so a change in a second trait would add to the effect of the first. These predictions do have high uncertainty given the variance across and within years in how traits change with soil moisture and how fitness components change with traits. They also entailed combining estimates from natural populations that could have different standard deviations in the traits. Considering those caveats, the largest decrease in fitness was mediated by a change in nectar production. Nectar production both decreases more sharply with soil moisture, as based on its standardized slope, and has a higher impact on both hummingbird visitation and rate of pollen export than any other floral trait (Table 2). Lower pollen export leads to lower male pollination success and lower overall reproductive success. Previous studies showed mixed effects of nectar production on female reproductive success in *I. aggregata*, with one study finding that increased nectar

This article is protected by copyright. All rights reserved.

production increased fruit production through increased hummingbird visitation (Mitchell 1994) and another study not detecting an effect on seed production (Campbell and Powers 2015). Long-term studies on *I. aggregata* have found a positive association between the intensity of natural selection on corolla length, in this case based on seed production rather than pollen export, and the date of spring snowmelt (Campbell and Powers 2015). If that result turns out to be mediated by soil moisture, our predictions of impacts of these drought treatments on relative female fitness could be overestimates, particularly for corolla length, since selection would be weaker as soil moisture decreases.

Another caveat is that most of the measurements of fitness effects for these floral traits compared plants of different phenotypes interspersed within the same population, with the exception of a study that measured selection in each year for a group of plants spread across approximately 1 km (Campbell et al. 2018) of a hybrid zone (Campbell and Powers 2015). Our estimates of how drought affects fitness components through changes in floral traits may thus not necessarily capture all the impacts of drought due to climate change, which presumably occur over larger spatial scales. Pollinators of *I. aggregata*, including hummingbirds, may respond to drought over large spatial scales by switching to different foraging locations or to alternative nectar sources, such as other plant species that in principle might be less influenced by drought. In such a case, there could be widespread drops in seed production, as seed production in *I. aggregata* is strongly pollen-limited in most years (Campbell 1991; Campbell and Halama 1993; Campbell et al. 2021). However, even if hummingbirds continued to forage on *I. aggregata* at the same sites, the large changes in nectar production with reduced soil moisture over a wide spatial extent could reduce average seed production due to insufficient availability of pollen on stigmas as a consequence of the expected decline in pollen export.

Accepted Article

This article is protected by copyright. All rights reserved.

Conclusions

Climate change is reducing snow cover and causing earlier snowmelt at high latitudes and elevations (Stewart et al. 2005). Here we showed that earlier snowmelt can cause changes in floral trait expression similar to those seen as plastic responses to reduced growing season precipitation in both *Ipomopsis aggregata* and other plant species (Campbell and Wendlandt 2013; Galen 2000; Gallagher and Campbell 2017). Earlier snowmelt can also amplify the effects of changes in summer precipitation on floral traits. These changes have the potential to influence pollinator visitation and other fitness components, as illustrated by predictions for *I. aggregata*. Whereas most studies of snowmelt timing have focused on impacts on phenology, these results provide a rare example of how snowmelt timing can also influence populations through alterations in expression of other traits with fitness effects (Anderson and Gezon 2015). We encourage future investigations of impacts of climate change on floral traits and other plant traits to consider responses to timing of key weather events such as snowmelt.

Acknowledgements

This study was conducted on the traditional and unceded land of the Ute People. We are grateful to Mary Dickson, David Dickson, Alex Malone, Samantha Siegfried, and Jackson Snow for assistance with the snowmelt manipulations and to Alexandra Faidiga, Jocelyn Navarro, Ayaka Paul, Siena Truex, Briana Vega, and Karen Wang for assistance with field work. The research was funded by NSF grant DEB-1654655 to DC.

Author Contributions

DC designed the study. HB constructed the rain-out shelters, and RD performed snow-melt manipulations. JP, HB, RD, XL, and DC watered plots, and collected the measurements of soil

This article is protected by copyright. All rights reserved.

moisture and floral traits. JP, HB, and DC organized and analyzed the data. JP and DC wrote the first version, and all authors contributed to revisions.

Data Availability

All data and code used to generate figures and tables are provided at https://jmpowers.github.io/snow-precip-floral/.

References

Al-Ghzawi, A. A.-M., Zaitoun, S., Gosheh, H., & Alqudah, A. (2009). Impacts of drought on pollination of *Trigonella moabitica* (Fabaceae) via bee visitations. *Archives of Agronomy and Soil Science*, *55*(6), 683–692. https://doi.org/10.1080/03650340902821666

Alstad, K. P., Welker, J. M., Williams, S. A., & Trlica, M. J. (1999). Carbon and water relations of *Salix monticola* in response to winter browsing and changes in surface water hydrology: An isotopic study using $\delta^{13}C$ and $\delta^{18}O$. *Oecologia*, *120*(3), 375–385. https://doi.org/10.1007/s004420050870

Anderson, J. T., & Gezon, Z. J. (2015). Plasticity in functional traits in the context of climate change: A case study of the subalpine forb *Boechera stricta* (Brassicaceae). *Global Change Biology*, *21*(4), 1689–1703. https://doi.org/10.1111/gcb.12770

Anderson, J. T., Inouye, D. W., McKinney, A. M., Colautti, R. I., & Mitchell-Olds, T. (2012). Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1743), 3843–3852. https://doi.org/10.1098/rspb.2012.1051

Andersson, S. (2005). Floral costs in *Nigella sativa* (Ranunculaceae): Compensatory responses to perianth removal. *American Journal of Botany*, *92*(2), 279–283. https://doi.org/10.3732/ajb.92.2.279

Assmann, J. J., Myers-Smith, I. H., Phillimore, A. B., Bjorkman, A. D., Ennos, R. E., Prevéy, J. S., Henry, G. H. R., Schmidt, N. M., & Hollister, R. D. (2019). Local snow melt and temperature—But not regional sea ice—Explain variation in spring phenology in coastal Arctic tundra. *Global Change Biology*, *25*(7), 2258–2274. https://doi.org/10.1111/gcb.14639

Bartoń, K. (2020). *MuMIn: Multi-model inference* (1.43.17) [Computer software]. https://CRAN.R-project.org/package=MuMIn

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bemmels, J. B., & Anderson, J. T. (2019). Climate change shifts natural selection and the adaptive potential of the perennial forb *Boechera stricta* in the Rocky Mountains. *Evolution*, *73*(11), 2247–2262. https://doi.org/10.1111/evo.13854

Blankinship, J. C., Meadows, M. W., Lucas, R. G., & Hart, S. C. (2014). Snowmelt timing alters shallow but not deep soil moisture in the Sierra Nevada. *Water Resources Research*, *50*(2), 1448–1456. https://doi.org/10.1002/2013WR014541

This article is protected by copyright. All rights reserved.

