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

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18 **Abstract**

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

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

44 **Introduction**

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

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

66 snowmelt timing (Blankinship et al. 2014). In such areas around the globe, warming winter and
67 spring temperatures are causing snow to melt earlier compared to preindustrial times (Clow
68 2010; Pederson et al. 2011; Stewart et al. 2005), which also reduces soil moisture during the
69 early parts of summer (Blankinship et al. 2014; Seager et al. 2013). Although it is well-known
70 that flowering time is advanced by early snowmelt (CaraDonna et al. 2014), the impact of
71 snowmelt timing on phenotypic expression of floral traits is unknown. A few studies have
72 investigated responses of reproductive traits such as inflorescence height, flower number, or
73 number of flowering stalks to snowmelt date (Bemmels and Anderson 2019; Iler et al. 2019), but
74 not, to our knowledge, traits of the flowers themselves. Depending on their life history strategy,
75 plants can source water from either winter precipitation (directly as winter rainfall or as snowmelt
76 in the spring), summer precipitation, or both, as revealed by stable isotope studies of xylem
77 water (Alstad et al. 1999; Ebbs 2016; Ehleringer et al. 1991; Gierke et al. 2016; Hu et al. 2010).
78 Therefore, it is unclear if enhanced precipitation during the summer can compensate for the
79 negative effects of early snowmelt on plant traits, or if a late-melting snowpack can compensate
80 for summer drought. Anticipating when such compensation might occur is made more difficult
81 because most field studies of water-mediated changes in floral traits do not simultaneously
82 measure any physiological indicator of water stress to the plant (Descamps et al. 2021), but see
83 Campbell and Wendlandt (2013). A recent meta-analysis of drought effects on floral traits has
84 called for more studies that simultaneously address water stress (Kuppler and Kotowska 2021)
85 through mechanisms such as reduced stomatal conductance (Cowan 1978).

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

92 2018; Walter 2020) or in a flight cage (Kuppler et al. 2021), and all have manipulated summer
93 precipitation only.

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

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

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

141

142 **Materials and Methods**

143 *Study system*

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

153 *Snowmelt and precipitation manipulations*

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

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

174 Observations and projections of earlier snowmelt with climate change are driven by both
175 warmer spring temperatures and less winter snow accumulation (Clow 2010). In Gothic (1.5 km
176 north and 40 m higher in elevation than the study site), spring snowpack depth has decreased
177 from 1973 - 2016, and snowmelt timing has advanced by 1.4 ± 0.5 days per decade from 1935 -
178 2021 (slope \pm SE, $R^2 = 0.08$, $P = 0.007$, data from Wadgyamar et al. 2018 updated with latest
179 values from billy barr, <http://www.gothicwx.org/ground-cover.html>, Figure S2). Depending on the
180 year and plot, the black cloth treatments accelerated snowmelt by 3 - 11 days (mean \pm SD, $6 \pm$
181 2 days) compared to the average unmanipulated plot (Figure 2). This acceleration is equivalent
182 to 42 ± 22 y of future snowmelt advancement assuming continuation of climate change at the
183 same rate. During the three years of the study, the combination of snowmelt treatments and
184 interannual variation spanned the range of snowmelt dates observed over 1990 - 2017 (Figure
185 2).

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

192 tap water evenly to each 4 m² 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 (Yahjadian
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

215 *Trait measurements*

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

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

240 plants (9.4 per subplot per year). The numbers of unique plants are slightly lower because 4%
241 of plants that flowered survived to flower a second year, usually from a second rosette after an
242 inflorescence was browsed by deer (Brody et al. 2007). Minimum and maximum stamen length
243 were strongly correlated with corolla length at the plant level ($r = 0.88$ and 0.86 , $N = 494$, $P <$
244 0.001). We did not consider it possible to separate effects on those traits from effects on corolla
245 length, so they were not analyzed. All remaining traits had absolute correlations < 0.7 at the
246 plant level, with the highest correlations between style length and corolla length ($r = 0.65$),
247 corolla width and corolla length ($r = 0.40$), and inflorescence height and flower number ($r =$
248 0.37). There was a weak negative correlation between nectar production and concentration ($r =$
249 -0.27).

