Flowering phenology in alpine grassland strongly responds to shifts in snowmelt but weakly to summer drought

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Abstract

Alpine plants complete their seasonal phenological cycle during two to three snow-free months. Under climate change, snowmelt advances and the risk of summer droughts increases. Yet, photoperiodism may prevent alpine plants from benefiting from an earlier start of the growing season. To identify the drivers of flowering phenology in the seven main species of an alpine grassland, we experimentally shifted the snowmelt date through snow manipulations, and excluded precipitation during summer. With “time-to-event” models, we analysed the beginning of main flowering with respect to temperature sums, time after snowmelt, and calendar day (photoperiod). We identified two phenology types: four species tracking snowmelt dates directly or with a certain lag set by temperature sums, including the dominant sedge *Carex curvula*, *Anthoxanthum alpinum*, *Helictotrichon versicolor*, and *Trifolium alpinum*, and three species tracking photoperiod: *Geum montanum*, *Leontodon helveticus* and *Potentilla aurea*. Photoperiodism did not act as daylength threshold but rather modulated the thermal sums at flowering. Hence, photoperiod delayed flowering after earlier snowmelt. The grass *A. alpinum* was the only one of seven species that clearly responded to drought by earlier and longer flowering. The remarkably high importance of snowmelt dates for both phenology types suggests an earlier onset of flowering in a warmer climate, particularly for non-photoperiod-sensitive species, with an increasing risk for freezing damages and potential disruptions of biotic interactions in the most frequent type of alpine grassland across the Alps. Consequentially, the distinct microclimate and species-specific responses to photoperiod challenge temperature-only based projections of climate warming effects on alpine plant species.

Keywords Alps · Climate change · Growing season · High elevation · Photoperiod · Snow cover · Survival analysis

Introduction

In alpine regions, the length of the growing season is determined by snow cover duration and alpine plant development is closely linked to snowmelt timing (Körner 2021). During recent decades, shifts in snow cover have been observed particularly below the treeline, but also for alpine and nival zones (Marty 2008; Scherrer et al. 2013; Klein et al. 2016; Hock et al. 2019). Further massive reductions in snow cover duration are predicted under ongoing and future climate change (Keller et al. 2005; Steger et al. 2013; Hock et al. 2019). Summer droughts are expected to occur more frequently and to be more severe (IPCC 2018), and may,

therefore, limit alpine plant species that otherwise profit from an earlier growing season.

Photoperiodism

Given the long-lasting snow cover, alpine plants have to complete their growth and reproduction very rapidly within a 10–12-week growing season. Besides bud preformation (Erschbamer et al. 1994; Meloche and Diggle 2001), mechanisms are required to precisely control plant phenology. About half of 23 species studied in the high alpine belt (2600–3200 m a.s.l.) have displayed pronounced photoperiodism in the greenhouse (response to daylength, thus to photoperiod; Keller and Körner 2003). Photoperiodism prevents plant development during warm spells in late winter or early spring and facilitates synchronised flowering, presumably increasing reproductive success (Heide 2001; Keller and Körner 2003). Heide (1985, 1990, 1992, 2005; Heide et al. 1990) provided compelling evidence that photoperiod plays

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a decisive role in many arctic plant species. The significance of photoperiod has predominantly been studied in form of thresholds or long-day requirements (e.g. Heide 2001; Keller and Körner 2003). In the context of climatic change, photoperiodism may prevent species from benefiting from earlier snow melt. Species that are tightly linked to photoperiod cues could have a competitive disadvantage over more non-photoperiod-sensitive species. Wadgymer et al. (2018) highlighted that the flowering phenology of six subalpine forbs has not advanced as rapidly as the snowmelt dates (1973–2016: 1 week earlier snowmelt induced 3.5–5 days earlier flowering only).

However, in situ evidence for photoperiodism in the alpine belt is still scarce. Recently, several studies with transplanted montane and alpine plants at different elevations (common gardens) underline that plant species from higher elevation flowered earlier when brought to lower elevation with earlier snowmelt (Gugger et al. 2015), especially early-flowering species or graminoids seem to be more responsive to earlier snowmelt than late flowering species (Wadgymer et al. 2018). Although common gardens have many advantages such as allowing a differentiation between genotypic and phenotypic acclimatisation, pre-cultivation of alpine plant species at lowland conditions (in the greenhouse) and commonly offering nutrient rich soil substrates or restricting rooting volumes by pots may affect plant performances and also phenological responses in common gardens.

In general, natural differences in photoperiod under variable snowmelt in the field are typically far smaller than those often applied in greenhouse and transplant experiments.

Furthermore, higher temperatures are expected to accelerate plant development in addition to photoperiod signals (Heide 1992). Without photoperiod control, temperature sums alone may drive plants to respond to early snowmelt, causing earlier flowering, but simultaneously increasing the risk of freezing damages.

The cascade of processes in a plant after the photoperiod threshold for flowering is passed, the interaction with temperature in particular, is not well understood. To predict future plant responses to an earlier onset of the growing season such interactions between drivers have to be accounted for. Here, we aim at deciphering these interactions experimentally by manipulating the onset of the growing season by snow manipulation under alpine field conditions.

The effect of snowmelt date and temperature on phenology

A 31-year-long study in the Rocky Mountains revealed a close correlation of first flowering and snowmelt dates, provided snowmelt did not occur exceptionally early in the year (Inouye 2008). A tight coupling of plant development with snowmelt dates was also observed in other high-elevation

and high-latitude ecosystems, which differed in daylength (e.g. Canaday and Fonda 1974; Ram et al. 1988; Wipf and Rixen 2010). For alpine plant species not assumed to be photoperiod sensitive, post-snowmelt temperatures were considered to control the phenology (e.g. Kudernatsch et al. 2008; Livensperger et al. 2016; warming with open-top chambers). Earlier attempts at identifying drivers of alpine plant phenology have already considered both, temperature and photoperiod, but have not addressed their potential interaction (Molau et al. 2005; Hülber et al. 2010).

When studying temperature effects on alpine plant species, it is important to account for the actual growing conditions of meristematic tissues. Given that the compressed, small stature of alpine plants creates a warmer microclimate, weather station data, as often used for phenological models, are not a reliable data source for temperatures that are driving alpine plant development (Scherrer and Körner 2010; Dietrich and Körner 2014; Körner and Hiltbrunner 2018).

Summer drought

Despite the typically positive water balance at high elevations in temperate mountains (Weingartner et al. 2007), recent heat waves and precipitation deficits in the Alps (2003, 2015, 2018) have shown that summer drought occurs above the upper treeline and plants have been spotted wilting (personal observations). In a low elevation grassland, drought both advanced flowering and prolonged flower duration by 4 days (Jentsch et al. 2009). Complete rain exclusion during 43 days in an otherwise very humid region increased the seed mass of plant species occurring at higher elevations, presumably promoting seedling recruitment in a calcareous grassland (Rosbakh et al. 2017). An experimental drought for 17 days reduced phytomass production in alpine grassland (de Boeck et al. 2016). Schmid et al. (2011) observed reductions of 12–35% in above-ground biomass of a similar grassland type under summer drought. None of these studies included phenological observations. Nevertheless, the combination of shifting snowmelt dates and summer drought may have a large impact on alpine grassland, in particular on developmental processes (phenology), with implications for biotic interactions and gene flow, as well as for future species distribution.

Main objectives

In this study, we aimed at identifying the drivers of flowering phenology and flower duration for the main plant species in a late successional alpine grassland and to explore how summer drought interferes with these drivers. To assess drivers and their interactions, we established a snow manipulation and rain exclusion experiment at 2500 m a.s.l. This late successional grassland, dominated by *Carex*

curvula, is the most widespread type of alpine grassland on siliceous bedrock in the European Alps (Oberdorfer 2001; Leuschner and Ellenberg 2017). We present a phenological dataset covering the 3 years 2016–2018, supplemented with detailed microclimatic data for the growing seasons.

As snowmelt commonly occurs around summer solstice at our field site, we hypothesise (1) that temperature after snowmelt plays a more crucial role for phenology than does photoperiod, with (2) an influence of photoperiod after exceptionally early snowmelt only. As soil moisture continuously decreases under ongoing drought, we expect (3) late flowering species to be significantly more affected by drought than early-flowering species.

