

# Intraseasonal climate and habitat-specific variability controls the flowering phenology of high alpine plant species

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## Summary

1. High alpine plants endure a cold climate with short growing seasons entailing severe consequences of an improper timing of development. Hence, their flowering phenology is expected to be rigorously controlled by climatic factors.

2. We studied ten alpine plant species from habitats with early and late melting snow cover for 2 years and compared the synchronizing effect of temperature sums (TS), time of snowmelt (SM) and photoperiod (PH) on their flowering phenology. Intraseasonal and habitat-specific variation in the impact of these factors was analysed by comparing predictions of time-to-event models using linear mixed-effects models.

3. Temperature was the overwhelming trigger of flowering phenology for all species. Its synchronizing effect was strongest at or shortly after flowering indicating the particular importance of phenological control of pollination. To some extent, this pattern masks the common trend of decreasing phenological responses to climatic changes from the beginning to the end of the growing season for lowland species. No carry-over effects were detected.

4. As expected, the impact of photoperiod was weaker for snowbed species than for species inhabiting sites with early melting snow cover, while for temperature the reverse pattern was observed.

5. Our findings provide strong evidence that alpine plants will respond quickly and directly to increasing temperature without considerable compensation due to photoperiodic control of phenology.

**Key-words:** Central European Alps, climate warming, temperature sum, snow cover duration

## Introduction

Global warming is predicted to be most pronounced in arctic and alpine environments in the northern hemisphere (Maxwell 1992; IPCC 2007). Within the 21st century mean summer temperature is predicted to rise about 4 °C above the treeline in the European Alps (Raible *et al.* 2006). A significant reduction in snow cover since the early 1980s (Latenser & Schneebeli 2003) has resulted in an overall shortening of snow cover duration (Beniston, Keller & Goyette 2003). Hence, the key abiotic factors of temperature, snow cover and time available for development, which con-

trol alpine plant life, will strongly be altered making mountain environments especially vulnerable to global climate change (Grabherr, Gottfried & Pauli 1994; Price & Waser 1998; Theurillat & Guisan 2001 and citations therein; Dunne, Harte & Taylor 2003).

Phenology is perhaps the aspect of plant life most responsive to climate warming (Sparks & Menzel 2002). Phenological responses of plants to increasing temperature are well documented on a global scale (Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003). Considerable changes in the seasonality of species as a consequence of altered seasonal patterns of temperature were also demonstrated for a wide array of species (Scheifinger *et al.* 2002; Stenseth & Mysterud 2002; Walther 2003). The most unambiguous trend is an

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enhancement of early phenophases while autumn phenology is less strictly coupled with temperature. In a meta-analysis of a comprehensive data set comprising more than 500 plant species 78% of records on spring and summer phenology across Europe had advanced during the last three decades (Menzel *et al.* 2006a).

Large-scale surveys as mentioned above are dominated by phenological records of lowland plants including those from moderate altitudes. However data on seasonal variability of flowering phenology from the cold limit of plant life are very rare or even lacking. Phenological responses of alpine plants need not necessarily follow the general trend of decreasing phenological variability (i.e. changes) from spring to autumn. The long-lasting snow cover releases plants under mid-summer conditions and thus shortens the growing season, particularly in alpine snowbeds. Furthermore, carry-over effects, which are a common adaptation to cope with the shortness of the growing season in high alpine regions all over the world (Körner 2003), may mask the association of phenology and current climatic conditions especially for early phenophases. Such carry-over effects are realized via bud preformation and hence mirror the weather of the previous year(s).

In cold areas like the high alpine regions phenology is even more temperature-related (Ratchke & Lacey 1985; Cleland *et al.* 2007). The strong temperature increase from winter to early spring is thought to cause phenological shifts particularly in mountain plants (Inouye & Wielgolaski 2003; Studer, Appenzeller & Defila 2005 and citations therein; Miller-Rushing & Primack 2008). However, a bulk of studies provide clear evidence, that besides temperature the date of snowmelt (e.g. Walker, Ingersoll & Webber 1995; Wagner & Reichegger 1997; Larl & Wagner 2005) and photoperiod (i.e. day length; e.g. Heide 1990, 1992, 1997) are key factors controlling plant phenology in alpine habitats.