250 *Statistical analyses*

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

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

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

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

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

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

305 *Question 3: Soil moisture as a mechanism*

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

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

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

326 To examine how floral trait changes could be mediated by changes in physiological
327 status, we combined the floral trait measurements with data from a separate study of how the
328 same manipulations in the same experiment influenced leaf gas exchange (photosynthetic rate
329 and stomatal conductance expressed on a per area basis) of vegetative plants (Navarro et al.
330 2021). Flowering plants of *I. aggregata* divert all of their resources into flowers as their leaves
331 senesce over the summer, lowering their rates of photosynthesis gradually and complicating
332 assessment of their physiological status from leaves (Campbell et al. 2005), so as a proxy we
333 used the average gas exchange values of the vegetative plants measured in the same subplot
334 and year as the flowering plants. To explore the extent to which traits respond directly to soil
335 moisture versus indirectly through its effects on leaf gas exchange, we used structural equation
336 modeling. All data points, including both the exogenous variable of soil moisture and all of the
337 endogenous variables, were mean values for a subplot and thus independent units. Structural
338 equation modeling allows specification of a causal network of paths (Grace et al. 2010) in which
339 leaf gas exchange can potentially play a role translating effects of soil moisture into responses
340 of floral traits. We compared three *a priori* nested models using log-likelihood ratio tests based

341 on differences in chi-square values (Mitchell 1992). First we examined a full model (Model 1) in
342 which soil moisture (the one exogenous variable) could influence each floral trait directly or
343 indirectly, as mediated by photosynthetic rate or stomatal conductance, with correlations
344 allowed between the two physiological measurements, and among all floral traits. We did not
345 include sepal width as we had measurements for that trait from only two years. We used nectar
346 sugar rather than concentration because concentration combines the influence of water and
347 carbohydrates. Photosynthetic rate could mediate effects on floral traits by increasing
348 carbohydrate resources for making larger flowers or more nectar sugar. Stomatal conductance
349 could mediate effects on nectar production (nectar volume per day) by changing water loss from
350 the plant. Direct effects of soil moisture not mediated by leaf gas exchange could reflect
351 changes in uptake of soil nutrients, or for nectar production simply a change in water available
352 in the soil. Model 2 contained only the direct paths without intermediaries of photosynthetic rate
353 or stomatal conductance. Model 3 contained only the indirect paths through photosynthetic rate
354 or stomatal conductance. Structural equation modeling employed PROC CALIS in SAS version
355 9.3.

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

357 We examined the predicted effects of floral trait changes on fitness components for traits that
358 met two criteria: soil moisture had a significant effect on the trait, and previous studies had
359 measured how much a relative fitness component changes with a change in mean value for the
360 trait. Traits that met both criteria were corolla length, corolla width, style length, and nectar
361 production. Pollinator visitation rates can increase with longer corollas, wider corollas, and
362 nectar production (Campbell et al. 1991; Mitchell 1993; Campbell et al. 1997). Pollen receipt on
363 stigmas increases with longer styles, and pollen exported to flowers on other plants of this self-
364 incompatible species increases with wider corollas and higher nectar production (Campbell
365 1989a; Mitchell 1993). These studies had ranges for trait values similar to those in the current

366 study. Although one nectar study (Mitchell 1993) was a manipulative study, the nectar addition
367 of 5 μL was within the natural range produced per day in our study (range = 0 - 12 μL with one
368 outlier of 18 μL). Seed production also increases with corolla length and corolla width in a hybrid
369 zone with a wider range of trait values, although the intensity of this selection varies greatly
370 across years with stronger selection associated with later snowmelt (Campbell and Powers
371 2015). We used standardized selection differentials from these studies, which provide the
372 change in relative fitness for each change of one standard deviation across plants in the trait,
373 i.e. a standardized trait. We multiplied the slopes of the standardized traits on soil moisture
374 determined under Question 3 (averaged across the three years) with these standardized
375 selection differentials to predict the change in a relative fitness component per change in soil
376 moisture, recognizing that there is considerable uncertainty around the quantitative estimates of
377 selection.

378 **Results**

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

380 We first examined the effects of the year, the summer precipitation and snowmelt treatments,
381 and their interactions on floral traits using the replicated split-plot models (Table 1, Figure 3).
382 Whereas the snowmelt treatment elicited no main effects on floral traits in these models (all $P >$
383 0.08), it did influence nectar production and flower number in ways that depended on the year
384 (Table 1; interaction $P < 0.01$). Compared to controls, precipitation reduction reduced corolla
385 length, style length, and sepal width, and precipitation addition increased corolla length, corolla
386 width, and nectar production, and decreased nectar concentration (post-hoc tests in Table 1).
387 The effects of the precipitation treatments only varied across years for sepal width (interaction P
388 < 0.01), which showed a stronger effect of precipitation in an early snowmelt year (2020), than
389 in a late snowmelt year (2019). There were differences among years for all floral traits except