Materials and methods

Site description

The study site is located at 2500 m a.s.l. near the Furka pass in the Swiss central Alps (46° 33' 47" N, 8° 23' 28" E) in a late successional grassland on siliceous podsol. For an earlier site description and productivity data, see Schächli and Körner (1996). The growing season lasts approximately 3 months with snowmelt usually occurring in June and senescence starting in the second half of August. Mean air temperatures during June, July and August are 6.0 °C, 8.7 °C and 8.3 °C (Furka pass, www.alpfor.ch). As a result of the continuous snowpack at the site, soils commonly do not freeze in winter. Summer precipitation amounts to ca. 400 mm (Jun–Aug, Furka pass). With an inclination of 10°, the terrain is relatively flat for alpine terrain and well suited for an experiment with snow manipulations and summer drought. Most of the roots and the apical shoot meristems are located in the upper 5 cm of the soil profile and the mean rooting depth is around 20 cm (few roots down to 1 m depth). Besides the dominant sedge *Carex curvula* All., other frequently occurring species are the grasses *Anthoxanthum alpinum* Á. Löve & D. Löve, *Helictotrichon versicolor* (Vill.) Pilg. and *Poa alpina* L., the forbs *Geum montanum* L., *Leontodon helveticus* Mérat, *Potentilla aurea* L., *Sibbaldia procumbens* L. and *Soldanella pusilla* Baumg., and the N₂-fixing forb *Trifolium alpinum* L. (species nomenclature according to Lauber et al. 2018).

Fruticose lichens (*Cetraria islandica* L. and various *Caldonia* species) are abundant in this alpine grassland. However, as the age of the lichens cannot be determined and lichens may dry out for longer periods, we did not include them in the field observations.

Snow manipulation and summer drought

We implemented all combinations of summer drought (control, moderate-5-week drought spanning the main period for the above-ground biomass production, intense-10.5-week drought covering almost the entire growing season) and snow manipulations (control, addition, removal) in a fully factorial experimental design. We had 45 parcels (2 × 2.5 m), organised in 5 replicated blocks. In each block, the nine parcels were randomly assigned to one fixed treatment combination. To avoid any boundary effects of the drought treatment, we defined a central plot (1 × 1 m) within each parcel.

We conducted the snow manipulations in late spring 2016–2018 (beginning of June 2016, end of May 2017, first half of June 2018), 2–3 weeks before natural snowmelt (Fig. 1). In 2016 and 2017, we decreased the snow depth from roughly 1–0.5 m to achieve earlier snowmelt, and we increased the snow depth to 2.2–2.5 m to delay snowmelt. An unstable weather period in 2018 postponed the snow manipulation, so that the mean snow depth was only 0.5 m, thinner than desired for the treatment. We, therefore, removed snow down to 0.3 m and added it up to 0.5–0.7 m, depending on snow availability. Then, because of the lower snow depth on the snow addition parcels, we covered the snow addition parcels with a white, water permeable fleece

Fig. 1 Snow manipulations and rainout shelters at the field site at 2500 m a.s.l. in 2017. The insert with snow manipulations was retrieved from <https://www.webcam-4insiders.com/de/Oberwald/15221-Oberwald.php> (on-site webcam)

(Datex KN 25, Fritz Landolt AG, CH), which was removed after 10 days when snow height was 0.3 m.

We applied the drought treatments using rainout shelters, starting directly after snowmelt: on June 16th, 2017 and on July 2nd, 2018 (no drought treatment in the year 2016).

The basal area of the shelters was 2.5×3 m, thus, they were 0.5 m larger than the parcels in either direction. The tent-like shelters had a ridge height of 1.2 m, with both long edges reaching down to 10 cm above the ground and covered by UV-B permeable foil (Lumisol AF clear, Hortuna AG, CH). The triangular openings of the short sides were oriented in the main wind direction (W–E), ensuring a constant air flow to minimise microclimatic effects. Wooden strips at both long sides of the shelter drained the excluded rainwater outside the lower end of the parcel. These rainout shelters were constructed to withstand harsh alpine weather conditions and have already been successfully implemented for a drought experiment (Schmid et al. 2011, photo of rainout shelter in the Fig. 1).

Temperature sensors in the centre of each plot (HOBO UTBI-001 TidbiT v2 Temp, Onset, US, 1-h measurement intervals) measured the soil temperature adjacent to most alpine plants' meristems (3–4 cm depth). Diurnal temperature fluctuations after snowmelt revealed exact snowmelt dates within each plot. We additionally used the soil temperatures for assessing temperature effects of rainout shelters (day- and night-time effects separated: 11 a.m.–10 p.m. and 11 p.m.–10 a.m. These 12-h intervals consider daily minima and maxima of soil temperatures, lagging 2 h behind air temperatures. During the growing seasons 2017 and 2018, every 10 min, two weather stations (Vantage Pro2, Davis Instruments Corp., USA) recorded precipitation, global radiation and air temperatures at 1.5 m above ground. Surface temperatures were measured with an IR thermal camera (VarioCAM®, Infratec, Dresden, GER). Thermograms were taken in each plot on six sunny days with all rainout shelters removed (two times in 2017, four times in 2018) from a distance of 180 cm southwards of the plots at an angle that covered the whole plot. Pixel-based temperatures were extracted using the software IRBIS 2.20 (Infratec, Dresden, GER; temperatures are shown in ESM 1.1 and 1.2).

We manually measured the soil moisture of the top 5 cm (Theta probe ML2x, Delta-T Devices, UK), with a 1–2-week interval. For assessing the drought effect in both years, we averaged the soil moisture values over five separate time periods as rainout shelters were immediately installed after snowmelt, and therefore, differed in the date between the 2 years (N indicates the number of measuring campaigns during the corresponding period). Two time periods with all rainout shelters installed (moderate and intense drought, 1st and 2nd half), two time periods during intense drought (1st and 2nd half), and one after the removal of all rainout shelters. Eight soil moisture retention curves (pF curves, pF

as the $\log_{10}$ of the matrix potential) served as a reference for the actual drought effect (10 and 30 cm soil depth, measured with a HYPROP 2, METER Environment/UMS, GER). The growing season 2018 was exceptionally dry and we observed wilting adjacent to our study site, therefore, we watered the controls twice (1st and 28th of August), with 17 L m^{-2} each, to prevent any drought damages in the controls.

Phenology

We assessed phenology twice a week directly after snowmelt, weekly throughout the main season, and biweekly at the end of the season (after flower senescence). This resulted in 7, 12 and 10 phenology assessments in the years 2016, 2017 and 2018, respectively. For each plot and each species growing on it, we determined its phenological stage. We characterised main flowering as the state when the majority ($\geq 50\%$) of flowering individuals on a plot had fully open flowers, and clearly visible open anthers and stigmas in case of sedge and grass species. We assessed flower senescence when the majority of flowering individuals had dried or fallen off petals or dried and broken off anthers for the graminoids. We then defined the transition to main flowering (TMF) as the start date of main flowering, and the flower duration as the time span until flower senescence. TMF was used for the analysis instead of the transition to earliest flowering because of its distinct signal at plant species level (e.g. CaraDonna et al. 2014).

Although we selected the most abundant species only, not all of these occurred in each plot. Dominant graminoids (*C. curvula*, *H. versicolor*) had often more than 50 individuals per plot, while forb species were much less abundant (6–20 individuals per plot). We, therefore, restricted our analysis to species that occurred at least three times per implemented treatment combination (snow and drought treatments) in all 3 years ($n=3-5$). These were the sedge *C. curvula*, the grasses *A. alpinum* and *H. versicolor* as well as the forbs *G. montanum*, *L. helveticus*, *P. aurea*, and *T. alpinum*. In 2016, flowering was not recorded in *A. alpinum*.

Drivers for flowering phenology and interval censoring

We differentiated between flowering phenology driven by (1) snowmelt or by snowmelt and the subsequent temperature regime, and (2) photoperiod (or an interaction between photoperiod and temperature). A special case of (1) would be a fully opportunistic plant species that starts flowering immediately after snowmelt with concurrent temperature allowing for a delay of only a few days till TMF. For the transition to main flowering (TMF), we thus considered (1) the day of the year (DOY) with its specific photoperiod (PP), (2) the time in days elapsed since snowmelt (DSM), and

(3) temperature, expressed by thermal sums (TS, $^{\circ}\text{h} \geq 0^{\circ}\text{C}$ or $\geq 5^{\circ}\text{C}$) measured close to apical meristems (at 3–4 cm soil depth; TS $\geq 5^{\circ}\text{C}$ are presented in the ESM 2 only).

DSM and TS are highly correlated across the whole growing season, but not necessarily during the first few days after snowmelt. Especially for early-flowering species, these temperatures at the very start of the growing season may be decisive for TMF, and therefore, both drivers were considered here, but analysed separately.