675 Brody, A. K., Price, M. V., & Waser, N. M. (2007). Life-history consequences of vegetative
676 damage in scarlet gilia, a monocarpic plant. *Oikos*, *116*(6), 975–985.
677 https://doi.org/10.1111/j.0030-1299.2007.15705.x
678 Burkle, L. A., & Runyon, J. B. (2016). Drought and leaf herbivory influence floral volatiles
679 and pollinator attraction. *Global Change Biology*, *22*(4), 1644–1654.
680 https://doi.org/10.1111/gcb.13149
681 Campbell, D. R. (1989a). Measurements of selection in a hermaphroditic plant: Variation in
682 male and female pollination success. *Evolution*, *43*(2), 318–334.
683 https://doi.org/10.1111/j.1558-5646.1989.tb04230.x
684 Campbell, D. R. (1989b). Inflorescence size: Test of the male function hypothesis.
685 *American Journal of Botany*, *76*(5), 730–738. https://doi.org/10.1002/j.1537-
686 2197.1989.tb11367.x
687 Campbell, D. R. (1991). Effects of floral traits on sequential components of fitness in
688 *Ipomopsis aggregata*. *The American Naturalist*, *137*(6), 713–737.
689 https://doi.org/10.1086/285190
690 Campbell, D. R. (1992). Variation in sex allocation and floral morphology in *Ipomopsis*
691 *aggregata* (Polemoniaceae). *American Journal of Botany*, *79*(5), 516–521.
692 https://doi.org/10.1002/j.1537-2197.1992.tb14587.x
693 Campbell, D. R. (1997). Genetic and environmental variation in life-history traits of a
694 monocarpic perennial: A decade-long field experiment. *Evolution*, *51*(2), 373–382.
695 https://doi.org/10.1111/j.1558-5646.1997.tb02424.x
696 Campbell, D. R. (2019). Early snowmelt projected to cause population decline in a
697 subalpine plant. *Proceedings of the National Academy of Sciences*, *116*(26), 12901–
698 12906. https://doi.org/10.1073/pnas.1820096116
699 Campbell, D. R., Crawford, M., Brody, A. K., & Forbis, T. A. (2002). Resistance to pre-
700 dispersal seed predators in a natural hybrid zone. *Oecologia*, *131*(3), 436–443.
701 https://doi.org/10.1007/s00442-002-0900-1
702 Campbell, D. R., Faidiga, A., & Trujillo, G. (2018). Clines in traits compared over two
703 decades in a plant hybrid zone. *Annals of Botany*, *122*(2), 315–324.
704 https://doi.org/10.1093/aob/mcy072
705 Campbell, D. R., Galen, C., & Wu, C. A. (2005). Ecophysiology of first and second
706 generation hybrids in a natural plant hybrid zone. *Oecologia*, *144*(2), 214–225.
707 https://doi.org/10.1007/s00442-005-0064-x
708 Campbell, D. R., & Halama, K. J. (1993). Resource and pollen limitations to lifetime seed
709 production in a natural plant population. *Ecology*, *74*(4), 1043–1051.
710 https://doi.org/10.2307/1940474
711 Campbell, D. R., & Powers, J. M. (2015). Natural selection on floral morphology can be
712 influenced by climate. *Proceedings of the Royal Society of London B: Biological*
713 *Sciences*, *282*(1808), 20150178. https://doi.org/10.1098/rspb.2015.0178
714 Campbell, D. R., Price, M. V., Waser, N. M., Irwin, R. E., & Brody, A. K. (2021).
715 Comparative impacts of annual variation in snowmelt and species interactions on
716 population dynamics of a subalpine plant.
717 Campbell, D. R., Sosenski, P., & Raguso, R. A. (2019). Phenotypic plasticity of floral
718 volatiles in response to increasing drought stress. *Annals of Botany*, *123*(4), 601–610.
719 https://doi.org/10.1093/aob/mcy193
720 Campbell, D. R., Waser, N. M., & Melendez-Ackerman, E. J. (1997). Analyzing pollinator-
721 mediated selection in a plant hybrid zone: Hummingbird visitation patterns on three
722 spatial scales. *The American Naturalist*, *149*(2), 295–315.
723 Campbell, D. R., Waser, N. M., & Price, M. V. (1994). Indirect selection of stigma position in
724 *Ipomopsis aggregata* via a genetically correlated trait. *Evolution*, *48*(1), 55–68.
725 https://doi.org/10.1111/j.1558-5646.1994.tb01294.x

This article is protected by copyright. All rights reserved.

Campbell, D. R., Waser, N. M., & Price, M. V. (1996). Mechanisms of hummingbird-mediated selection for flower width in *Ipomopsis aggregata*. *Ecology*, *77*(5), 1463–1472. https://doi.org/10.2307/2265543

Campbell, D. R., Waser, N. M., Price, M. V., Lynch, E. A., & Mitchell, R. J. (1991). Components of phenotypic selection: Pollen export and flower corolla width in *Ipomopsis aggregata*. *Evolution*, *45*(6), 1458–1467. https://doi.org/10.1111/j.1558-5646.1991.tb02648.x

Campbell, D. R., Waser, N. M., & Wolf, P. G. (1998). Pollen transfer by natural hybrids and parental species in an *Ipomopsis* hybrid zone. *Evolution*, *52*(6), 1602–1611. https://doi.org/10.1111/j.1558-5646.1998.tb02241.x