Alpine ecosystems are characterized by rough topography and steep environmental gradients, generating a mosaic of habitats with very heterogeneous snow distribution on small spatial scales. At one extreme, wind-blown ridges can be snowfree during the whole year, exposing plants to strong winter frosts. At the other extreme, snowbeds are characterized by long-lasting snow cover that surrounds plants for much greater proportion of the growing season until the occurrence of snowmelt in mid-summer. It can be assumed that the initiation of growth and reproduction is triggered in different ways for species inhabiting these contrasting habitats (Molau, Nordenhäll & Eriksen 2005). Strong effects of photoperiod, which protects plants from starting too early and subsequently suffering from frost damage (Inouye 2000, 2008), can be expected for plants in exposed habitats, while the timing of snowmelt should be the key factor for plant development in snowbeds.

Phenological responses of mountain plants to climate warming are highly species-specific (Arft *et al.* 1999), even among closely related taxa (Miller-Rushing & Primack 2008) and within the same type of habitat (Körner 2003): Species may be triggered by different environmental factors (Defila & Clot 2001), respond to changes in the same factor but at dif-

ferent rates (Galen & Stanton 1995; Post *et al.* 2008) or even in opposite directions (Kudo 1992; Sherry *et al.* 2007). Additionally, the magnitude of alpine species' response to an environmental factor shows strong seasonal variation (Wagner & Mitterhofer 1998; Ladinig & Wagner 2007). Thus, to assess the impact of climate warming on flowering phenology the whole sequence of reproductive development as opposed to a single event (e.g. flowering) needs to be examined.

Due to the short growing season in alpine areas, the timing of developmental processes is critical for the reproductive success of species. Here, we used parametric time-to-event models and linear mixed-effects models to study the synchronizing effects of temperature, photoperiod and snowmelt on the reproductive phenology of ten alpine species. In particular, the following questions were addressed:

- (1) Is the early season phenology of species at the cold limit of vascular plant life more strongly coupled to climatic conditions like temperature, snowmelt and photoperiod than later phenophases?
- (2) Do temperature, snowmelt and photoperiod show different effects on plant phenology in habitats with early and late snowmelt, respectively?
- (3) Do the patterns of phenological responses differ between an average and an exceptionally warm year?

## Materials and methods

### STUDY SITE

The study was conducted on the north-western slope of the lateral moraine of the Schwarzenberger-Seespitze glacier (Stubai Alpen, Tyrol, Austria; 11 °06'E, 47 °03'N) at an altitude between 2630 and 2680 m a. s. l. The area is characterized by a cold temperate, continental climate with about 0 and -5.5 °C average annual temperature and annual precipitation of 800–900 and 1600–1700 mm in 2000 and 3000 m a. s. l. respectively (Klimadaten von Österreich 1971–2000). Siliceous bedrock predominates in the surrounding mountains, hence the substrate of the moraine consists of unsorted, siliceous debris with a high proportion of small-sized gravel and no organic soil layer. Extending over a horizontal distance of less than 100 m, the site covers a continuous gradient from a basin-shaped depression with very high snow accumulation to an upper slope with an average snow cover.

### DATA COLLECTION

Fourteen data loggers (Stowaway Tidbit TBI32-20 + 50, Onset Corporation, Bourne, MA, USA, range -20 °C to +50 °C) were placed along a snowmelt gradient on the moraine slope. The loggers were buried 5 cm below the soil surface, the layer of the most compact rooting. This approach prevents direct sun insolation and disturbance from tourists or avalanches. From October 2001 to October 2003 measurements were taken at 60-minute intervals (i.e. 24 measurements per day and logger).

Ten abundant species representative of high alpine habitats of the central Alps were selected for phenological observations (see Tab 1). Nomenclature and habitat affiliations follow Adler, Oswald &

**Table 1.** Ecological requirements of study species. TS represents predictions of time-to-event models representing the thermal demands (mean  $\pm$  standard deviation) of individuals – given as accumulated temperature sums above 1 °C – to reach flowering. Habitat requirements are extracted from Adler, Oswald & Fischer (1994)