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

399 We examined the responses of floral traits to the actual snowmelt dates and the total
400 summer precipitation experienced by the flowering plants using our second set of models that
401 incorporated both experimental effects and natural variation in those climatic variables (Table
402 S2, Figure 4). For snowmelt date, these models detected effects that were not significant in the
403 first models, because of low replication of the snowmelt manipulation and the greater statistical
404 power achieved with incorporating the full range of snowmelt dates over a period of 46 days
405 rather than an average manipulation of 6 days. Earlier snowmelt date reduced corolla length,
406 style length, corolla width, sepal width, nectar production, and inflorescence height, and
407 increased nectar concentration (all $P < 0.02$), but had no detected effect on flower number ($P =$
408 0.60). The standardized effects of snowmelt timing varied by trait, with inflorescence height and
409 nectar concentration responding most strongly. Lower total summer precipitation (calculated
410 based on the treatments applied to each subplot) reduced corolla length, style length, corolla
411 width, and sepal width ($P < 0.05$), but did not have detected effects on other floral traits ($P >$
412 0.05). The negative effect of reduced precipitation on corolla length and sepal width
413 strengthened with earlier snowmelt (interaction $P < 0.01$), but no other traits showed this
414 interaction between the two climate variables ($P > 0.06$). For the traits that showed effects of the
415 two climate variables but not an interaction, we estimated the amount of additional total summer

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

421 *Question 3: Soil moisture as a mechanism*

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

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

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

444 The relationships of floral traits to soil moisture were partially mediated by how soil
445 moisture altered leaf gas exchange. The full model with direct paths from soil moisture to traits
446 as well as paths mediated through photosynthetic rate or stomatal conductance fit better than
447 either of the nested models (difference in chi-square = 30.3, 5 df and 25.7, 5 df). All of the floral
448 traits tested (corolla length, style length, corolla width, nectar production, and nectar sugar)
449 responded to soil moisture through direct mechanisms that were not mediated by photosynthetic
450 rate or stomatal conductance, while only three of the traits showed responses mediated by gas
451 exchange (Figure 6). Subplots with higher average photosynthetic rate also had plants with
452 wider corollas (standardized path coefficient = 0.37, $P = 0.0011$) and longer style (standardized
453 coefficient = 0.35, $P = 0.0031$), while subplots with higher stomatal conductance and thus less
454 water stress also had plants with higher nectar production (standardized path = 0.23, $P =$
455 0.0012). The strongest path detected was between soil moisture and nectar production
456 (standardized path = 0.46, $P < 0.0001$). Although the path from soil moisture to stomatal
457 conductance was not significant ($P > 0.05$), stomatal conductance and photosynthetic rate were
458 highly correlated ($P < 0.0001$; Figure 6). The reduced models gave similar results, with evidence
459 for direct paths from soil moisture to each floral trait (Figure S5A) and indirect paths mediated
460 by gas exchange for 4 of the traits, corolla length as well as style length, corolla width, and
461 nectar production (Figure S5B).

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

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

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

477 **Discussion**

478 *Changes in floral trait expression in response to snowmelt and precipitation*

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

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

498 These results add to studies of other species that have also reported general reductions
499 in flower size with reduced water during the growing season (Descamps et al. 2021; Gallagher
500 and Campbell 2017; Suni et al. 2020). Responses of nectar and pollen to water availability have
501 been mixed; for example, nectar volume was higher for dry plants in *Phlox drummondii* (Suni et
502 al. 2020), but higher for wet plants in *Epilobium angustifolium* (Carroll et al. 2001) and *Mertensia*
503 *ciliata* (Gallagher and Campbell 2017). In our analysis of the effect of soil moisture, we found
504 that decreased water availability strongly reduced nectar production in *I. aggregata* (0.22
505 $\mu\text{L}/\text{day}/\% \text{VWC}$), complementing other work in this species showing reductions in both pollen
506 and nectar production with soil moisture (Waser and Price 2016; estimated effect on nectar
507 production was 0.40 $\mu\text{L}/\text{day}/\% \text{VWC}$). Our work is unusual in that we examined how traits of
508 individual flowers respond to snowmelt timing. This research is timely because in tundra and
509 subalpine ecosystems around the world (Pederson et al. 2011; Assmann et al. 2019; Sun et al.
510 2019), there are strong trends towards earlier snowmelt dates with recent and predicted climate
511 change, while predictions for summer precipitation have high variability (IPCC 2014). For that
512 reason, we urge other investigators of high latitude or high elevation systems to pay attention to
513 floral plasticity in response to aspects of winter snowpack, such as snowmelt timing, as well as
514 summer precipitation.