Campbell, D. R., & Wendlandt, C. (2013). Altered precipitation affects plant hybrids differently than their parental species. *American Journal of Botany*, *100*(7), 1322–1331. https://doi.org/10.3732/ajb.1200473

Campbell, D. R., Wu, C. A., & Travers, S. E. (2010). Photosynthetic and growth responses of reciprocal hybrids to variation in water and nitrogen availability. *American Journal of Botany*, *97*(6), 925–933. https://doi.org/10.3732/ajb.0900387

CaraDonna, P. J., Iler, A. M., & Inouye, D. W. (2014). Shifts in flowering phenology reshape a subalpine plant community. *Proceedings of the National Academy of Sciences*, *111*(13), 4916–4921. https://doi.org/10.1073/pnas.1323073111

Carroll, A. B., Pallardy, S. G., & Galen, C. (2001). Drought stress, plant water status, and floral trait expression in fireweed, *Epilobium angustifolium* (Onagraceae). *American Journal of Botany*, *88*(3), 438–446. https://doi.org/10.2307/2657108

Caruso, C. M. (2006). Plasticity of inflorescence traits in *Lobelia siphilitica* (Lobeliaceae) in response to soil water availability. *American Journal of Botany*, *93*(4), 531–538. https://doi.org/10.3732/ajb.93.4.531

Caruso, C. M., Maherali, H., & Sherrard, M. (2006). Plasticity of physioolgy in *Lobelia*: Testing for adaptation and constraint. *Evolution*, *60*(5), 980–990. https://doi.org/10.1111/j.0014-3820.2006.tb01176.x

Clow, D. W. (2010). Changes in the timing of snowmelt and streamflow in Colorado: A response to recent warming. *Journal of Climate*, *23*(9), 2293–2306. https://doi.org/10.1175/2009JCLI2951.1

Cowan, I. R. (1978). Stomatal behaviour and environment. In R. D. Preston & H. W. Woolhouse (Eds.), *Advances in Botanical Research* (Vol. 4, pp. 117–228). Academic Press. https://doi.org/10.1016/S0065-2296(08)60370-5

Descamps, C., Quinet, M., Baijot, A., & Jacquemart, A.-L. (2018). Temperature and water stress affect plant–pollinator interactions in *Borago officinalis* (Boraginaceae). *Ecology and Evolution*, *8*(6), 3443–3456. https://doi.org/10.1002/ece3.3914

Descamps, C., Quinet, M., & Jacquemart, A.-L. (2021). The effects of drought on plant–pollinator interactions: What to expect? *Environmental and Experimental Botany*, *182*, 104297. https://doi.org/10.1016/j.envexpbot.2020.104297

Ebbs, L. M. (2016). *Response of Arctic shrubs to deeper winter snow is species and ecosystem dependent: An isotopic study in northern Alaska* [M.S., University of Alaska Anchorage]. https://search.proquest.com/docview/1810727612/abstract/B7C9706A4E72440DPQ/1

Ehleringer, J. R., Phillips, S. L., Schuster, W. S. F., & Sandquist, D. R. (1991). Differential utilization of summer rains by desert plants. *Oecologia*, *88*(3), 430–434. https://doi.org/10.1007/BF00317589

Franks, S. J., Weber, J. J., & Aitken, S. N. (2014). Evolutionary and plastic responses to climate change in terrestrial plant populations. *Evolutionary Applications*, *7*(1), 123–139. https://doi.org/10.1111/eva.12112

This article is protected by copyright. All rights reserved.

Galen, C. (2000). High and dry: Drought stress, sex-allocation trade-offs, and selection on flower size in the alpine wildflower *Polemonium viscosum* (Polemoniaceae). *The American Naturalist*, *156*(1), 72–83. https://doi.org/10.1086/303373

Gallagher, M. K., & Campbell, D. R. (2017). Shifts in water availability mediate plant–pollinator interactions. *New Phytologist*, *215*(2), 792–802. https://doi.org/10.1111/nph.14602

Gallagher, M. K., & Campbell, D. R. (2021). Experimental test of the combined effects of water availability and flowering time on pollinator visitation and seed set. *Frontiers in Ecology and Evolution*, *9*, 163. https://doi.org/10.3389/fevo.2021.641693

Gierke, C., Newton, B. T., & Phillips, F. M. (2016). Soil-water dynamics and tree water uptake in the Sacramento Mountains of New Mexico (USA): A stable isotope study. *Hydrogeology Journal*, *24*(4), 805–818. https://doi.org/10.1007/s10040-016-1403-1

Glenny, W. R., Runyon, J. B., & Burkle, L. A. (2018). Drought and increased CO_2 alter floral visual and olfactory traits with context-dependent effects on pollinator visitation. *New Phytologist*, *220*(3), 785–798. https://doi.org/10.1111/nph.15081

Grace, J. B., Anderson, T. M., Olff, H., & Scheiner, S. M. (2010). On the specification of structural equation models for ecological systems. *Ecological Monographs*, *80*(1), 67–87. https://doi.org/10.1890/09-0464.1

Grant, V., & Wilken, D. H. (1986). Taxonomy of the *Ipomopsis aggregata* group (Polemoniaceae). *Botanical Gazette*, *147*(3), 359–371. https://doi.org/10.1086/337603

Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknes, A.-L., & Totland, Ø. (2009). How does climate warming affect plant-pollinator interactions? *Ecology Letters*, *12*(2), 184–195. https://doi.org/10.1111/j.1461-0248.2008.01269.x

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, *50*(3), 346–363. https://doi.org/10.1002/bimj.200810425

Hu, J., Moore, D. J. P., Burns, S. P., & Monson, R. K. (2010). Longer growing seasons lead to less carbon sequestration by a subalpine forest. *Global Change Biology*, *16*(2), 771–783. https://doi.org/10.1111/j.1365-2486.2009.01967.x

Iler, A. M., Compagnoni, A., Inouye, D. W., Williams, J. L., CaraDonna, P. J., Anderson, A., & Miller, T. E. X. (2019). Reproductive losses due to climate change-induced earlier flowering are not the primary threat to plant population viability in a perennial herb. *Journal of Ecology*, *107*(4), 1931–1943. https://doi.org/10.1111/1365-2745.13146

Inouye, D. W. (2008). Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology*, *89*(2), 353–362. https://doi.org/10.1890/06-2128.1

IPCC. (2014). *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* (R. K. Pachauri & L. Meyer, Eds.). Intergovernmental Panel on Climate Change.