Species	Habitat	Pollination	TS
<i>Agrostis rupestris</i> (Poaceae)	Swards	Anemophilous	11678 $\pm$ 437
<i>Cardamine resedifolia</i> (Brassicaceae)	Snowbeds, moist rocks, open soil	Entomophilous	2328 $\pm$ 791
<i>Gnaphalium supinum</i> (Asteraceae)	Snowbeds, moist swards	Entomophilous†	6894 $\pm$ 289
<i>Leucanthemopsis alpina</i> (Asteraceae)	Snowbeds, swards, scree	Entomophilous	6905 $\pm$ 649
<i>Oxyria digyna</i> (Polygonaceae)	Swards, scree	Anemophilous	4432 $\pm$ 2344
<i>Poa alpina</i> (Poaceae)*	Scree, nutrient rich swards and pastures	Anemophilous	10427 $\pm$ 632
<i>Poa laxa</i> (Poaceae)	Wind-exposed rocks, scree	Anemophilous	9111 $\pm$ 407
<i>Sedum alpestre</i> (Crassulaceae)	Snowbeds, rocks, scree	Entomophilous	4679 $\pm$ 627
<i>Saxifraga bryoides</i> (Saxifragaceae)	Wind-exposed rocks, scree	Entomophilous	11260 $\pm$ 2281
<i>Veronica alpina</i> (Scrophulariaceae)	Snowbeds, moist swards, richly manured pastures	Entomophilous	7009 $\pm$ 63

\**Poa alpina* has a twofold strategy of reproduction with flowering and pseudoviviparous individuals.

†Some species of *Gnaphalium* and the related genus *Antennaria* are apomictic or are at least suspected to be apomicts. However, for this species no information is available.

Fischer (1994). For each species, 90 adult individuals (86 for *Saxifraga bryoides*) in close proximity to the dataloggers (max. 2.5 m horizontal and 0.5 m altitudinal distance) were tagged for monitoring. Observations were made at c. 10-day intervals during the 2002 and 2003 growing seasons. This resulted in 9 sets of observations for 2002 and 10 sets for 2003. The growing season in 2002 was characterized by average temperatures (ZAMG 2002) while the summer in 2003 was exceptionally warm (ZAMG 2003). During each observation newly developed generative shoots were marked with coloured wool threads. Phenological phases of each shoot were recorded, except for *Sedum alpestre* for which we registered the phenological status of each flower. Phenological development of generative shoots within a year was classified in five to eight phases depending on the species. Easily distinguishable morphological traits were used to define these phases (Tab 2). For the 30 (i.e. 3.3%) individuals which died in the winter of 2002, we measured its nearest neighbour of the same species in the growing season of 2003.

The study area was enclosed with an electric fence to deter large herbivores from grazing.

#### DATA PRE-PROCESSING

We checked for deviations among the 14 data loggers by storing them together at room temperature for several days before and after deployment in the field. Measurements taken in the field were

corrected according to differences among the loggers during that time.

Three environmental variables were used to analyse flowering phenology of study species. Two of them were derived from the raw temperature data stored by the data loggers:

(i) Temperature sums (TS) were calculated from the first of April until each of the nine or ten observation dates for each logger in 2002 and 2003, respectively. As alpine plants may be photosynthetically active during periods of low temperature, we used a threshold value of 1 °C. The measurement values exceeding this threshold were summed. Calculations using other threshold temperatures (from 0 °C to 10 °C) revealed very similar results but did not fit as well.

(ii) The time since snowmelt (SM) is given as the number of days from the start of the growing season to each observation where the ground above the logger was snow free. Ground was determined to be snow covered if data loggers indicated temperatures ranging from –0.5 to 0.5 °C and temperature amplitudes (variations) were low. The daily temperature amplitudes were analysed using a moving window of 3 days. Measurements from the first of April – the first measurement without snow cover was taken in June – to each observation without snow cover were counted for each logger and divided by 24 (i.e. the number of measurements each day).

(iii) The third variable photoperiod (PH) was defined as minutes of daylight without snow cover at the day of observation.

**Table 2.** Description of distinctive marks used to morphologically differentiate phenophases of ten high alpine plant species. Phenophases given in bold mark the anthesis of the species (compare Table 4)

Species	Phenophases
<i>Agrostis rupestris</i>	Panicle visible – panicle elongated – <b>flowers</b> – anthers dry – caryopsis propagating
<i>Cardamine resedifolia</i>	Buds – <b>flowers</b> – fruit with corolla – fruit, corolla dropped off – pod dehiscent
<i>Gnaphalium supinum</i>	Buds covered with leaves – buds visible – <b>flowers</b> – corolla shrivelled – involucre turned yellow – fruits dehiscent
<i>Leucanthemopsis alpina</i>	Buds sessil – buds pedicellate – ligulate flowers visible – <b>I. tubular flower open</b> – all tubular flowers open – tubular flowers dark coloured – fruits immature – fruits dehiscent
<i>Oxyria digyna</i>	Buds – <b>flowers</b> – stigmas emerged – fruits winged – tubercles brownish – fruits dry
<i>Poa alpina</i> (flowering)	Panicle visible – panicle elongated – <b>flowers</b> – postanthesis – caryopsis propagating – dry panicle
<i>Poa alpina</i> (pseudoviviparous)	Panicle visible – panicle elongated – pseudo-bulbs kneeled – spikelet dry with bulbs – spikelet dry without bulbs
<i>Poa laxa</i>	Panicle visible – panicle elongated – <b>flowers</b> – anthers dry – glumes dry – caryopsis propagating
<i>Sedum alpestre</i>	Buds – <b>corolla bright yellow</b> – corolla darkened – fruits immature – fruits dehiscent
<i>Saxifraga bryoides</i>	Buds – corolla closed – <b>corolla opened</b> – carpels red – corolla dropped off – dispersal
<i>Veronica alpina</i>	Blue coloured bracts – corolla visible – <b>corolla opened</b> – fruit < calyx – fruit = > calyx – fruit dehiscent