515 Since predictions for summer precipitation have such high variability, it is of interest to
516 know if high summer precipitation could compensate for the predicted earlier snowmelt driven
517 by climate change. In this study system, compensation appears possible for most floral traits,
518 with the caveat that we measured the impacts in an experiment that did not manipulate all
519 aspects of climate change. Effects of snowmelt timing and precipitation could be different under
520 higher summer temperatures in the future, as high temperature can dry soils and increase
521 evapotranspiration (Seager et al. 2013). We detected no significant differences between control
522 plots and early snowmelt plots that received additional water, except where water addition
523 overcompensated for early snowmelt. The observed changes in floral traits in response to early
524 snowmelt and reduced precipitation are associated with reductions in soil moisture. Our early
525 snowmelt treatment reduced soil moisture by less than our water additions increased it (0.5% vs
526 1.8%), so it is not a surprise that compensation occurred under those treatments. Our results
527 indicate that a doubling of average summer precipitation could compensate for any changes in
528 trait values that occurred under an earlier snowmelt of 6 ± 2 days (mean \pm SD), which we
529 estimated to be equivalent to 44 ± 22 y of further climate change. However, such a doubling of
530 precipitation throughout the growing season is very unlikely, especially over the course of
531 multiple seasons. Climate models downscaled for this region of North America predict
532 reductions in precipitation during spring through June, with some predicting a potential increase
533 of 2 - 4% in mid-summer by 2070 - 2099, as timing of the summer monsoon shifts (Seth et al.
534 2011). Since we estimated that a 3 - 6% increase in total summer precipitation would
535 compensate for one day earlier snowmelt (for corolla width or style length), a 4% increase in
536 future precipitation, even if it extended throughout the summer, could not compensate for the 11
537 days earlier snowmelt predicted by 2099 if snowmelt timing continues to change at its historical
538 estimated rate of 1.4 days per decade (Figure S2). Moreover, since 1990 in Gothic, the average
539 daily summer precipitation has decreased by $14 \pm 5\%$ per decade, and the proportion of
540 summer days with precipitation has declined by $11 \pm 5\%$ per decade (mean \pm SE, Figure S6).

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

544 *Potential mechanisms*

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

566 In only a few cases do we know if shifts in floral traits with drought can alter pollinator
567 visitation or other fitness components (Al-Ghzawi et al. 2009; Burkle and Runyon 2016;
568 Gallagher and Campbell 2017; Glenny et al. 2018; Walter 2020; reviewed in Descamps et al.
569 2021; Kuppler et al. 2021). Results have been mixed, with some showing negative responses of
570 pollinator visitation rate to decreased soil moisture (Gallagher and Campbell 2017; Kuppler et al.
571 2021) and others finding results dependent upon the species of plant or pollinator (Burkle and
572 Runyon 2016; Glenny et al. 2018). By combining our results with previous studies of *I.*
573 *aggregata* going back as far as three decades (e.g., Campbell 1989a), we were able to predict
574 that pollinator visitation by hummingbirds, in response to a single trait change, could decrease
575 by 2 - 8% with a 1% decrease in soil moisture (depending on the trait), and other relative fitness
576 components could decrease by up to 11%. Because multiple floral traits responded to soil
577 moisture, it is likely that decreases in pollinator visitation would be greater than those estimated
578 for any single floral trait; traits with positive associations with soil moisture have positive
579 correlations with each other, but those correlations are only partial so a change in a second trait
580 would add to the effect of the first. These predictions do have high uncertainty given the
581 variance across and within years in how traits change with soil moisture and how fitness
582 components change with traits. They also entailed combining estimates from natural
583 populations that could have different standard deviations in the traits. Considering those
584 caveats, the largest decrease in fitness was mediated by a change in nectar production. Nectar
585 production both decreases more sharply with soil moisture, as based on its standardized slope,
586 and has a higher impact on both hummingbird visitation and rate of pollen export than any other
587 floral trait (Table 2). Lower pollen export leads to lower male pollination success and lower
588 overall reproductive success. Previous studies showed mixed effects of nectar production on
589 female reproductive success in *I. aggregata*, with one study finding that increased nectar

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

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

613 *Conclusions*

614 Climate change is reducing snow cover and causing earlier snowmelt at high latitudes and
615 elevations (Stewart et al. 2005). Here we showed that earlier snowmelt can cause changes in
616 floral trait expression similar to those seen as plastic responses to reduced growing season
617 precipitation in both *Ipomopsis aggregata* and other plant species (Campbell and Wendlandt
618 2013; Galen 2000; Gallagher and Campbell 2017). Earlier snowmelt can also amplify the effects
619 of changes in summer precipitation on floral traits. These changes have the potential to
620 influence pollinator visitation and other fitness components, as illustrated by predictions for *I.*
621 *aggregata*. Whereas most studies of snowmelt timing have focused on impacts on phenology,
622 these results provide a rare example of how snowmelt timing can also influence populations
623 through alterations in expression of other traits with fitness effects (Anderson and Gezon 2015).
624 We encourage future investigations of impacts of climate change on floral traits and other plant
625 traits to consider responses to timing of key weather events such as snowmelt.