From the phenology census, we identified the interval of the transition for TMF and flower senescence, respectively. The last observation prior to TMF corresponds to the lower interval boundary and the first observation of main flowering represents the upper interval boundary after the transition. For these intervals with the phenological shift, we have continuous records of the three potential drivers (DOY/PP, DSM, and TS).

Data analysis

Drivers of TMF

For each driver and each plant species separately, we analysed whether snow manipulation, summer drought or the different years led to a significant shift (delay/advance) of TMF. We used time-to-event analysis (R package survival v 2.43.3, Therneau 2015) with our census observations to delineate TMF. Time-to-event regression is specifically designed for situations when only the interval of an event occurrence is known but not its exact time. Here, “event” refers to a phenological transition (TMF, flower senescence), and “time” denotes a phenological driver (DOY/PP, DSM, and TS).

The so-called hazard function describes the probability of TMF to occur at time x and the corresponding survival curve provides the probability of the phenological transition to have already occurred by the time x (Klein and Moeschberger 2003). With the time-to-event regression, we fit a parametrical hazard function to the interval censored data. For each driver, each plant species and the two transitions, we tested three parametric distributions (exponential, Weibull, and log-logistic) and the best fit was chosen based on the log-likelihood. In addition, we compared parametric to non-parametric stepwise models, and we graphically analysed response residuals. For each treatment and each year, we determined TMF at the driver’s value with a 50% probability for individuals within plots to have transitioned ($p50$). We calculated the TMF’s $p50$ values and their confidence intervals for each treatment combination in each year.

As summer drought was implemented in 2017 and 2018 only, we tested its effect for these 2 years separately (model with drought, snow manipulations and years, $n = 3$ –5). In case of a significant drought effect, only parcels without

drought treatments were used for the further analysis of the snow treatments across all three years (2016–2018). For all analyses, we allowed twofold interactions, as higher number of interactions could not be interpreted in an ecologically reasonable manner for the given setup. Significant treatment and year effects were assessed using type III ANOVA. Since TMF occurred before the end of the moderate drought treatment, we averaged the values for the moderate and intense drought treatments. We present absolute values, but the drivers for TMF were standardised to values between 0 and 1 to allow direct comparisons among drivers. The predictive power of a driver was judged by its degree of concurrence with the observed onset of TMF. The best fitting driver was identified by a very small difference between the earliest and the latest onset of a phenological shift across experimental treatments in all 3 years (standardised range of TMF).

Photoperiod-dependent temperature sums

In addition to the treatment effects, we investigated the linear relation of TS ($^{\circ}\text{h} \geq 0^{\circ}\text{C}$) at TMF and snowmelt dates (with its respective photoperiod) for each species, again with time-to-event analysis, using a Gaussian hazard distribution. For those species with a drought effect in the prior analysis, we also tested the response to drought, allowing for the interaction of drought and snowmelt dates.

Flower duration

We assessed the flower duration as the time difference between TMF and the transition to flower senescence (both $p50$ values). $p50$ values were extracted from survival models, based on the driver days since snowmelt (DSM). Particularly later in the growing season, DSM and TS are highly correlated, and therefore, we here report flower durations expressed in DSM (days) but not in TS ($^{\circ}\text{h}$). For flower duration, we considered 2017 and 2018 only. The difference in natural snowmelt dates among the 2 years was far larger than what we achieved through snow manipulations. Thus, for flower duration, we accounted for differences between years and for the effect of drought, but not for the effect of snow manipulation. Thereof, we derived one flower duration per treatment combination and year. This resulted in a replicate of $n = 3$ per drought treatment and year. We applied stepwise backwards model selection to the full model with interaction effects between species, years, and drought treatment. Contrasts were calculated through Tukey HSD post hoc comparisons (R package emmeans v1.4.2., Lenth et al. 2019). All analyses were performed with the statistical software R-3.5.2 (R Core Team 2019).

Results

Snow manipulation and snowmelt dates

2016 was a relatively normal year with respect to snow cover and snowmelt date (Fig. 2; compared to the data for the 2013–2020 period from the Furka weather station). Very little snow in the winter 2017 and an exceptionally warm spring led snowmelt to occur 24 days earlier than in the previous year, and 14 days earlier than in 2018. Snow manipulation in 2016 caused a 9-day earlier snowmelt (snow removal) and a delay of 1 day only through snow addition. In 2017, snow removal advanced melt by 6 days and snow addition delayed it by 4 days. After a period with thunderstorms in spring 2018, snow manipulation was late and the combination of snow addition and fleece postponed snowmelt by 6 days, while the removal of snow from an already thin snowpack advanced snowmelt by 2 days only. Across all 3 years with snow manipulations, the range of snowmelt dates covered 38 days.

Drought treatment and microclimatic effects

The drought treatments (moderate and intense) during the growing seasons 2017 and 2018 successfully reduced soil volumetric water contents (Table 1). Compared to the relatively normal summer precipitation in 2017 (+17% compared to the 2013–2016 mean for June–August), the 2018 growing season was very dry (–40% compared to 2013–2016) and temporarily, soil moisture in the controls of 2018 was lower than in the extreme drought treatment of 2017. Throughout the second half of the moderate drought treatment, soil moisture was on average 7.8 vol% (2017) and 7.3 vol% (2018) lower than in the control parcels. During the second half of the intense drought treatment, soil

moisture was 15.2 vol% (2017) and 10.9 vol% (2018) lower than in controls, respectively. Mean soil moisture values did not drop below the permanent wilting point of 10.1 vol% (derived of eight pF curves at 10 cm soil depth; 8.8 vol% at 30 cm soil depth), but in single parcels, soil moisture reached these values. After termination of the moderate drought treatment, average soil moisture values recovered to values in the range of the control parcels. Our weekly assessments showed that the snow manipulations did not affect the soil water contents beyond 2 weeks after the start of the drought treatment in 2017, and 3 weeks in 2018 (data not shown).

The rainout shelters induced slightly higher soil temperatures (0.3–1.4 K, Table 1), because of the inhibition of radiative cooling during night (0.1–0.4 K for the period with the intense drought treatment). Further, an increased warming effect under intense drought compared to moderate drought indicated less evaporative cooling under extreme drought. The overall soil temperature increase under rainout shelters amounted to 0.9 K.

Surface temperatures (thermal imaging) at single, sunny days (rainout shelters briefly removed) were typically higher under experimental drought (up to 3.9 K under intense drought), pointing to stomatal closures and elevated sensible heat fluxes from leaves and soil surface (ESM 1.1 and 1.2).

Transition to main flowering (TMF)

The early snowmelt in 2017 induced early TMF in all species. Correspondingly, snow removal consistently induced an earlier, snow addition a later TMF in all species (DOY in Fig. 3). Thus, no critical threshold in photoperiod could be observed. Nevertheless, we identified two groups of species, differing in their responsiveness to early snowmelt dates. The early snowmelt in 2017 (24 days earlier) advanced flowering by 20–24 days in *C. curvula*, *H. versicolor* and *T. alpinum* (no records for *A. alpinum* in 2016), indicating that TMF of this group of species is driven by the snowmelt date and the subsequent temperature regime. In a second, less responsive group, consisting of the forbs *G. montanum*, *L. helveticus* and *P. aurea*, flowering set in only 10–13 days earlier in 2017.

The driver DOY/PP consistently exhibited the broadest variation across all years and snow manipulations, whereas DSM and TS were always less variable (smaller horizontal grey bars in Fig. 3). Without snow manipulation, DSM at TMF only varied by 4 days for the species *C. curvula*, *A. alpinum*, *H. versicolor* and *T. alpinum*, but by 7–13 days for *G. montanum*, *L. helveticus* and *P. aurea*. Thus, these results suggest that within the observational period of our study, DSM and TS exerted a substantially larger effect than DOY/PP, even in a year with exceptionally early melt and additional snow removal. In the following, we present the

Fig. 2 Snowmelt dates (mean $\pm$ SD) in three consecutive years (2016–2018) with snow manipulations (see Fig. 1)

Table 1 Soil moisture (mean $\pm$ SD) in the topsoil (0–5 cm, manually measured) of plots with moderate and intense drought during selected time periods 2017 and 2018 ($n=5$ per treatment, 5 measuring points each) and soil temperature (mean $\pm$ sd) in 3–4 cm depth (continuous measurements)