Each plant was assigned individually to the nearest datalogger and included with its TS, SM and PH values in the following analyses.

#### DATA ANALYSIS

Plants without generative shoots and obviously diseased or damaged shoots were excluded from analyses.

To examine the synchronizing effect of the environmental factors TS, SM and PH on plant phenology, parametric time-to-event models for interval censored data (Hosmer & Lemeshow 1999; Klein & Möschberger 2003) were used. For each phenophase of each species in each of the two observation years models with TS, SM and PH as response variables were fitted as null models, i.e. we modelled the probability that an individual would not have reached a specific phenophase above a certain TS, SM or PH.

$$f(T) = \beta_0 + \sigma \varepsilon$$

where  $f()$  is a link function depending on the assumed standard distribution of responses,  $T$  is either TS, SM or PH,  $\beta_0$  is the intercept,  $\sigma$  is the scale parameter and  $\varepsilon$  is the error. To account for random effects of individuals a penalized variable with an assumed gamma distribution (frailty term) was included in the models. We explored models with ten standard distributions: minimum extreme value, Weibull, normal, lognormal, logistic, loglogistic, exponential, log-exponential, Rayleigh and log-Rayleigh. The model with the smallest Akaike information criterion (AIC; Sakamoto, Ishiguro & Kitagawa 1986) – calculated as  $-2 \times \log\text{-likelihood} + 2 \times n$ , where  $n$  is the number of parameters in the model – was regarded as the model with the best fit.

Applying the time-to-event models, the median 'time' [expressed in accumulated °C for temperature sums (TS), number of days since snowmelt for SM and daylight minutes for PH] to reach the phenological phases was predicted for each individual in each year. These individual predictions were used to assess how strongly the respective climatic factor synchronizes the phenological development of species. We assumed that an environmental factor acting as a strong trigger will lead to very similar predicted values for all individuals of a species in both years, whereas factors with only weak impacts on phenology will result in greatly varying individual median 'times' between years and along the snowmelt gradient. To quantify the variance of individual predictions the standard deviation (SD) was calculated for each phase and year. High SD-values indicate a weak or missing impact of the respective factor, whereas a SD of zero represents perfect synchronization. The magnitude of SD depends on the absolute values of individual predictions. Hence, to allow for comparisons among the three environmental factors, which have different units, as well as among phenophases within one factor, where late phenophases have higher values than early ones (i.e. in both cases large differences in absolute values can be expected), predictions of each time-to-event model were standardized to cover a range from zero to one by using the formula  $(x-x_{\min})/(x_{\max}-x_{\min})$ , where  $x$  is a value of the environmental variable and  $x_{\min}$  and  $x_{\max}$  are the minimum and maximum of these variable occurring in the data for the respective model.

Linear mixed-effects models (Laird & Ware 1982) were developed with the following parameters (unless explicitly specified): we assumed a gaussian error distribution, a maximum likelihood algorithm was chosen to approximate the log-likelihood criterion of parameter estimation, within-group errors were allowed to have

unequal variances, the potential non-independence of SDs within species as well as between years was accounted for by using both variables as group levels in the calculation of random effects, we allowed for random intercepts as well as random effects of these groups for each fixed effect (i.e. the fixed effect of a model was also used as random effect).

To compare the synchronizing effect of environmental factors on flowering phenology SDs as response, and TS, SM and PH were used as levels of the fixed-effects variable. To investigate the reliability of SDs derived from TS, SM and PH, comparisons between the exceptionally warm year 2003 and the average year 2002 were carried out by applying a linear mixed-effects model for each environmental factor using the year of observation as a binomial predictor and allowing for random intercept for species, which were used as the grouping variable.