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632 **Author Contributions**

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

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

637 **Data Availability**

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

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904 **Tables and Figures**905 **Table 1**

906 Linear mixed model results for replicated split-plot analysis of the effects of year and the snowmelt and precipitation treatments on traits. P values
 907 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
 908 effects. P values for post-hoc tests for the main effects of precipitation (excluding interactions) are listed comparing the precipitation addition and
 909 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

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Table 2

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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 \pm 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).

Trait	Slope of standardized trait vs. VWC	Standardized selection differential (S')				Percent change in relative fitness per increase in 1% VWC			
		Visits	Pollen receipt	Seeds	Pollen export	Visits	Pollen receipt	Seeds	Pollen export
Corolla length	0.12 \pm 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 \pm 0.04	NA	0.23 ³	ns ⁵	ns ³		3.4%		
Corolla width	0.16 \pm 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 \pm 0.04	0.37 ¹ or 0.19 ⁶	ns ⁵	ns ⁴	0.53 ⁶	8.0% or 4.1%			11.5%

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¹Within-population slopes on standardized traits calculated from field observations in 1989 (Campbell et al.

921

1991). S' for corolla length and nectar production were not reported but were calculated from the original data.

922

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

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

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

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

930 ⁶Estimated from change in visit rate comparing control and nectar addition plants in 1987 - 1991 (Mitchell
931 1993). Standard deviation of the trait was not reported and so was estimated from the current study.

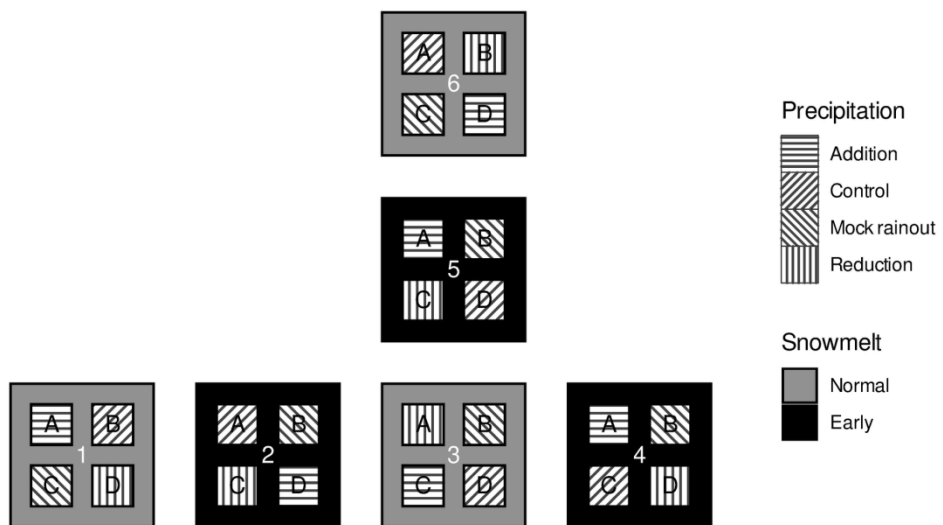


Figure 1. Layout of snowmelt manipulation plots (7 m × 7 m, denoted by numbers) and precipitation manipulation subplots (2 m × 2 m, denoted by letters). Plot sizes are to scale, but not distances between plots.

165x101mm (300 x 300 DPI)