Time period	Drought	Soil moisture (vol%)		Soil temperature ($^{\circ}$ C)			
		2017		2018		2017	
		N		N		Day	Night
Mod. Drought 1st half	Control	32.2 $\pm$ 4.6	2	24.7 $\pm$ 4.4	2	16.1 $\pm$ 3.9	10.7 $\pm$ 2.4
	Moderate	24.4 $\pm$ 6.2		19.5 $\pm$ 6.1		16.1 $\pm$ 3.6	11.5 $\pm$ 2.5
	Intense	25.4 $\pm$ 5.7		20.2 $\pm$ 5.2		16.4 $\pm$ 3.8	11.5 $\pm$ 2.5
Mod. drought 2nd half	Control	30.0 $\pm$ 6.7	4	20.9 $\pm$ 5.4	4	15.2 $\pm$ 3.6	11.2 $\pm$ 2.1
	Moderate	22.2 $\pm$ 5.8		13.6 $\pm$ 4.6		15.3 $\pm$ 3.4	11.9 $\pm$ 2.0
	Intense	22.2 $\pm$ 5.9		13.9 $\pm$ 4.8		15.6 $\pm$ 3.5	11.9 $\pm$ 2.0
Intense drought 1st half	Control	34.0 $\pm$ 3.5	1	29.1 $\pm$ 5.5	2	14.4 $\pm$ 3.7	11.2 $\pm$ 1.9
	Moderate	27.6 $\pm$ 5.8		21.1 $\pm$ 5.8		14.4 $\pm$ 3.8	11.0 $\pm$ 1.9
	Intense	21.4 $\pm$ 5.8		15.2 $\pm$ 6.5		15.0 $\pm$ 3.1	12.0 $\pm$ 1.8
Intense drought 2nd half	Control	38.3 $\pm$ 4.4	1	25.1 $\pm$ 3.9	2	14.7 $\pm$ 3.2	10.1 $\pm$ 2.0
	Moderate	35.0 $\pm$ 4.8		19.8 $\pm$ 4.5		14.8 $\pm$ 3.3	10.0 $\pm$ 2.0
	Intense	23.1 $\pm$ 5.8		14.2 $\pm$ 4.9		15.7 $\pm$ 2.6	11.5 $\pm$ 1.7
After drought	Control	22.6 $\pm$ 3.4	1	29.2 $\pm$ 3.7	1	8.3 $\pm$ 4.8	6.0 $\pm$ 3.5
	Moderate	21.1 $\pm$ 4.0		25.8 $\pm$ 3.8		8.5 $\pm$ 4.9	6.1 $\pm$ 3.5
	Intense	17.1 $\pm$ 3.3		20.6 $\pm$ 5.5		8.4 $\pm$ 5.0	6.0 $\pm$ 3.6

N indicates the number of soil moisture measuring campaigns during the corresponding time period

best fitting driver for TMF for each species of the two groups (Table 2).

Temperature sums and days since snowmelt at the transition to main flowering

TMF in *C. curvula* was characterised by very similar TS (between 2300 and 3400 $^{\circ}$ h $\geq 0^{\circ}$ C) across years and snow manipulations (Table 2). DSM ranged between 9 and 15 days, but the total range of TMF (scaled) for TS was 45% smaller than for DSM. In control plots, *C. curvula* started flowering after accumulating 2300–2900 $^{\circ}$ h, with lowest values in 2018. Significant differences between years and snow manipulations (Table 2) were slightly smaller than TS typically accumulated during two average days in July (ca. 600 $^{\circ}$ h $\geq 0^{\circ}$ C day $^{-1}$). This dominant sedge flowers very quickly after snowmelt and thus, represents a fully opportunistic flowering behaviour with respect to snowmelt date.

Similarly, but not as extreme as in *C. curvula*, for *T. alpinum*, TS was the best describing driver for TMF and compared to DSM, the range of TS at TMF was 15% smaller. *T. alpinum*'s TMF started at 10200 $^{\circ}$ h on control plots without any significant differences between years. Snow manipulation significantly influenced TS at the TMF ($p=0.03$), with a delay after snow removal (+900 $^{\circ}$ h) and acceleration following snow addition (–700 $^{\circ}$ h). This slight compensatory effect within years increased the temporal synchronisation of flowering (Fig. 3). Nevertheless, flowering after snow removal started up to 5 days earlier than on control plots.

TS at TMF did not increase after snow removal in the early melt year 2017.

For *H. versicolor*, TS and DSM predicted the TMF equally well (2% difference in the range of TMF between the two drivers). Following natural snowmelt, it took *H. versicolor* 42–46 days to start flowering. Across all years, snow manipulations increased DSM by 1–4 days, except for snow addition in 2017, which accelerated TMF by 4 days compared to the control (interaction between snow manipulation and years, $p=0.04$). The same pattern was observed for the driver TS (Fig. 3). TMF in *A. alpinum* on average occurred 28 days after snowmelt without any significant differences between years nor snow manipulations and with very a similar course for TS.

In contrast to the species above, TMF of *L. helveticus* showed large differences in both TS and DSM among years and snow manipulations (Fig. 3). TMF started 33 (2016) to 43 (2017) days after natural snowmelt ($p_{\text{year}} < 0.01$). Snow removal prolonged the time between snowmelt and flowering by 0.5–2.5 days, while snow addition caused contrasting responses among years (snow manipulation: $p=0.01$, snow manipulation $\times$ year interaction: $p=0.05$, Table 2). The same pattern was observed for the driver TS (Fig. 3). For *G. montanum* and *P. aurea*, the total range of TMF (scaled) across years and snow manipulations was slightly smaller for TS than for DSM (12% and 9%). Although the difference between years was not as pronounced as for *L. helveticus*, it was statistically significant for both forbs ($p < 0.01$). Highest TS were accumulated in the early melt year 2017 and lowest TS after late melt in 2016 (Table 2). Main flowering

Fig. 3 TMF for the three drivers DOY, DSM and TS ($^{\circ}\text{h} \geq 0^{\circ}\text{C}$) of each plant species in 2016–2018 (DOY: day of the year, DSM: days since snowmelt, TS: temperature sum). Error bars represent 95% confidence intervals of TMF ($n=3\text{--}5$). Grey bars indicate the range of

the driver at the TMF (earliest vs. latest TMF). Species were ordered by functional groups (sedge, grass, and forb). No data for *A. alpinum* in 2016

in *G. montanum* started at 3200 $^{\circ}\text{h}$ (2016) to 5500 $^{\circ}\text{h}$ (2017), in *P. aurea* at 6300 $^{\circ}\text{h}$ (2016) to 9900 $^{\circ}\text{h}$ (2017). For *G. montanum*, snow manipulation had a marginal influence on TS ($p=0.06$), with higher TS after snow removal (delaying effect), whereas for *P. aurea* there was no significant influence of the snow manipulations. The patterns for DSM were very similar as for TS for both species (Fig. 3).

Overall, for the species *C. curvula*, *A. alpinum*, *H. versicolor*, and *T. alpinum*, one single driver explained TMF adequately well. Relatively constant TS or DSM defined their TMF. These patterns with respect to TMF did not vary much between thresholds of 0°C and 5°C . The total variability in TMF was slightly larger for the 5°C threshold (ESM 2). In contrast, the forbs *G. montanum*, *L. helveticus*, and *P. aurea* exhibited a much larger variation in DSM and

TS. For those species, photoperiod signals are likely to influence TS at TMF.

Photoperiod-dependent temperature sums

To further investigate photoperiod effects, we additionally analysed the TS at TMF in relation to the date of snowmelt. For the four apparently non-photoperiod sensitive species (Table 3), the TS at TMF did not depend on the date of snowmelt (all $p > 0.1$), evidenced by horizontal regression lines (Fig. 4). The TS changes per 1-week difference in snowmelt dates did not evoke changes that were higher than 300 $^{\circ}\text{h}$ (a typical, daily $^{\circ}\text{h}$ -value in July). Thus, the TMFs of these species were fully insensitive to photoperiod (Table 3).