Another model examined the intra-seasonal trends of the effect of temperature by using second order polynomials of mean temperature sums of the phenophases as fixed effects. The significance of the first order polynomial indicates a linear increasing or decreasing impact of temperature as a trigger of plant development during the growing season. A significant second order term indicates a maximum or minimum of impact of temperature in mid-season.

Climatic conditions of the previous summer may influence the phenological development due to a varying degree of maturation of the preformed buds. Hence, the accumulated temperature of the total growing season of 2002 was used to uncover such carry-over effects from 2002 to 2003. The respective TS of each individual for 2002 was added to that of each prefloral phenophase in 2003 before applying the time-to-event analysis.

PH can be expected to have a stronger influence on species in habitats with early melting snow cover compared to snowbed species, which should be triggered by energy input. Accordingly, the five snowbed species were compared to the five species inhabiting other habitats like swards, scree or rocks (compare Table 1).

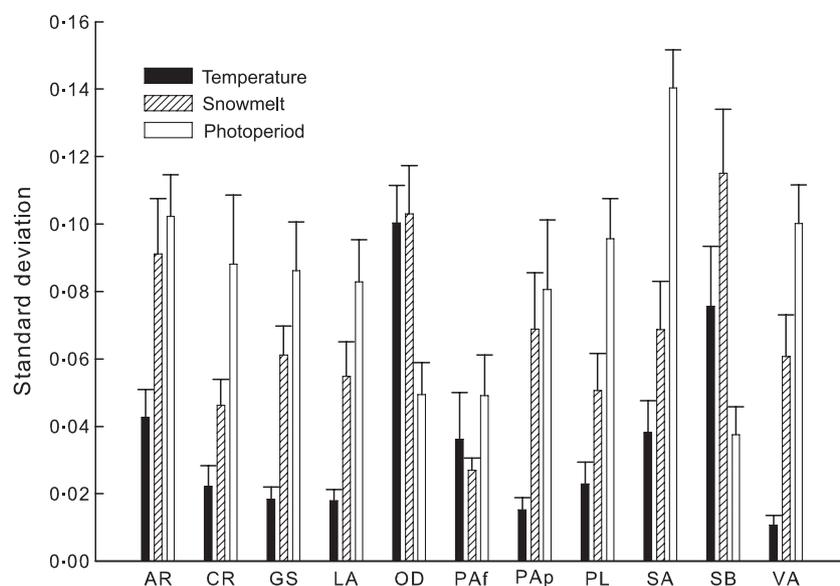
For each mixed-effects model the total number of observations ( $n_{\text{obs}}$ ), the number of groups ( $n_{\text{gr}}$ ), the denominator degrees of freedom, the t-test statistic and the associated  $P$ -value are given for the respective fixed effect.

All Statistical analyses were performed using S-Plus 2000 (Math-Soft Inc. 1988–1999).

## Results

For eight out of ten study species mean SDs of TS were the smallest followed by that of SM and PH (Fig. 1). In contrast, *Oxyria digyna* and *Saxifraga bryoides* had the lowest SDs for PH compared to other environmental factors and to PH of the remaining species. Additionally, flowering *Poa alpina*'s SDs of TS were slightly higher than for SM. Linear mixed-effects models revealed significantly lower SDs for TS than for SM ( $n_{\text{obs}} = 375$ ,  $n_{\text{gr}} = 22$ , d.f. = 351,  $t = 6.54$ ,  $P < 0.001$ ) and PH ( $n_{\text{obs}} = 375$ ,  $n_{\text{gr}} = 22$ , d.f. = 351,  $t = 11.45$ ,  $P < 0.001$ ).

Mean SDs were higher in 2003 than in 2002 showing a more pronounced difference between TS and the two other environmental factors in 2003 (Tab 3). The differences in SDs between 2002 and 2003 were not significant for TS (mixed-effects model:  $n_{\text{obs}} = 125$ ,  $n_{\text{gr}} = 11$ , d.f. = 113,  $t = 1.04$ ,  $P = 0.299$ ) but highly significant for SM ( $n_{\text{obs}} = 125$ ,



**Fig. 1.** Comparison of the synchronizing effect of environmental factors on the flowering phenology of alpine species. The median 'time' expressed in minutes of daylight for photoperiod (PH) as well as accumulated °C for temperature sums (TS) and number of days since snowmelt (SM) were predicted for each phenophase of each plant in both years of observation using time-to-event models for interval censored data. From these individual predictions the standard deviations (SD) were calculated for each species. To assure comparability among environmental factors predictions were standardized to cover the range from zero to one for each model. Illustrated are the means ( $\pm$  standard error) of SDs averaged over phenophases and years. Species are coded as: AR (*Agrostis rupestris*), CR (*Cardamine resedifolia*), GS (*Gnaphalium supinum*), LA (*Leucanthe-mopsis alpina*), OD (*Oxyria digyna*), PAF (flowering *Poa alpina*), PAp (pseudoviviparous *Poa alpina*), PL (*Poa laxa*), SA (*Sedum alpestre*), SB (*Saxifraga bryoides*), VA (*Veronica alpina*).