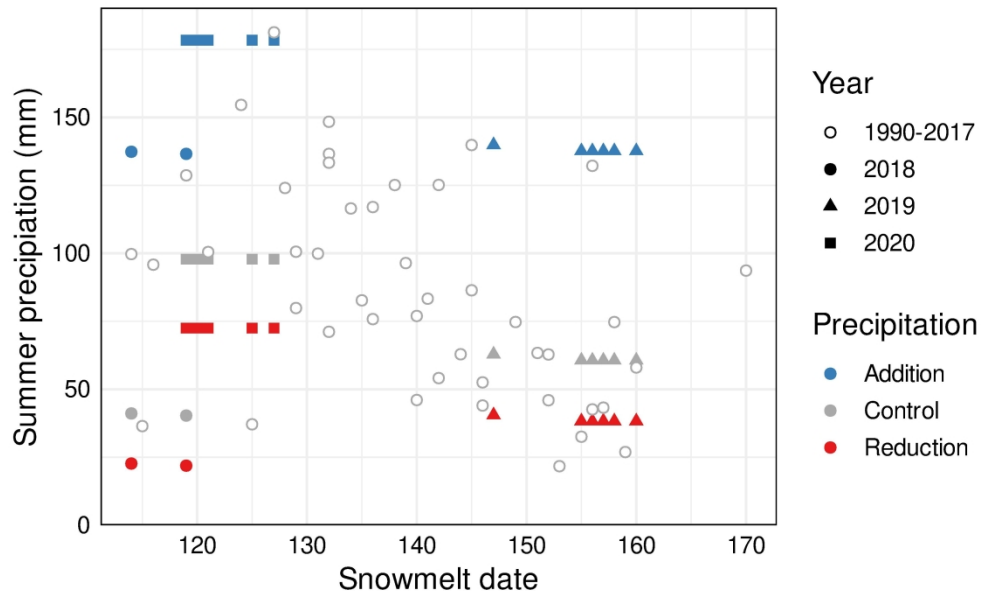


Figure 2. The range of environmental variation produced by snowmelt and summer precipitation treatments compared to 30 y of historic variation. The snowmelt date and summer precipitation from the snowmelt date to Julian day 214 in Gothic, Colorado, USA are shown as open circles for 1990 - 2017. The snowmelt 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)

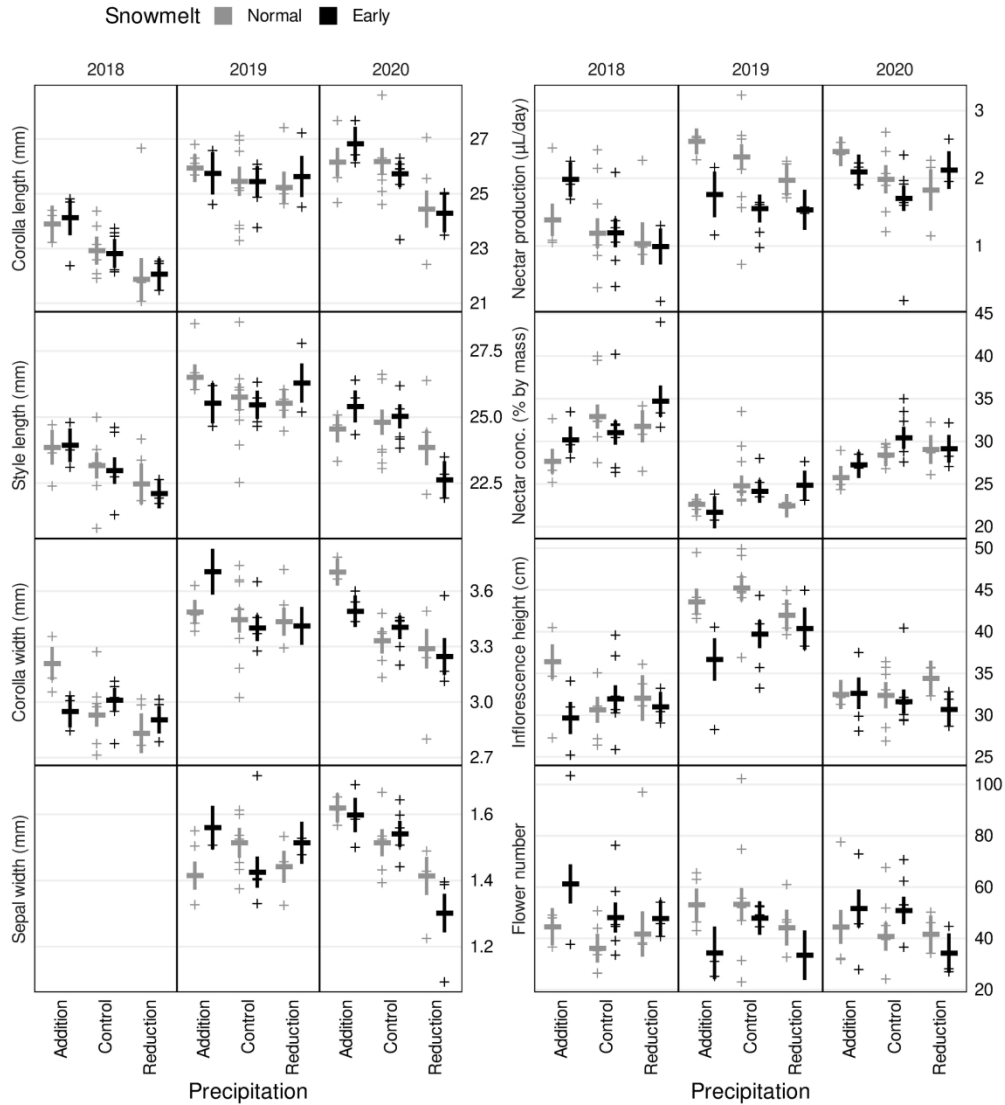


Figure 3. The effects of snowmelt and precipitation treatments on traits across three years. Horizontal bars show the estimated marginal means from a model fitted to plant means with random effects of plot and subplot, with ± 1 standard error as a vertical bar, and small crosses show subplot means. Sepal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