On the contrary, TS in *L. helveticus* and similarly in *G. montanum* and *P. aurea* (Table 3) significantly decreased

Table 2 Best fitting driver for TMF (transition to main flowering) of each plant species (2016–2018)

Species	Best fitting driver	Y	TMF in control	Difference to control		Expl. var	LR χ^2 (df)	p value	Expl. var	LR χ^2 (df)	p value
				Rem	Add						
<i>Sedge</i>											
<i>C. curvula</i>	TS (°h)	2016	2900	500	− 100	S	11.27 (2)	<0.01	D	2.23 (1)	0.14
		2017	2700	600	− 300	Y	10.20 (2)	0.01	D × S	3.67 (2)	0.16
		2018	2300	300	0	S × Y	1.39 (4)	0.85	D × Y	1.58 (1)	0.21
<i>Grasses</i>											
<i>A. alpinum</i>	DSM (days)	2016	−	−	−	S	2.14 (2)	0.34	D	14.57 (1)	<0.01
		2017	29	0	− 2	Y	0.06 (1)	0.80	D × S	1.59 (2)	0.45
		2018	29	− 3	0	S × Y	2.86 (2)	0.24	D × Y	0.35 (1)	0.55
<i>H. versicolor</i>	DSM (days)	2016	42	1	3	S	3.40 (2)	0.18	D	0.13 (1)	0.71
		2017	46	4	− 4	Y	3.81 (2)	0.15	D × S	2.43 (2)	0.30
		2018	44	2	1	S × Y	10.09 (4)	0.04	D × Y	0.70 (1)	0.40
<i>Forbs</i>											
<i>G. montanum</i>	TS (°h)	2016	3200	1000	300	S	5.65 (2)	0.06	D	2.48 (1)	0.12
		2017	5500	100	− 100	Y	59.21 (2)	<0.01	D × S	1.59 (2)	0.45
		2018	5200	300	− 300	S × Y	3.40 (4)	0.46	D × Y	0.47 (1)	0.49
<i>L. helveticus</i>	DSM (days)	2016	33	2	2	S	0.01 (2)	0.01	D	1.70 (1)	0.19
		2017	43	3	0	Y	92.67 (2)	<0.01	D × S	0.43 (2)	0.81
		2018	36	1	− 4	S × Y	3.74 (4)	0.05	D × Y	0.56 (1)	0.46
<i>P. aurea</i>	TS (°h)	2016	6300	300	1100	S	0.09 (2)	0.96	D	0.45 (1)	0.50
		2017	9900	− 900	− 700	Y	28.57 (2)	<0.01	D × S	0.20 (2)	0.90
		2018	9900	100	− 700	S × Y	6.05 (4)	0.2	D × Y	3.62 (1)	0.06
<i>T. alpinum</i>	TS (°h)	2016	9600	1400	− 300	S	6.97 (2)	0.03	D	3.13 (1)	0.08
		2017	10,900	− 300	− 1000	Y	0.74 (2)	0.69	D × S	0.36 (2)	0.83
		2018	10,200	1000	− 1300	S × Y	2.56 (4)	0.69	D × Y	0.08 (1)	0.77

Left: thermal sums accumulated at TMF and days since snowmelt at TMF on controls (derived from time-to-event models, $n = 3-5$). Values following snow removal (snow rem.), snow addition (snow add.) and drought are shown as difference to the control (units according to the driver). The difference of the drought treatment to the control is averaged over snow treatments. Right: test statistics (LR χ^2) for explaining variables for TMF (bold p values indicate statistically significant differences). D drought treatment, Y year

with later snowmelt dates, revealing a high photoperiod sensitivity (Fig. 4). Across our observational period, one week of difference in snowmelt dates caused TS at TMF of *L. helveticus* to decrease by 825°h, and for the other two species, TS decreased in the range of 440–490°h (Table 3).

Drought effects on TMF

Only for three out of seven species, the TMF was affected by summer drought (Table 2), and *A. alpinum* and *T. alpinum* both responded directly (without drought × year interaction). Under drought, TMF of *A. alpinum* occurred 5 days earlier than in controls ($p < 0.01$), and irrespective of the snowmelt date, drought reduced TS at TMF by 2000°h ($p < 0.01$, Fig. 4). For *T. alpinum*, drought accelerated TMF by reducing TS by 600–700°h compared to the controls ($p = 0.04$, Fig. 4). The drought response in *P. aurea* was less uniform, accentuated by a marginally significant interaction between drought and years ($p = 0.06$). Drought in 2017 reduced TS at TMF (800°h on average) but increased it in 2018 (400°h) in relation to controls.

Flower duration

The flower durations in 2017 and 2018 were estimated as the time difference between TMF and the transition to flower senescence for each species and drought treatment. The flower durations in 2017, with very early melt, were longer than those in 2018 ($p < 0.01$, Table 4), and drought increased the flower duration significantly ($p = 0.04$). However, the effects of both, early snowmelt and the drought treatment, were very species specific. We did not find an interaction effect between drought and years ($p = 0.61$).

Table 3 The linear relation between TS at TMF (temperature sums in °h ≥ 0 °C) and plot-specific snowmelt dates (2016–2018)

Species	Change TS per week (°h/week)	<i>n</i>	Log-likelihood deviance	<i>p</i> -value	PP sensitive
<i>C. curvula</i>	– 24	135	0.17 (1)	0.68	No
<i>A. alpinum</i> ^a	3	75	0.02 (1)	0.89	No
<i>H. versicolor</i>	– 181	117	2.10 (1)	0.15	No
<i>G. montanum</i>	– 441	96	32.95 (1)	< 0.01	Yes
<i>L. helveticus</i>	– 825	132	85.80 (1)	< 0.01	Yes
<i>P. aurea</i>	– 491	111	19.16 (1)	< 0.01	Yes
<i>T. alpinum</i>	20	98	0.36 (1)	0.85	No

The ‘change TS per week’ indicates the change in TS per 1-week later snowmelt. Test statistics are presented by log-likelihood deviances and *p*-values (ANOVA, *n* is total number of observed intervals)

^aYears 2017, 2018 only

For individual species, only the two grasses *A. alpinum* and *H. versicolor* strongly differed in flower durations between the 2 years. *A. alpinum* flowered 15 days in the early snowmelt year 2017 and 6 days in 2018. Similarly, *H. versicolor*’s flower duration in 2017 lasted 15 days and 10 days in 2018, respectively ($p < 0.01$). In the forb *T. alpinum*, the flower duration was marginally longer in 2017 than in 2018, (10 days in 2017 and 6 days in 2018; $p = 0.06$). For the species with a short flower duration (*C. curvula*, *G. montanum*, *L. helveticus* and *P. aurea*) in the range of 1–5 days, no significant differences between the 2 years were observed.

Only one species, *A. alpinum*, flowered significantly longer under drought (8 days in both years; $p < 0.01$, Fig. 5). As mentioned above, our results suggest slightly longer flower durations for all species in 2017 than in 2018, except for *C. curvula*. In 2017, the mean July air temperatures at the site were 1.0 K lower than in 2018 (ESM 3 for on-site weather conditions).

Discussion

This snow manipulation and summer precipitation exclusion experiment at 2500 m a.s.l. revealed that the flowering phenology of the main species in this alpine grassland closely pursue snowmelt date and the microclimatic conditions thereafter. Drought had a minor influence on TMF, most likely because flowering started before the soil had gone through the most severe dehydration. DOY/PP at snowmelt varied by 38 days among the three different years (2016–2018) and the snow manipulations. We were able to distinguish between non-photoperiod-sensitive species (*C. curvula*, *A. alpinum*, *H. versicolor*, and *T. alpinum*) and species that closely track the photoperiod (*L. helveticus*, *G. montanum*, *P. aurea*). In species exhibiting photoperiodism, later snowmelt accelerated TMF and caused a higher degree of flowering synchrony. This increased synchrony may be of larger importance for plant species that depend on pollinators, as all three photoperiod sensitive species are insect-pollinated forbs. The non-photoperiod sensitive species (all but one wind pollinated) showed very similar TS at TMF across experimental manipulations and years.

The role of snowmelt and microclimate

The number of days elapsed since snowmelt (DSM) at TMF was consistently less variable than DOY at TMF, even for photoperiod-sensitive species. Snow removal led to earlier flowering irrespective of DOY and snow addition caused later flowering. This confirms other snow manipulation studies performed in (sub-) alpine and arctic ecosystems (e.g. Totland and Alatalo 2002; Lambert et al. 2010; Wipf and

Fig. 4 TS at TMF (temperature sums at the transition to main flowering) in relation to the snowmelt date in 2016–2018, with census intervals, regression line (blue: no drought, orange: drought, black: no significant drought effect) and 95% CI (grey)

Rixen 2010). Particularly for *C. curvula*, TS at the TMF varied by 45% less than DSM. Hence, in these species, TMF was determined by the snowmelt date, but with a time lapse defined by species-specific heat sum requirements. Low temperatures immediately after snowmelt may delay the floral development. The later snowmelt occurs, the stronger the correlation of TS and DSM. For late flowering species (e.g.