$n_{gr} = 11$ , d.f. = 113,  $t = 17.87$ ,  $P < 0.001$ ) and PH ( $n_{obs} = 125$ ,  $n_{gr} = 11$ , d.f. = 113,  $t = 3.43$ ,  $P < 0.001$ ).

SD values of TS were slightly higher at the end compared to the beginning of the growing season. However, the synchronization of phenological development with TS was strongest at or shortly after the anthesis of species (Tab 4) with a considerable decrease of the impact of temperature – indicated by higher SD values – towards both earlier and later phenophases for most species. As in the comparison of environmental factors, results for *Oxyria digyna* (strongest effect of temperature during fruit ripening) and *Saxifraga bryoides* (quadratic shape with the maximum variation during mid-season) departed from the general trend.

The general pattern was consistent with the results from a mixed-effects model: we found a highly significant linear

( $n_{obs} = 125$ ,  $n_{gr} = 22$ , d.f. = 101,  $t = 3.96$ ,  $P < 0.001$ ) and quadratic ( $n_{obs} = 125$ ,  $n_{gr} = 22$ , d.f. = 101,  $t = 7.10$ ,  $P < 0.001$ ) term for the mean time of phenophases.

To test whether the higher SDs of prefloral phenophases compared to flowering may be caused by carry-over effects, models for 2003 (including the thermal input of 2002) were compared to corresponding models based on the thermal input of 2003 only. The mean SDs ( $\pm$  standard error) were  $0.156 \pm 0.016$  for models including and  $0.097 \pm 0.016$  for models excluding temperature sums of 2002. Mixed-effects models confirmed that SDs of the former models were significantly higher ( $n_{obs} = 44$ ,  $n_{gr} = 11$ , d.f. = 32,  $t = -7.38$ ,  $P < 0.001$ ) for all study species except for *Cardamine resedifolia* (Tab 5).

Mean SDs of TS were lower for snowbed species ( $0.021 \pm 0.003$ ) compared to species adapted to habitats with early melting snow cover ( $0.050 \pm 0.006$ ). In contrast, mean SDs for PH were higher for species from late ( $0.098 \pm 0.007$ ) than mean SDs from early ( $0.068 \pm 0.006$ ) melting snow cover. The comparison of species from habitats with early and late melting snow cover revealed significant differences for TS (mixed-effects model:  $n_{obs} = 125$ ,  $n_{gr} = 22$ , d.f. = 20,  $t = -3.06$ ,  $P = 0.006$ ) and for PH ( $n_{obs} = 125$ ,  $n_{gr} = 22$ , d.f. = 20,  $t = 2.11$ ,  $P = 0.050$ ), but not for SM ( $n_{obs} = 125$ ,  $n_{gr} = 22$ , d.f. = 20,  $t = -0.97$ ,  $P = 0.345$ ). However, when comparing TS to PH the SDs of the former ( $0.042 \pm 0.010$ ) were significantly lower than the latter ( $0.060 \pm 0.008$ ) even for early phenophases of species of habitats with early melting snow cover ( $n_{obs} = 40$ ,  $n_{gr} = 12$ , d.f. = 27,  $t = 4.43$ ,  $P < 0.001$ ).

**Table 3.** Effect of accumulated temperature sums (TS), days since snowmelt (SM) and photoperiod (PH) on flowering phenology of ten high alpine species observed over 2 years. Standard deviations (SDs) of individual predictions derived from time-to-event models were calculated for each phenophase of each species and year as a measure for the synchronizing effect of these environmental factors

Year	TS	SM	PH
2002	0.031 $\pm$ 0.004	0.036 $\pm$ 0.004	0.070 $\pm$ 0.006
2003	0.040 $\pm$ 0.006	0.096 $\pm$ 0.006	0.094 $\pm$ 0.006

Values (mean  $\pm$  standard error) represent averages of SDs over species and phenophases. Low values indicate strong synchronization.