228x254mm (300 x 300 DPI)

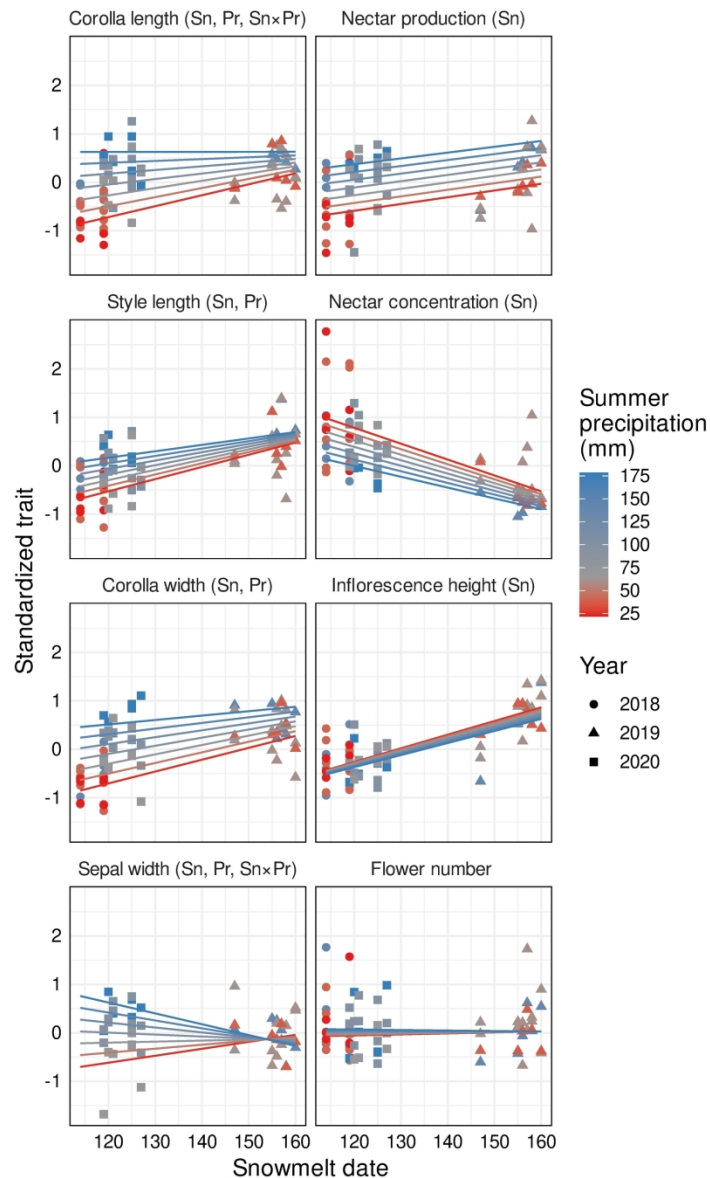


Figure 4. The effects of the snowmelt date and estimated summer precipitation on traits across three years. Each trait was standardized by dividing by the standard deviation of plant means. Lines show the estimated marginal trends for the amounts of summer precipitation listed in the legend, from a model 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)