Juenger, T., & Bergelson, J. (1997). Pollen and resource limitation of compensation to herbivory in scarlet gilia, *Ipomopsis aggregata*. *Ecology*, *78*(6), 1684–1695. https://doi.org/10.1890/0012-9658(1997)078[1684:PARLOC]2.0.CO;2

Kudo, G., & Ida, T. Y. (2010). Carbon source for reproduction in a spring ephemeral herb, *Corydalis ambigua* (Papaveraceae). *Functional Ecology*, *24*(1), 62–69. https://doi.org/10.1111/j.1365-2435.2009.01601.x

Kuppler, J., & Kotowska, M. M. (2021). A meta-analysis of responses in floral traits and flower-visitor interactions to water deficit. *Global Change Biology*, *n/a*(n/a). https://doi.org/10.1111/gcb.15621

Kuppler, J., Wieland, J., Junker, R. R., & Ayasse, M. (2021). Drought-induced reduction in flower size and abundance correlates with reduced flower visits by bumble bees. *AoB PLANTS*, *13*(plab001). https://doi.org/10.1093/aobpla/plab001

This article is protected by copyright. All rights reserved.

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*(1), 1–26. https://doi.org/10.18637/jss.v082.i13

Lambrecht, S. C., Loik, M. E., Inouye, D. W., & Harte, J. (2007). Reproductive and physiological responses to simulated climate warming for four subalpine species. *New Phytologist*, *173*(1), 121–134. https://doi.org/10.1111/j.1469-8137.2006.01892.x

Legendre, P., & Legendre, L. F. J. (1998). *Numerical Ecology*. Elsevier.

Lenth, R., Singmann, H., Love, J., Buerkner, P., & Herve, M. (2018). *emmeans: Estimated marginal means, aka least-squares means* (1.4.3) [Computer software]. https://CRAN.R-project.org/package=emmeans

Leonard, L. T., Wilmer, C., Steltzer, H., Williams, K. H., & Sharp, J. O. (2020). Accelerated snowmelt protocol to simulate climate change induced impacts on snowpack dependent ecosystems. *Bio-Protocol*, *10*(6), e3557–e3557.

Merilä, J., & Hendry, A. P. (2014). Climate change, adaptation, and phenotypic plasticity: The problem and the evidence. *Evolutionary Applications*, *7*(1), 1–14. https://doi.org/10.1111/eva.12137

Mitchell, R. J. (1992). Testing evolutionary and ecological hypotheses using path analysis and structural equation modelling. *Functional Ecology*, *6*(2), 123–129. https://doi.org/10.2307/2389745

Mitchell, R. J. (1993). Adaptive significance of *Ipomopsis aggregata* nectar production: Observation and experiment in the field. *Evolution*, *47*(1), 25–35. https://doi.org/10.1111/j.1558-5646.1993.tb01196.x

Mitchell, R. J. (1994). Effects of floral traits, pollinator visitation, and plant size on *Ipomopsis aggregata* fruit production. *The American Naturalist*, *143*(5), 870–889. https://doi.org/10.1086/285637

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Navarro, J., Powers, J. M., & Campbell, D. R. (2021). *Leaf gas exchange in* Ipomopsis aggregata *under manipulated snowmelt timing and summer precipitation* [Data set]. Dryad. https://datadryad.org/stash/share/KjP8YcH8WGykmtvSfviMdxKwIGntKy7PQq2CtscuBb4

Pederson, G. T., Gray, S. T., Woodhouse, C. A., Betancourt, J. L., Fagre, D. B., Littell, J. S., Watson, E., Luckman, B. H., & Graumlich, L. J. (2011). The unusual nature of recent snowpack declines in the North American cordillera. *Science*, *333*(6040), 332–335. https://doi.org/10.1126/science.1201570

Price, M. V., Waser, N. M., Irwin, R. E., Campbell, D. R., & Brody, A. K. (2005). Temporal and spatial variation in pollination of a montane herb: A seven-year study. *Ecology*, *86*(8), 2106–2116. https://doi.org/10.1890/04-1274

Seager, R., Ting, M., Li, C., Naik, N., Cook, B., Nakamura, J., & Liu, H. (2013). Projections of declining surface-water availability for the southwestern United States. *Nature Climate Change*, *3*(5), 482–486. https://doi.org/10.1038/nclimate1787

Seth, A., Rauscher, S. A., Rojas, M., Giannini, A., & Camargo, S. J. (2011). Enhanced spring convective barrier for monsoons in a warmer world? *Climatic Change*, *104*(2), 403–414. https://doi.org/10.1007/s10584-010-9973-8

Sloat, L. L., Henderson, A. N., Lamanna, C., & Enquist, B. J. (2015). The effect of the foresummer drought on carbon exchange in subalpine meadows. *Ecosystems*, *18*(3), 533–545. https://doi.org/10.1007/s10021-015-9845-1

This article is protected by copyright. All rights reserved.

Stewart, I. T., Cayan, D. R., & Dettinger, M. D. (2005). Changes toward earlier streamflow timing across western North America. *Journal of Climate*, *18*(8), 1136–1155. https://doi.org/10.1175/JCLI3321.1

Sun, F., Berg, N., Hall, A., Schwartz, M., & Walton, D. (2019). Understanding end-of-century snowpack changes over California's Sierra Nevada. *Geophysical Research Letters*, *46*(2), 933–943. https://doi.org/10.1029/2018GL080362

Suni, S. S., Ainsworth, B., & Hopkins, R. (2020). Local adaptation mediates floral responses to water limitation in an annual wildflower. *American Journal of Botany*, *107*(2), 209–218. https://doi.org/10.1002/ajb2.1434

Villarreal, A. G., & Freeman, C. E. (1990). Effects of temperature and water stress on some floral nectar characteristics in *Ipomopsis longiflora* (Polemoniaceae) under controlled conditions. *Botanical Gazette*, *151*(1). https://doi.org/10.1086/337797