**Table 4.** Synchronization of phenophases of study species with temperature sums (TS) using a threshold of 1 °C. Values represent averaged annual standard deviations (SD) for the years 2002 and 2003. A low SD indicates high synchronization of the phenophase with the accumulated thermal input

Species	Pre-anthesis		Anthesis	Post-anthesis			
<i>Agrostis rupestris</i>	0.052	0.043	<b>0.021</b>	0.054	0.043		
<i>Cardamine resedifolia</i>		0.024	<b>0.010</b>	0.014	0.020	0.043	
<i>Gnaphalium supinum</i>	0.015	0.012	0.014	<b>0.008</b>	0.021	0.041	
<i>Leucanthemopsis alpina</i>	0.034	0.018	<b>0.003</b>	0.008	0.028	0.017	0.020
<i>Oxyria digyna</i>		0.118	0.100	0.097	<b>0.078</b>	0.099	0.118
<i>Poa alpina</i> (flowering)	0.027	0.011	0.053	<b>0.009</b>	0.022	0.139	
<i>Poa laxa</i>	0.014	0.018	0.019	<b>0.005</b>	0.023	0.059	
<i>Sedum alpestre</i>		0.054	0.035	<b>0.031</b>	0.034	0.046	
<i>Saxifraga bryoides</i>	<b>0.005</b>	0.032	0.150	0.110	0.114	0.041	
<i>Veronica alpina</i>	0.008	0.014	0.004	<b>0.002</b>	0.007	0.029	

Best synchronized phenophases are given in bold. Pre- and post-anthesis denotes all phenophases of a species preceding and following anthesis. For a detailed description of phenophases including the identification of the anthesis see Table 2.

## Discussion

Temperature was the main driver of flowering phenology for the species in the present study. This finding is consistent with global meta-analyses (Parmesan & Yohe 2003; Root *et al.* 2003) as well as with regional studies of comparable alpine systems (Studer, Appenzeller & Defila 2005; Huelber *et al.* 2006). SDs of TS were lower than those of SM and PH in both years of observation, but also show by far the lowest variability between the average and the warmer year, corroborating temperature sums (Molau, Nordenhäll & Eriksen 2005; Kudo & Hirao 2006) as the best indicators of phenological development of high alpine plants. However, the synchronizing effect of temperature varies considerably among species. Flowering phenology of species with low SDs can be expected to respond instantaneously to annual fluctuations as well as long-term trends (compare Fig. 1).

**Table 5.** Carry-over effects of temperature on the synchronization of prefloral phenophases. Values represent SDs individual predictions for 2003 derived from mixed-effects models including and excluding the thermal input of 2002 in the calculation of accumulated temperature sums (TS)

Species	Excluding 2002	Including 2002
<i>Agrostis rupestris</i>	0.131–0.101	0.188–0.164
<i>Cardamine resedifolia</i>	0.001	0.216
<i>Gnaphalium supinum</i>	0.050–0.061	0.204–0.246
<i>Leucanthemopsis alpina</i>	0.191–0.102	0.244–0.159
<i>Oxyria digyna</i>	0.288–0.239	0.289–0.271
<i>Poa alpina</i> (flowering)	0.006–0.067	0.045–0.116
<i>Poa laxa</i>	0.082–0.074	0.115–0.127
<i>Sedum alpestre</i>	0.179	0.061
<i>Saxifraga bryoides</i>	0.003–0.135	0.057–0.179
<i>Veronica alpina</i>	0.047–0.069	0.124–0.158

Lower values for models including data from 2002 indicate an influence of thermal conditions of the previous growing season on early phenophases of the species.

## INTRASEASONAL VARIATION

The phenotypic plasticity shown by individuals as a response to environmental variability and change differs among phenophases (Post *et al.* 2008). For high altitudes in the Alps, Weber *et al.* (1997) observed significant temperature changes within the second half of the 20th century only for winter and spring. Early spring phenophases show the greatest year to year variability due to particularly strong relations between air temperatures and phenological events (Studer, Appenzeller & Defila 2005 and citations therein; Miller-Rushing & Primack 2008) and therefore the greatest long-term advancement in supraregional observations of lowland (Fitter & Fitter 2002; Menzel *et al.* 2006b and citations therein) and mountain areas (Defila & Clot 2001).