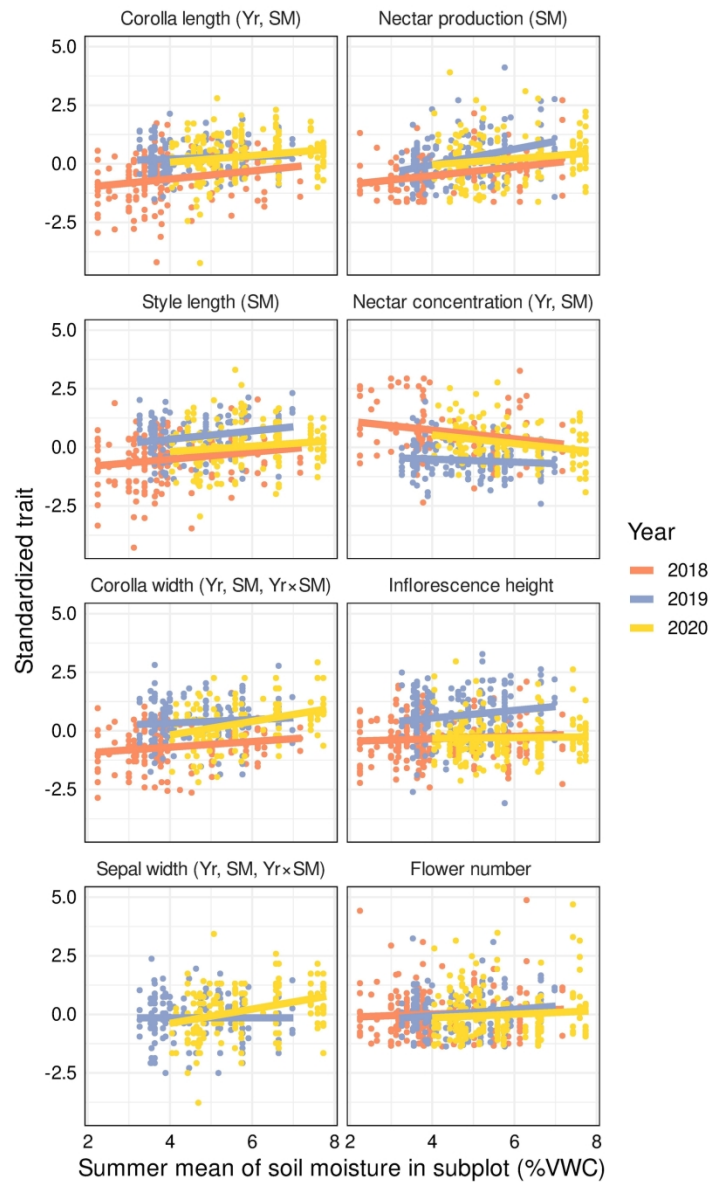


Figure 5. The effects of soil moisture (averaged across the measurement period in each subplot) on traits across three years. The standardized mean trait values for each plant in each year are shown as points. The estimated marginal trend is shown as a line for each year. Sepal width was not measured 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)

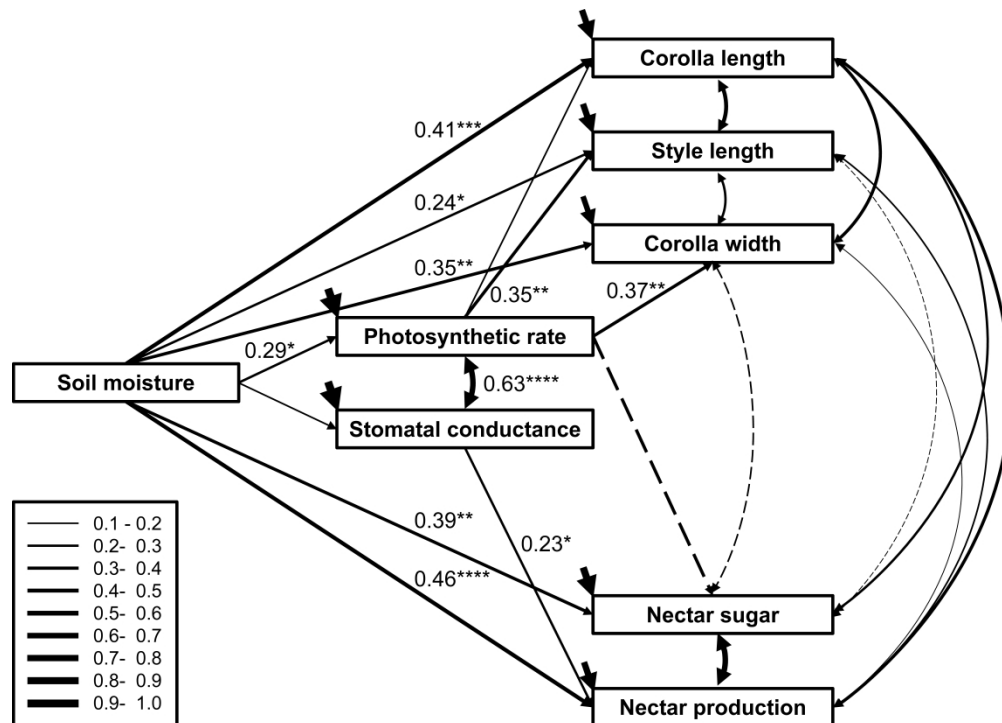


Figure 6. Structural equation paths showing direct effects of soil moisture on floral traits as well as those mediated through leaf gas exchange (photosynthetic rate and stomatal conductance). The figure shows the standardized paths from a full model including all paths from soil moisture to floral traits, 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)