Wadgymar, S. M., Ogilvie, J. E., Inouye, D. W., Weis, A. E., & Anderson, J. T. (2018). Phenological responses to multiple environmental drivers under climate change: Insights from a long-term observational study and a manipulative field experiment. *New Phytologist*, *218*(2), 517–529. https://doi.org/10.1111/nph.15029

Walter, J. (2020). Dryness, wetness and temporary flooding reduce floral resources of plant communities with adverse consequences for pollinator attraction. *Journal of Ecology*, *108*(4), 1453–1464. https://doi.org/10.1111/1365-2745.13364

Waser, N. M., & Price, M. V. (2016). Drought, pollen and nectar availability, and pollination success. *Ecology*, *97*(6), 1400–1409. https://doi.org/10.1890/15-1423.1

Yahdjian, L., & Sala, O. E. (2002). A rainout shelter design for intercepting different amounts of rainfall. *Oecologia*, *133*(2), 95–101. https://doi.org/10.1007/s00442-002-1024-3

Zhang, F., Biederman, J. A., Dannenberg, M. P., Yan, D., Reed, S. C., & Smith, W. K. (2021). Five decades of observed daily precipitation reveal longer and more variable drought events across much of the western United States. *Geophysical Research Letters*, *48*(7), e2020GL092293. https://doi.org/10.1029/2020GL092293

Accepted Article

This article is protected by copyright. All rights reserved.

Accepted Article

Tables and Figures

Table 1

Linear mixed model results for replicated split-plot analysis of the effects of year and the snowmelt and precipitation treatments on traits. P values are listed for each trait under the fixed effects and interactions, and R^2_m is the marginal R^2 for the proportion of variance explained by the fixed effects. P values for post-hoc tests for the main effects of precipitation (excluding interactions) are listed comparing the precipitation addition and reduction treatments to the controls.

Trait	Year	Snowmelt	Precipitation	Year × Snowmelt	Year × Precipitation	Snowmelt × Precipitation	Year × Snowmelt × Precipitation	R^2_m	Addition vs. Control	Reduction vs. Control
Corolla length	< 0.001	0.895	0.003	0.991	0.147	0.735	0.893	0.228	0.030	0.011
Style length	< 0.001	0.763	0.020	0.980	0.102	0.931	0.275	0.185	0.253	0.039
Corolla width	< 0.001	0.719	0.002	0.525	0.627	0.434	0.061	0.303	< 0.001	0.254
Sepal width	0.499	0.930	0.009	0.180	0.003	0.313	0.022	0.114	0.170	0.022
Nectar production	< 0.001	0.209	0.035	0.009	0.704	0.635	0.463	0.168	0.022	0.846
Nectar concentration	< 0.001	0.523	0.008	0.758	0.661	0.492	0.173	0.308	< 0.001	0.999
Inflorescence height	< 0.001	0.080	0.989	0.240	0.452	0.482	0.083	0.234	1.000	0.985
Flower number	0.713	0.804	0.368	0.010	0.257	0.627	0.722	0.040	0.886	0.409

This article is protected by copyright. All rights reserved.

Table 2

Predicted impacts of water-induced changes in floral traits on fitness components. The estimated slope of the standardized trait vs. soil moisture (volumetric water content, VWC) is reported averaged across years (mean ± SE). Standardized selection differentials (S' = change in relative fitness with unit change in standardized trait value) from previous studies are reported in cases where they differed significantly from zero (ns = not significantly different from zero, NA = information not available). The percent change in relative fitness per increase of 1% VWC was obtained by multiplying the slope of the standardized trait value on VWC by S' (blank if S' is ns or NA).

		Standardized selection differential (S')				**Percent change in relative fitness per increase in 1% VWC**			
Trait	**Slope of standardized trait vs. VWC**	**Visits**	**Pollen receipt**	**Seeds**	**Pollen export**	**Visits**	**Pollen receipt**	**Seeds**	**Pollen export**
Corolla length	0.12 ± 0.05	0.36[1] or 0.08[2]	ns[3]	0.04[4]	ns[3]	4.4% or 1.0%		0.5%	
Style length	0.15 ± 0.04	NA	0.23[3]	ns[5]	ns[3]		3.4%		
Corolla width	0.16 ± 0.04	0.23[1] or 0.36[2]	ns[3]	0.12[4]	0.24[3]	3.7% or 5.8%		1.9%	3.9%
Nectar production	0.22 ± 0.04	0.37[1] or 0.19[6]	ns[5]	ns[4]	0.53[6]	8.0% or 4.1%			11.5%

[1]Within-population slopes on standardized traits calculated from field observations in 1989 (Campbell et al. 1991). S' for corolla length and nectar production were not reported but were calculated from the original data.

[2]From field experiment with potted plants in 1994 (Campbell et al. 1997).

This article is protected by copyright. All rights reserved.

[3]Average S' from field observations in 1984 - 1986 (Campbell 1989a). Values for style length were taken from those measured for stigma exsertion.

[4]The estimate for corolla length is the average S' across 13 years between 2001 and 2016 (Campbell and Powers 2015). The estimate for corolla width is the average across 11 years, omitting two years in which hawkmoths were abundant visitors at one site, since those are not common at the site in the current study. The estimate for nectar production is the average across the 4 years it was measured (2010 - 2013).

[5]From field observations in 1984 - 1987 (Campbell 1991).

[6]Estimated from change in visit rate comparing control and nectar addition plants in 1987 - 1991 (Mitchell 1993). Standard deviation of the trait was not reported and so was estimated from the current study.

Accepted Article

This article is protected by copyright. All rights reserved.