This general trend of strong synchronization of plant phenology by climatic factors – mainly temperature – at the beginning of the season and weaker responses of phenology towards autumn senescence (Sparks & Menzel 2002) could also be observed on the local scale for the high alpine species of this study. However, it was accompanied by another strong trend. The phenology of the majority of the study species was most strongly synchronized with temperature during mid-summer at or shortly after the peak of flowering (Huelber *et al.* 2006), with weaker effects of temperature during early spring and late autumn phenophases. Thus, flowering can be regarded as the phenophase of generative reproduction most sensitive to climate change for study species.

The timing of flowering is crucial for the reproductive success of a species (Thórhallsdóttir 1998). In highly seasonal environments like temperate alpine regions this timing is under strong selective pressure to maximize fitness (Stinson 2004), reducing the intraspecific variability especially for that part of the development.

The highest synchronization at flowering instead of the earliest phenophases can also be explained by carry-over effects, which decouple the early phases of development from recent climatic conditions to some extent. However, we did not find substantial evidence of carry-over effects for the study species

(except for *Sedum alpestre*). The synchronization of early phenophases was not enhanced but diminished by accounting for the previous year's weather conditions, perhaps indicating that carry-over effects in the present study are of minor importance for phenological timing as in high arctic species (Thórhallsdóttir 1998). However, carry-over effects could be more significant for the abundance of flowers rather than for the timing.

Flowering shoots of *Oxyria digyna* and *Saxifraga bryoides* were strongly affected by pathogens, causing irregularities in the development and death of a considerable proportion of shoots. Hence, the proportion of early phenophases is increased which could be the reason for the deviations in phenological behaviour of the two species compared to the majority of study species.

#### HABITAT-SPECIFIC VARIATION

The date of snowmelt shows great annual variation (Beniston 1997), but the snow distribution pattern in the landscape remains constant among years (Friedel 1961; Walker *et al.* 1993; Molau, Nordenhäll & Eriksen 2005). Photoperiodic induction of reproduction prevents plants from developing flowers too early in the season due to thermal peculiarities. Consequently, the impact of the photoperiod should be greater for species of early melting habitats compared to snowbeds.

Although temperature was the most important environmental factor triggering phenology, significant habitat-specific differences were detected. The synchronizing effect of TS was higher for species adapted to habitats early released from snow cover compared to snowbed species, while for PH the opposite pattern was observed.

These results corroborate the only comparable study of habitat-specific responses in flowering phenology, in which considerable differences between snowbeds and wind exposed ridges were observed in mountain environments in Japan (Kudo & Hirao 2006). However, one reason for the impact of photoperiod being weaker than temperature in our study may originate in the selection of the study system. Unlike Kudo & Hirao (2006) we did not observe the total snowmelt gradient occurring at the study area. Our observations were restricted to the amplitude of sympatric occurrence of the study species, leading to a lack of sites with very early snowmelt. Consequently, snow release may have been too late to allow for a dominant photoperiodic control even in the sites with the earliest date of snow release in our study. Photoperiod and temperature most likely interact in controlling flowering phenology of alpine species. Arctic and alpine plants commonly show a dual floral induction (Heide 1990, 1992, 1997) initiating inflorescence primordia under short day and/or low temperature conditions, but anthesis and heading require long days and are enhanced by high temperatures. Keller & Körner (2003) argue that photoperiodic control becomes less strict after surpassing a certain threshold. Most of the species they studied were either insensitive to photoperiod or required a long-day induction of about 15 h of daylight. Major parts of our study area fulfilled these requirements as

plants were released from snow in mid-May to mid-July. Earlier snowmelt can be expected to unify the anthesis. Dates of flowering will be further advanced for plants on late melting sites, while plants on early melting sites stay around the 15-h threshold (i.e. end of May). Consequently, photoperiodic induction currently seems to be of little importance.

#### Conclusions

Flowering phenology of high alpine plant species proved to be highly temperature-sensitive. Notwithstanding global surveys (Walther *et al.* 2002; Menzel *et al.* 2006a) early phenophases were less strongly associated with temperature than flowering. Our results suggest that high alpine species will respond quickly and directly to increasing temperature. Climate-induced changes seem not to be attenuated by their reproductive system due to photoperiodic synchronization unless the changes reach a magnitude of at least 1 month (i.e. one hour daylight per day). The temperature sensitivity of flowering phenology of all study species gives no indication for drastic shifts in temporal patterns of flowering among species of different high alpine habitats, provided that the temperature increase is more or less consistent throughout the year. However, the increase is predicted to be greater in winter and spring (Weber *et al.* 1997), which may lead to temporal dispersions of flowering time and hence a diminished overlap among species, potentially changing species interactions and species composition of future plant assemblages.

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