H. versicolor), DSM and TS may thus be substituted by each other as drivers.

We assume that the highly opportunistic flowering behaviour of the dominant species *C. curvula* that was also observed by Wagner and Reichegger (1997), is related to a rather complete preformation of the inflorescences (Erschbamer et al. 1994), allowing such rapid flowering. The less complete inflorescences are preformed, the greater the

Table 4 ANOVA results for the flower duration (recalculated after removing non-significant variables from the full model)

	Sum Sq	df	F value	p value
Intercept	4638.8	1	835.5593	< 0.01
Drought	25.2	1	4.5446	0.04
Species	1346.1	6	40.4114	< 0.01
Year	229.8	1	41.3853	< 0.01
Species × drought	206.8	6	6.2083	< 0.01
Species × year	140.8	6	4.2281	< 0.01
Residuals	349.8	63		

influence of weather conditions after snowmelt on TMF. In some species, preformation (primary induction sensu Heide, 1990) may take up to 2 years prior to flowering (Diggle and Mulder 2019). The tight coupling of flowering with snowmelt (with only minor weather-dependent delay) in the wind pollinated *C. curvula* creates topography driven reproduction cohorts which flower simultaneously - tracking the distinct small-scale snowmelt patterns. This may promote ecotype formation (reproductive guilds) over longer time periods. TMF in *T. alpinum* also correlated with TS. This species forms very large and complex inflorescences, the full development of which requires more time, and thus, depends more strongly on the weather conditions in the weeks after snowmelt.

Covering a wide range of high-latitude and high-elevation phenological observations, Prevy et al. (2019) demonstrated that under current global warming, late flowering species may start flowering earlier in the season. In contrast to our results, Prevy and co-authors assumed that early-flowering species followed photoperiod more closely (in addition to snowmelt date), and late flowering species

pursued the temperature regime. In contrast, Wadgymar et al. (2018) observed that in six subalpine forb species, flowering advanced fastest in earlier flowering species. Our data show that both, an early-flowering species *C. curvula* as well as a later flowering species *T. alpinum* were triggered by thermal sums. Both species required higher TS till TMF after snow removal, but lower TS following snow addition, suggesting a slight flowering synchronisation in these two non-photoperiod-sensitive species.

Whether an earlier start of the seasonal phenological development will also yield reproductive benefits is rather questionable (Gugger et al. 2015). A potential trade-off of an earlier snowmelt date is the greater risk of late freezing events (Wipf et al. 2009). In a 31-year-long phenology study in the Rocky Mountains, Inouye (2008) found a higher degree of frost damage after early snowmelt. Number of flowers, leaf growth and survival of the evergreen forb *Gentiana nipponica* were significantly reduced in populations with 1-month earlier snowmelt (Kawai and Kudo 2018). However, occasional frost damages do not necessarily cause a population decline, given that these taxa are all long lived and, to variable degree, clonal. Observations in the subalpine sunflower *Helianthella quinquenervis* revealed that early snowmelt (between 1999 and 2012) increased the risk of frost damages, but it also enhanced the number of flowers in the following growing season (Iler et al. 2019). The authors suggested a higher allocation of assimilates to preforming buds for the next year, thus, overcompensating for the frost damages.

The role of photoperiod

The fact that TMF in three of the seven species was modulated by photoperiod underlines the observations by Keller

Fig. 5 Flowering duration (mean ± SE) for the seven plant species in 2017 and 2018 ($n=3$, without snow manipulations). Open symbols: controls, filled symbols: drought (moderate and intense averaged). Letters refer to Tukey post hoc comparisons by species

and Körner (2003) that half of 23 alpine and nival species revealed a photoperiod effect on flowering (though much stronger than observed here). Hence, these three species were unable to utilise an earlier onset of the snow-free period. The photoperiod control became less decisive once a minimum daylength requirement had been surpassed. Yet, the plants studied by Keller and Körner (2003) started the growing season in daylight growth chambers with a 4 h shorter photoperiod than would normally occur in the field. At our field site, such a difference would correspond to a snowmelt in mid-March and even the exceptionally early snowmelt in 2017 (3.5 weeks earlier) corresponds to a photoperiod difference in the range of minutes only (maximum of 10 min). At field conditions, it is, therefore, unlikely that differences in photoperiod of several hours will come into action in a warmer future. Iler et al. (2013) studied 58 subalpine plant species over 38 years and found that peak flowering linearly advanced with snowmelt dates in 38% of all species. However, roughly one-fifth of the species had longer development times when snowmelt occurred before a certain date. Using a similar time-to-event analysis as in our study, with temperature sums (soil temperature), snowmelt dates and photoperiod, Hülber et al. (2010) concluded that temperature was the dominant driver for the transition to flowering in all ten alpine species tested along a natural snowmelt gradient.

The challenge with such conclusions is that these three components, the date of snowmelt, the temperature conditions and photoperiod interact in a non-linear way on species that differ in their degree of flower bud preformation (and thus, the time required to grow an inflorescence). When conditions are favourable and plants enter the winter with almost completed flower buds, it seems that temperature after snowmelt is the only factor driving TMF. The role of photoperiod comes into action as a modulating factor when snowmelt occurs much earlier (as was observed in 2017). This gradual nature of the photoperiod influence complicates the interpretation. When species are released at a date at which they are sensitive to photoperiod, they seem to require more thermal energy (TS) after earlier snowmelt till flowering. We found such a gradual influence in *L. helveticus* and less pronounced in *G. montanum* and *P. aurea*. For the observed period, TS at TMF increased linearly with earlier snowmelt dates, including a year with 3.5-week earlier snowmelt than usual.

For snowbed species, reduced heat requirements for flowering have been observed after late snowmelt (Carbognani et al. 2016). Larl and Wagner (2006) noticed a substantially faster seasonal cycle of *Saxifraga oppositifolia* in subnival (2.5 months) than in alpine populations (4-month season), along with lower temperature sums for reaching all developmental stages. They hypothesised that the evolved genotypes at the subnival sites require less thermal energy. This is in line with results of Prock and Körner (1996), who unveiled

an origin-specific influence of photoperiod on flowering and plant senescence (but not for the *Rosaceae* species they included) by means of a cross-continental transplant experiment. The modulating effect of photoperiod on phenology may enhance such micro-evolutionary processes.

Drought effects

TMF was largely unaffected by summer drought. Only the grass *A. alpinum* showed a pronounced shift by a 5-day earlier flowering and a longer flower duration under drought (plus 8 days). A similar response was observed in a low-land grassland, where flowering under drought lasted 4 days longer (Jentsch et al. 2009). The TMF of *C. curvula*, *H. versicolor*, *G. montanum*, and *L. helveticus* remained completely unaffected by drought, similar to findings for the Bavarian Alps by Cornelius et al. (2013). These authors explored drought effects along an elevational gradient (800–2000 m a.s.l.) and in contrast to the lower elevation sites, plants at higher elevations did not respond to drought. However, the drought treatment in the study of Cornelius and co-authors started late (4 weeks after snowmelt, thus missing the most critical period). The transitions to flowering of 20 montane and alpine species was clearly advanced by an elevational down-shift of 1000 m a.s.l., but not by drought alone, revealed by a transplant experiment (Gugger et al. 2015). Sheltering off rain did also not affect flowering phenology in a montane grassland in the French Massif Central (Bloor et al. 2010). In these cases, it is very likely that rain exclusion did not evoke substantial responses in flowering phenology because flowering occurred early in the season when the soil profile still contained sufficient moisture, causing soil profile depth to become an important co-variable. However, our IR surface temperatures point to prevalent stomatal closures under drought, underpinning that our alpine plants experienced water shortage in situ.

Flower duration

The longer flower duration observed in the early melt year 2017 compared to 2018 could compensate for the cooler early season weather and presumably, less abundant pollinators. Several studies in montane grassland have noted prolonged flower durations in case of early snowmelt (e.g. Dunne et al. 2003; Pardee et al. 2019). Alpine forbs have been shown to be very plastic in their flower durations in the absence of pollinators and/or under bad weather conditions (Trunschke 2017; see the review in Körner 2021). Extended flowering may facilitate higher visitation numbers by insects (Pardee et al. 2019). And in case of a specific plant-pollinator dependency, flowering time can be

decoupled from pollinator activity, as was suggested for the ephemeral *Corydalis ambigua* and its bumblebee under early snowmelt (Kudo and Cooper 2019). However, alpine plants commonly receive a very broad pollinator spectrum (e.g. Erhardt 1993; Tiisanen et al. 2019) and often have several cohorts of flowers, making pollinator limitation for reproduction very unlikely (Wagner et al. 2016; Arroyo et al. 2017), in addition to the fact that many alpine plants grow clonally (Körner 2021).