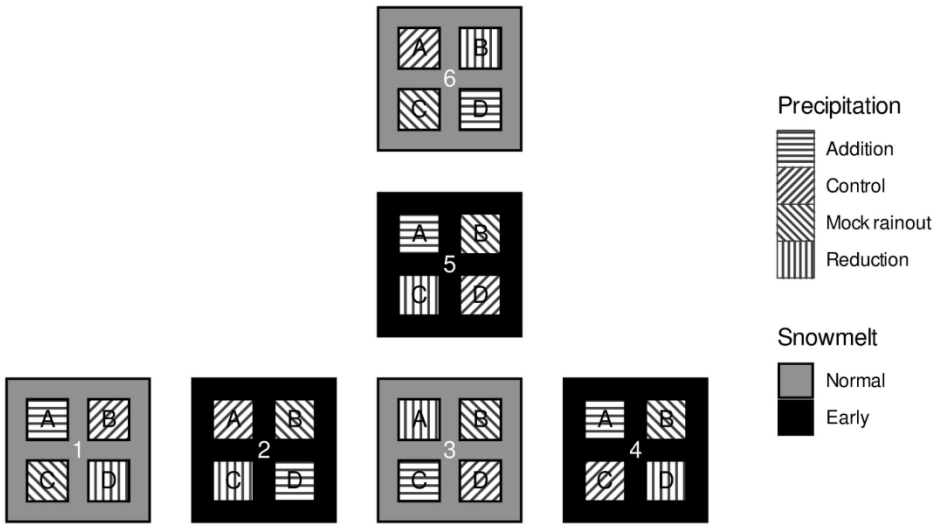


Figure 1. Layout of snowmelt manipulation plots (7 m × 7 m, denoted by numbers) and precipitation manipulation subplots (2 m × 2 m, denoted by letters). Plot sizes are to scale, but not distances between plots.

165x101mm (300 x 300 DPI)

This article is protected by copyright. All rights reserved.

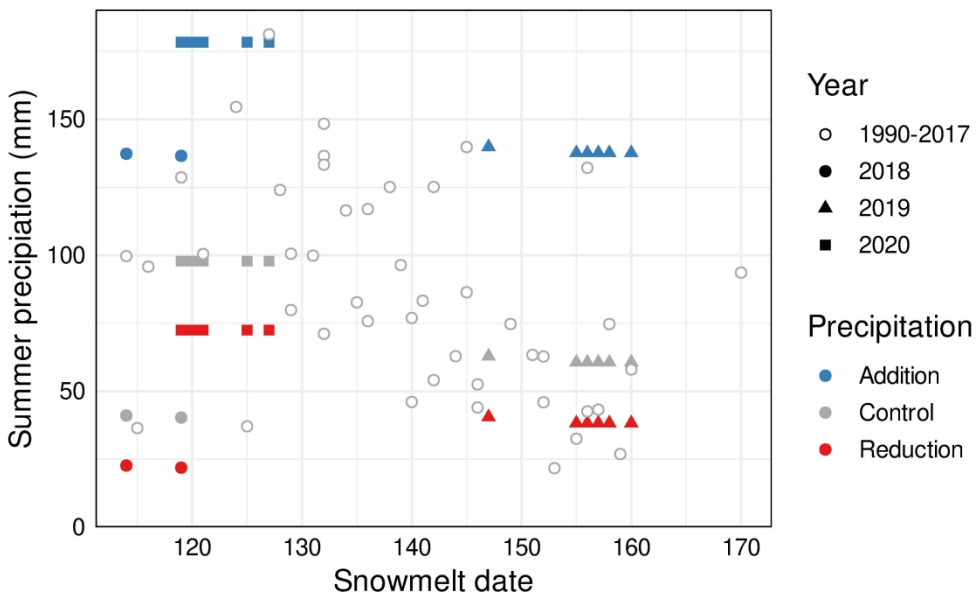


Figure 2. The range of environmental variation produced by snowmelt and summer precipitation treatments compared to 30 y of historic variation. The snowmelt date and summer precipitation from the snowmelt date to Julian day 214 in Gothic, Colorado, USA are shown as open circles for 1990 - 2017. The snowmelt date in each experimental plot in Maxfield Meadow and estimated summer precipitation from the snowmelt date in each subplot until the last floral measurement are shown as filled shapes colored by precipitation treatment for 2018 - 2020. Points for subplots with the same melt date overlap in 2018 and 2020, such that some points represent more than one plot. Specifically, in 2018 all three early snowmelt plots melted on day 114, and all three normal snowmelt plots melted on day 119. In 2020, two normal plots both melted on day 125.

165x101mm (600 x 600 DPI)

This article is protected by copyright. All rights reserved.