Conclusions

Our snowmelt manipulation and the natural variation of snowmelt date demonstrated the importance of snowmelt date and the subsequent microclimatic conditions for flowering phenology in late successional alpine grassland, with photoperiod playing a species-specific modulating role in at least three of the seven species studied. A 3.5-week earlier snowmelt in the exceptional year 2017 reinforced the photoperiod effect. Even subtle changes in the snowmelt regime modified the heat sum required till flowering, suggesting a complex interaction between temperature and photoperiod. We, therefore, warn against simplistic projections of correlations between climatic warming (commonly extrapolated from weather stations), snowmelt date and flowering phenology. The earlier snow melts, the stronger become photoperiod constraints, responses, presumably selected for escaping freezing damage. These evolutionary constraints to phenology will limit potential benefits in terms of growth and reproduction of current alpine grassland taxa and their currently abundant ecotypes by a longer alpine season in a warmer climate.

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Author contributions EH planned and designed the project, MV, CK and EH performed experiments and conducted fieldwork. MV and EH analysed the data, and MV, AK, CK and EH all wrote the manuscript.

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Declaration

Conflict of interest The authors declare no conflict of interest.

Ethical approval No ethical approval was required as we did not collect data from human participants or animals.

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References

- Arroyo MTK, Pacheco DA, Dudley LS (2017) Functional role of long-lived flowers in preventing pollen limitation in a high elevation outcrossing species. *AoB Plants* 9:1–12. <https://doi.org/10.1093/aobpla/plx050>
- Bloor JMG, Pichon P, Falcimagne R, Leadley P, Soussana J-F (2010) Effects of warming, summer drought, and CO₂ enrichment on aboveground biomass production, flowering phenology, and community structure in an upland grassland ecosystem. *Ecosystems* 13:888–900. <https://doi.org/10.1007/s10021-010-9363-0>
- Canaday BB, Fonda RW (1974) The influence of subalpine snowbanks on vegetation pattern, production, and phenology. *Bull Torrey Bot Club* 101:340–350
- CaraDonna P, Iler AM, Inouye DW (2014) Shifts in flowering phenology reshape a subalpine plant community. *Proc Nat Acad Sci* 111:4916–4921
- Carbognani M, Bernareggi G, Perucco F, Tomaselli M, Petraglia A (2016) Micro-climatic controls and warming effects on flowering time in alpine snowbeds. *Oecologia* 182:573–585. <https://doi.org/10.1007/s00442-016-3669-3>
- Cornelius C, Leingärtner A, Hoiss B, Menzel A (2013) Phenological response of grassland species to manipulative snowmelt and drought along an altitudinal gradient. *J Exp Bot* 64:241–251. <https://doi.org/10.1093/jxb/err313>
- de Boeck HJ, Bassin S, Verlinden M, Zeiter M, Hiltbrunner E (2016) Simulated heat waves affected alpine grassland only in combination with drought. *New Phytol* 209:531–541. <https://doi.org/10.1111/nph.13601>
- Dietrich L, Körner C (2014) Thermal imaging reveals massive heat accumulation in flowers across a broad spectrum of alpine taxa. *Alp Bot* 124:27–35. <https://doi.org/10.1007/s00035-014-0123-1>
- Diggle PK, Mulder CPH (2019) Diverse developmental responses to warming temperatures underlie changes in flowering phenologies. *Integr Comp Biol* 59:559–570. <https://doi.org/10.1093/icb/icz076>
- Dunne JA, Harte J, Taylor KJ (2003) Subalpine meadow flowering phenology responses to climate change: Integrating experimental and gradient methods. *Ecol Monogr* 73:69–86. [https://doi.org/10.1890/0012-9615\(2003\)073](https://doi.org/10.1890/0012-9615(2003)073)

- Erhardt A (1993) Pollination of the edelweiss, *Leontopodium alpinum*. Bot J Linn Soc 111:229–240. <https://doi.org/10.1111/j.1095-8339.1993.tb01900.x>
- Erschbamer B, Winkler J, Wagner J (1994) The vegetative and generative development of three *Carex curvula* in the Central Alps. Flora 189:277–286
- Gugger S, Kesselring H, Stöcklin J, Hamann E (2015) Lower plasticity exhibited by high- versus mid-elevation species in their phenological responses to manipulated temperature and drought. Ann Bot 116:953–962. <https://doi.org/10.1093/aob/mcv155>
- Heide OM (1985) Physiological aspects of climatic adaptation in plants with special reference to high-latitude environments. In: Plant Prod north Proc from plant Adapt Work Tromsø, Norway, September 4–9, 1983, pp 1–22
- Heide OM (1990) Dual floral induction requirements in *Phleum alpinum*. Ann Bot 66:687–694. <https://doi.org/10.1093/oxfordjournals.aob.a088083>
- Heide OM (1992) Flowering strategies of the high-arctic and high-alpine snow bed grass species *Phippsia algida*. Physiol Plant 85:606–610. <https://doi.org/10.1111/j.1399-3054.1992.tb04761.x>
- Heide OM (2001) Photoperiodic control of dormancy in *Sedum tel-ephium* and some other herbaceous perennial plants. Physiol Plant 113:332–337. <https://doi.org/10.1034/j.1399-3054.2001.1130305.x>
- Heide OM (2005) Ecotypic variation among European arctic and alpine populations of *Oxyria digyna*. Arctic, Antarct Alp Res 37:233–238. [https://doi.org/10.1657/1523-0430\(2005\)037\[0233:EVAEAA\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2005)037[0233:EVAEAA]2.0.CO;2)
- Heide OM, Pedersen K, Dahl E (1990) Environmental control of flowering and morphology in the high-arctic *Cerastium regelii*, and the taxonomic status of *C. jenisejense*. Nord J Bot 10:141–147. <https://doi.org/10.1111/j.1756-1051.1990.tb01761.x>
- Hock R, Rasul G, Adler C, Cáceres B, Gruber S, Hirabayashi Y, Jackson M, Kääb A, Kang S, Kutuzov S, Milner A, Molau U, Morin S, Orlove B, Steltzer H (2019) High mountain areas. In: Pörtner H-O, Roberts DC, Masson-Delmotte V, Zhai P, Tignor M, Poloczanska E, Mintenbeck K, Alegría A, Nicolai M, Okem A, Petzold J, Rama BNMW (ed) IPCC special report on the ocean and cryosphere in a changing climate. World Meteorological Organization, p 202–232 (in press)
- Hülber K, Winkler M, Grabherr G (2010) Intraseasonal climate and habitat-specific variability controls the flowering phenology of high alpine plant species. Funct Ecol 24:245–252. <https://doi.org/10.1111/j.1365-2435.2009.01645.x>
- Iler AM, Høye TT, Inouye DW, Schmidt NM (2013) Nonlinear flowering responses to climate: Are species approaching their limits of phenological change? Philos Trans R Soc B Biol Sci 368:13–16. <https://doi.org/10.1098/rstb.2012.0489>
- Iler AM, Compagnoni A, Inouye DW, Williams JL, Anderson A, Miller TEX, CaraDonna PJ (2019) Reproductive losses due to climate change-induced earlier flowering are not the primary threat to plant population viability in a perennial herb. J Ecol 107:1931–1943. <https://doi.org/10.1111/1365-2745.13146>
- Inouye DW (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology 89:353–362. <https://doi.org/10.1890/06-2128.1>
- IPCC (2018) Summary for policymakers. In: Masson-Delmotte V, Zhai P, Pörtner H et al (eds) Global Warming of 1.5 °C. An IPCC Special Report on the impacts of global warming of 1.5 °C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change. Geneva, Switzerland, pp 374–381
- Jentsch A, Kreyling J, Boettcher-Treschkow J, Beierkuhnlein C (2009) Beyond gradual warming: extreme weather events alter flower phenology of European grassland and heath species. Glob Change Biol 15:837–849. <https://doi.org/10.1111/j.1365-2486.2008.01690.x>
- Kawai Y, Kudo G (2018) Variations in ramet performance and the dynamics of an alpine evergreen herb, *Gentiana nipponica*, in different snowmelt conditions. Am J Bot 105:1813–1823. <https://doi.org/10.1002/ajb2.1186>
- Keller F, Körner C (2003) The role of photoperiodism in alpine plant development. Arctic, Antarct Alp Res 35:361–368. [https://doi.org/10.1657/1523-0430\(2003\)035\[0361:TROPIA\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2003)035[0361:TROPIA]2.0.CO;2)
- Keller F, Ephane ST, Beniston M (2005) Sensitivity analysis of snow cover to climate change scenarios and their impact on plant habitats in alpine terrain. Clim Change 72:299–319. <https://doi.org/10.1007/s10584-005-5360-2>
- Klein JP, Moeschberger ML (2003) Survival analysis. Techniques for censored and truncated data, 2nd edn. Springer, New York, p 535
- Klein G, Vitasse Y, Rixen C, Marty C, Rebetez M (2016) Shorter snow cover duration since 1970 in the Swiss Alps due to earlier snowmelt more than later snow onset. Clim Change 139:637–649. <https://doi.org/10.1007/s10584-016-1806-y>
- Körner C (2021) Alpine plant life. Functional plant ecology of high mountain ecosystems, 3rd edn. Springer, Cham, p 496
- Körner C, Hiltbrunner E (2018) The 90 ways to describe plant temperature. Perspect Plant Ecol Evol Syst 30:16–21. <https://doi.org/10.1016/j.ppees.2017.04.004>
- Kudernatsch T, Fischer A, Bernhardt-Römermann M, Abs C (2008) Short-term effects of temperature enhancement on growth and reproduction of alpine grassland species. Basic Appl Ecol 9:263–274. <https://doi.org/10.1016/j.baee.2007.02.005>
- Kudo G, Cooper EJ (2019) When spring ephemerals fail to meet pollinators: mechanism of phenological mismatch and its impact on plant reproduction. Proc R Soc Biol Sci 286:20190573
- Lambert AM, Miller-Rushing AJ, Inouye DW (2010) Changes in snowmelt date and summer precipitation affect the flowering phenology of *Erythronium grandiflorum* (glacier lily; Liliaceae). Am J Bot 97:1431–1437. <https://doi.org/10.3732/ajb.1000095>
- Larl I, Wagner J (2006) Timing of reproductive and vegetative development in *Saxifraga oppositifolia* in an alpine and a subnival climate. Plant Biol 8:155–166. <https://doi.org/10.1055/s-2005-872888>
- Lauber K, Wagner G, Gyax A (2018) Flora helvetica, 6th edn. Haupt Verlag, Bern, p 1686
- Lenth R, Henrik S, Love J, Buerkner P, Herve M (2019) R package *emmeans*: estimated marginal means, aka least-squares means, p 81
- Leuschner C, Ellenberg H (2017) Ecology of central European non-forest vegetation: coastal to alpine, natural to man-made habitats. Vegetation ecology of central Europe, volume II, extended v. Springer, Cham, p 1094
- Livensperger C, Steltzer H, Darrouzet-Nardi A, Sullivan PF, Wallenstein M, Weintraub MN (2016) Earlier snowmelt and warming lead to earlier but not necessarily more plant growth. AoB Plants 8:plw021. <https://doi.org/10.1093/aobpla/plw021>
- Marty C (2008) Regime shift of snow days in Switzerland. Geophys Res Lett 35:L12501. <https://doi.org/10.1029/2008GL033998>
- Meloche CG, Diggle PK (2001) Preformation, architectural complexity, and developmental flexibility in *Acomastylis rossii* (Rosaceae). Am J Bot 88:980–991. <https://doi.org/10.2307/2657079>
- Molau U, Nordenhäll U, Eriksen B (2005) Onset of flowering and climate variability in an alpine landscape: a 10-year study from Swedish Lapland. Am J Bot 92:422–431. <https://doi.org/10.3732/ajb.92.3.422>
- Oberdorfer E (2001) Pflanzensoziologische Exkursionsflora für Deutschland und angrenzende Gebiete, 8th edn. Ulmer, Germany, p 1051
- Pardee GL, Jensen IO, Inouye DW, Irwin RE (2019) The individual and combined effects of snowmelt timing and frost exposure on