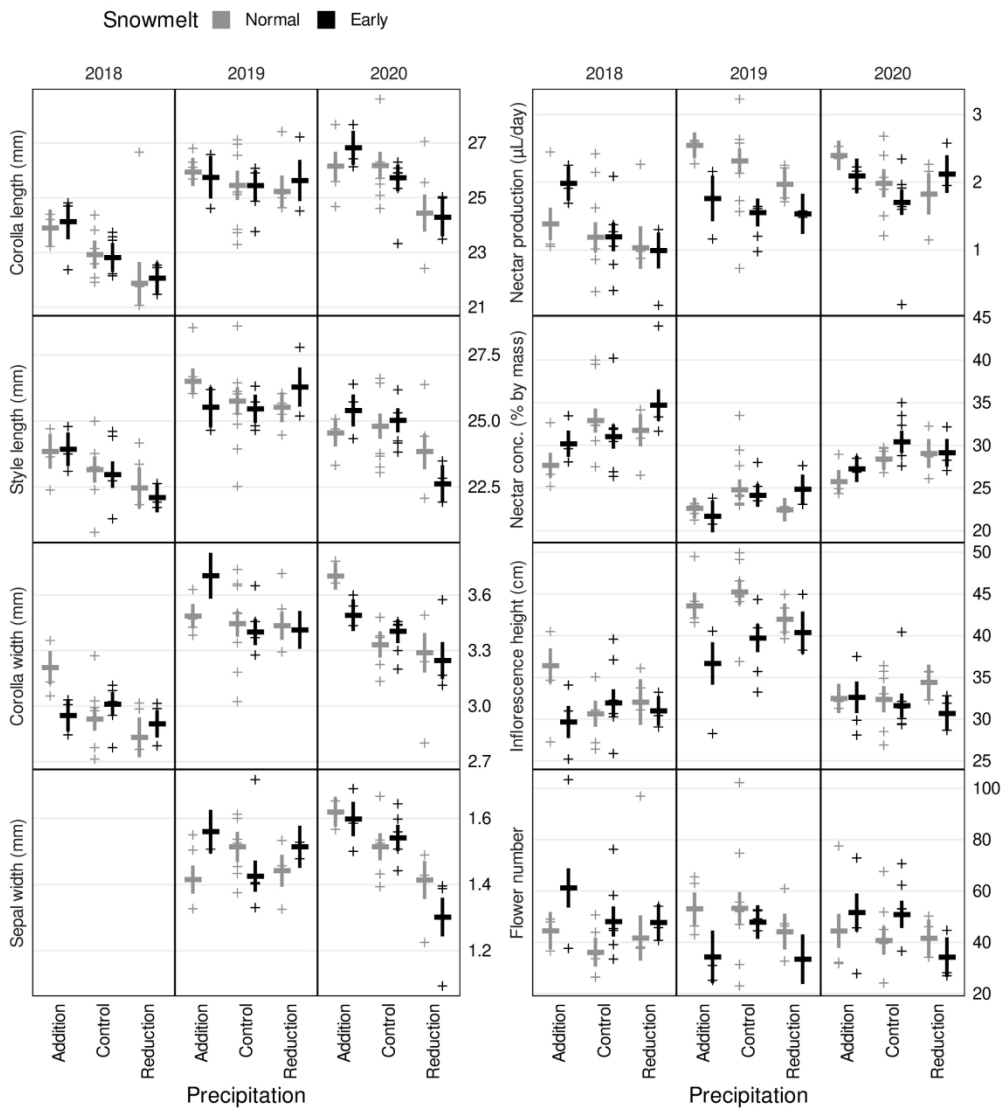


Figure 3. The effects of snowmelt and precipitation treatments on traits across three years. Horizontal bars show the estimated marginal means from a model fitted to plant means with random effects of plot and subplot, with ± 1 standard error as a vertical bar, and small crosses show subplot means. Sepal width was not measured in 2018.

228x254mm (300 x 300 DPI)

This article is protected by copyright. All rights reserved.

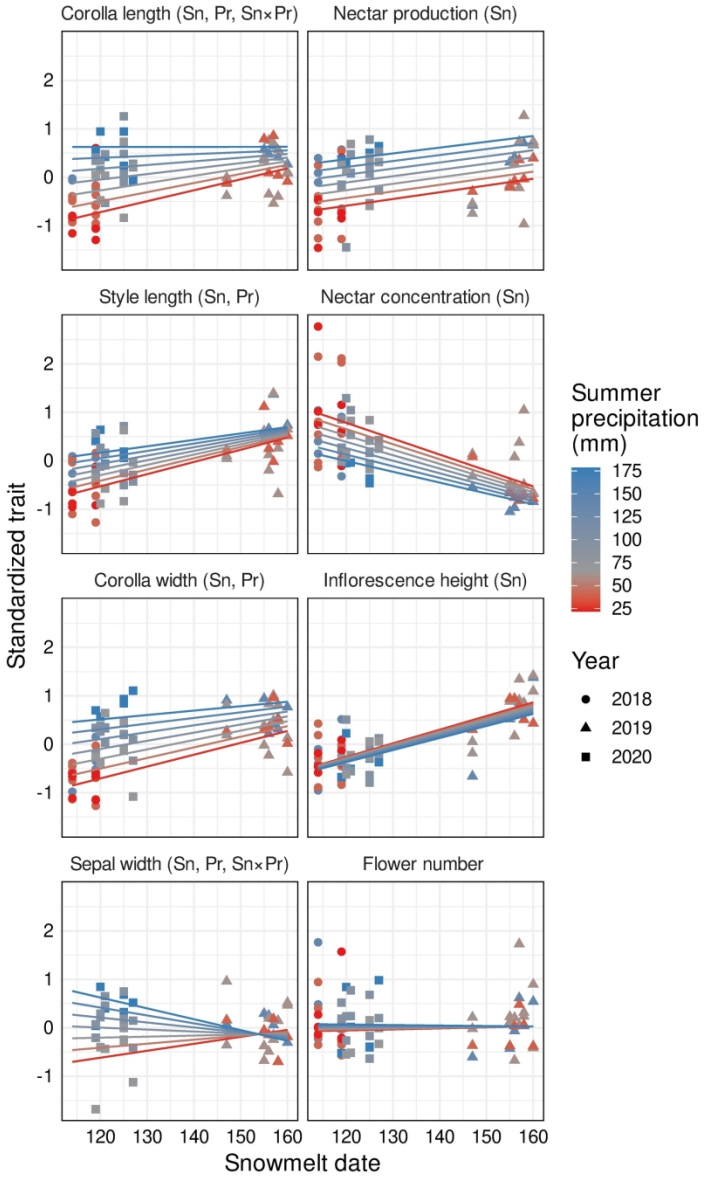


Figure 4. The effects of the snowmelt date and estimated summer precipitation on traits across three years. Each trait was standardized by dividing by the standard deviation of plant means. Lines show the estimated marginal trends for the amounts of summer precipitation listed in the legend, from a model fitted to plant means with random effects of plot and subplot. Points show the subplot means, colored by the estimated summer precipitation they received. Statistically significant effects of snowmelt date (Sn), summer precipitation (Pr), and their interaction are indicated for each trait. Full model results are given in Table S2.

152x254mm (300 x 300 DPI)

This article is protected by copyright. All rights reserved.