- the reproductive success of montane forbs. *J Ecol* 107:1970–1981. <https://doi.org/10.1111/1365-2745.13152>
- Prevy JS, Rixen C, Rger N, Hye TT, Bjorkman AD, Myers-smith IH, Elmendorf SC, Ashton IW, Cannone N, Chisholm CL, Clark K, Cooper EJ, Elberling B, Fosaa AM, Henry GHR, Hollister RD, Jnsdttir IS, Klanderud K, Kopp CW, Lvesque E, Mauritz M, Molau U, Natali SM, Schuur E, Semenchuk PR, Smith JG, Suding KN, Totland , Troxler T, Venn S, Wahren C-H, Welker JM, Wipf S (2019) Warming shortens flowering seasons of tundra plant communities. *Nat Ecol Evol* 3:45–52. <https://doi.org/10.1038/s41559-018-0745-6>
- Prock S, Krner C (1996) A cross-continental comparison of phenology, leaf dynamics and dry matter allocation in Arctic and temperate zone herbaceous plants from contrasting altitudes. *Ecol Bull* 45:93–103
- R Core Team (2019) R: a language and environment for statistical computing
- Ram J, Singh SP, Singh JS (1988) Community level phenology of grassland above treeline in Central Himalaya, India. *Arct Alp Res* 20:325–332
- Rosbakh S, Leingrtner A, Hoiss B, Krauss J, Steffan-dewenter I, Poschold P (2017) Contrasting effects of extreme drought and snowmelt patterns on mountain plants along an elevation gradient. *Front Plant Sci* 8:1–17. <https://doi.org/10.3389/fpls.2017.01478>
- Schppi B, Krner C (1996) Growth responses of an alpine grassland to elevated CO₂. *Oecologia* 105:43–52
- Scherrer D, Krner C (2010) Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Glob Change Biol* 16:2602–2613. <https://doi.org/10.1111/j.1365-2486.2009.02122.x>
- Scherrer SC, Wthrich C, Croci-Maspoli M, Weingartner R, Appenzeller C (2013) Snow variability in the Swiss Alps 1864–2009. *Int J Climatol* 33:3162–3173. <https://doi.org/10.1002/joc.3653>
- Schmid S, Hiltbrunner E, Spehn E, Lscher A, Scherer-Lorenzen M (2011) Impact of experimentally induced summer drought on biomass production in alpine grassland. *Grassl Sci Eur* 16:214–216
- Steger C, Kotlarski S, Jonas T, Schr C (2013) Alpine snow cover in a changing climate: a regional climate model perspective. *Clim Dyn* 41:735–754. <https://doi.org/10.1007/s00382-012-1545-3>
- Therneau TM (2015) A package for survival analysis in S
- Tiusanen M, Huotari T, Hebert PDN, Andersson T, Asmus A, Bty J, Davis E, Gale J, Hardwick B, Hik D, Krner C, Lanctot RB, Loonen MJJE, Partanen R, Reischke K, Saalfeld ST, Senez-Gagnon F, Smith PA, ulavk J, Syvnper I, Urbanowicz C, Williams S, Woodard P, Zaika Y, Roslin T (2019) Flower-visitor communities of an arcto-alpine plant—global patterns in species richness, phylogenetic diversity and ecological functioning. *Mol Ecol* 28:318–335. <https://doi.org/10.1111/mec.14932>
- Totland O, Alatalo JM (2002) Effects of temperature and date of snowmelt on growth, reproduction, and flowering phenology in the Arctic/Alpine herb, *Ranunculus glacialis*. *Oecologia* 133:168–175
- Trunschke J (2017) Plasticity of flower longevity in alpine plants is increased in populations from high elevation compared to low elevation populations. *Alp Bot* 127:41–51. <https://doi.org/10.1007/s00035-016-0176-4>
- Wadgymar SM, Ogilvie JE, Inouye DW, Weis AE, Anderson JT (2018) Phenological responses to multiple environmental drivers under climate change: insights from a long-term observational study and a manipulative field experiment. *New Phytol* 218:517–529. <https://doi.org/10.1111/nph.15029>
- Wagner J, Reichegger B (1997) Phenology and seed development of the alpine sedges *Carex curvula* and *Carex firma* in response to contrasting topoclimates. *Arct Alp Res* 29:291–299
- Wagner J, Lechleitner M, Hosp D (2016) Pollen limitation is not the rule in nival plants: a study from the European Central Alps. *Am J Bot* 103:375–387. <https://doi.org/10.3732/ajb.1500214>
- Weingartner R, Viviroli D, Schdler B (2007) Water resources in mountain regions: a methodological highland-lowland-system. *Hydrol Process* 21:578–585. <https://doi.org/10.1002/hyp>
- Wipf S, Rixen C (2010) A review of snow manipulation experiments in arctic and alpine tundra ecosystems. *Polar Res* 29:95–109. <https://doi.org/10.1111/j.1751-8369.2010.00153.x>
- Wipf S, Stoeckli V, Bebi P (2009) Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Clim Change* 94:105–121. <https://doi.org/10.1007/s10584-009-9546-x>

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