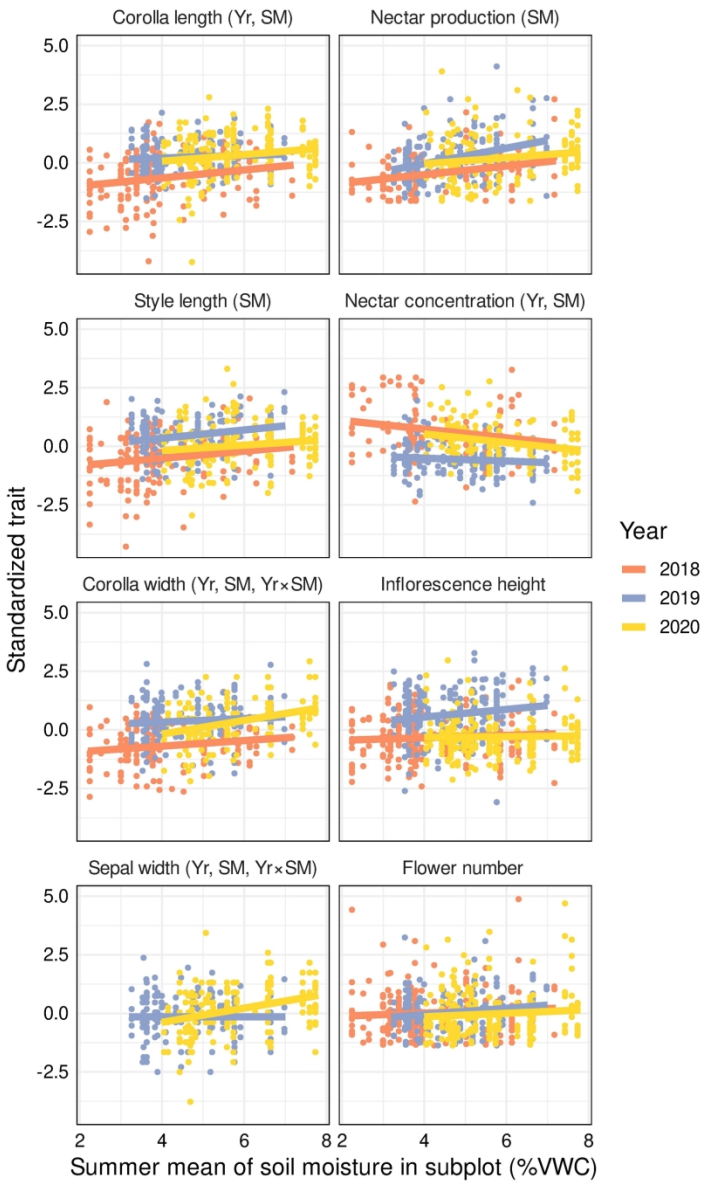


Figure 5. The effects of soil moisture (averaged across the measurement period in each subplot) on traits across three years. The standardized mean trait values for each plant in each year are shown as points. The estimated marginal trend is shown as a line for each year. Sepal width was not measured in 2018. Statistically significant effects of year (Yr), soil moisture (SM), and their interaction are indicated for each trait. Full model results are given in Table S3.

152x254mm (300 x 300 DPI)

This article is protected by copyright. All rights reserved.

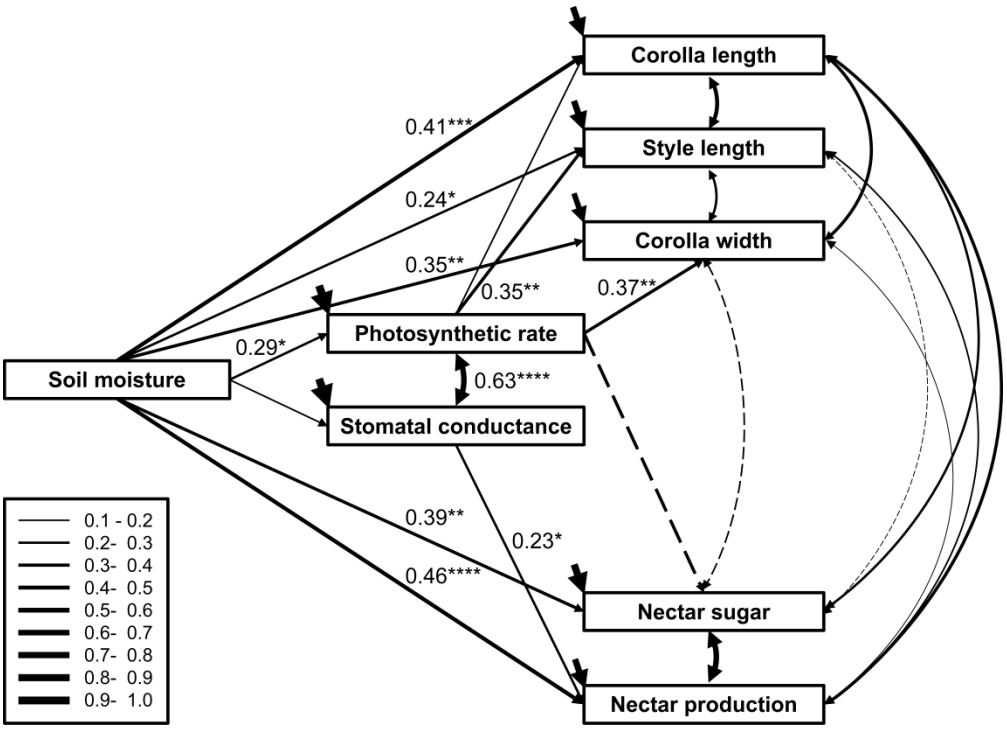


Figure 6. Structural equation paths showing direct effects of soil moisture on floral traits as well as those mediated through leaf gas exchange (photosynthetic rate and stomatal conductance). The figure shows the standardized paths from a full model including all paths from soil moisture to floral traits, from soil moisture to photosynthetic rate and stomatal conductance, from photosynthetic rate to all floral traits, from stomatal conductance to nectar traits, and correlations between all traits, as well as unexplained variance in each measurement. Width of the arrow indicates the strength of the standardized path coefficient. Solid lines indicate positive paths, and dashed lines indicate negative paths. Double headed curved arrows indicate correlations. Diagonal arrows with no start point indicate unexplained variance. For ease in viewing the figure, path coefficients are not depicted for non-significant one-way paths to floral traits or for double-headed correlations between traits. All traits were significantly correlated ($P < 0.05$) except for nectar production and nectar sugar with corolla width and nectar production and nectar sugar with style length. Figure S5 shows nested models that contain only the direct paths from soil moisture or only the indirect paths mediated by gas exchange.

778x559mm (600 x 600 DPI)

This article is protected by copyright. All rights reserved.