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Phenological response of grassland species to manipulative snowmelt and drought along an altitudinal gradient

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Abstract

Plant communities in the European Alps are assumed to be highly affected by climate change, as the temperature rise in this region is above the global average. It is predicted that higher temperatures will lead to advanced snowmelt dates and that the number of extreme weather events will increase. The aims of this study were to determine the impacts of extreme climatic events on flower phenology and to assess whether those impacts differed between lower and higher altitudes. In 2010, an experiment simulating advanced and delayed snowmelt as well as a drought event was conducted along an altitudinal transect approximately every 250 m (600–2000 m above sea level) in the Berchtesgaden National Park, Germany. The study showed that flower phenology was strongly affected by altitude; however, there were few effects of the manipulative treatments on flowering. The effects of advanced snowmelt were significantly greater at higher than at lower sites, but no significant difference was found between both altitudinal bands for the other treatments. The response of flower phenology to temperature declined through the season and the length of flowering duration was not significantly influenced by treatments. The stronger effect of advanced snowmelt at higher altitudes may be a response to differences in treatment intensity across the gradient. Consequently, shifts in the date of snowmelt due to global warming may affect species more at higher than at lower altitudes, as changes may be more pronounced at higher altitudes. These data indicate a rather low risk of drought events on flowering phenology in the Bavarian Alps.

Key words: advanced snowmelt, Alps, BBCH, climate change, delayed snowmelt, flowering.

Introduction

Over the past 100 years, global annual mean temperatures have increased by about 0.7 °C (IPCC, 2007). However, some regions have been more affected by climate change than others. For the European Alps, a much stronger temperature increase of about 2 °C has been detected (Auer *et al.*, 2007). In the future, it is predicted that temperatures will further rise, that rainfall distribution will change, and that extreme weather events, such as torrential rain and drought, will increase significantly in frequency (IPCC, 2007). Furthermore, a general reduction in the duration of snow

cover will be caused by warmer temperatures, because the zero-degree isotherm will be displaced to higher altitudes (Beniston, 2003; Laghari *et al.*, 2012). However, climate change scenarios for future snow conditions are rather vague. An increase in heavy snowfall events in winter may therefore also lead to a prolongation of snow cover duration.

As a result of the changing environment, alpine plant communities have already experienced and will suffer further negative impacts (e.g. Korner, 1992; Grabherr *et al.*, 1994; Sala *et al.*,

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2000; Erschbamer *et al.*, 2009). The effects of climate change on alpine vegetation will be especially pronounced at high altitudes, as abiotic factors such as climate prevail over biotic factors in these regions (Korner and Miglietta, 1994; Theurillat and Guisan, 2001).

Phenology, the study of the timing of recurring natural events, can be a tool for assessing climate change impacts on plant growth and development. Several studies have shown that the most important factors for plant development in alpine areas are temperature, date of snowmelt, and photoperiod (e.g. Price and Waser, 1998; Blionis *et al.*, 2001; Keller and Korner, 2003). However, in the future, drought may also play an important role in the development of plants in the Alps due to an increasing probability of the occurrence of extreme weather events.

Shifts in plant phenology due to warmer temperatures have already been widely documented by analysing long-term datasets (e.g. Schwartz and Reiter, 2000; Sparks *et al.*, 2000; Abu-Asab *et al.*, 2001; Fitter and Fitter, 2002; Menzel *et al.*, 2005, 2006) or have been confirmed by experimental studies (Marion *et al.*, 1997; Hollister and Webber, 2000; Kudernatsch *et al.*, 2008; De Frenne *et al.*, 2010). Higher temperatures mainly advance plant phenology (e.g. Sparks *et al.*, 2000; Menzel *et al.*, 2006; Kudernatsch *et al.*, 2008), which increases the risk of late frost damage in spring (Inouye, 2000, 2008; Wipf *et al.*, 2009) and may cause shifts in plant community composition due to die off (Molau, 1997). Furthermore, changes in plant flowering patterns can cause an overlap of the flowering times of different species, which, in early summer, can lead to greater competitive pressure, because pollinator activity is very low at this time of year (Molau, 1997). Shifts in plant flowering times may also decrease population levels of pollinators (Inouye and McGuire, 1991), which may in turn also increase competitive pressure.

Timing, depth, and duration of snow cover determine the beginning of the growing season in alpine areas (Inouye and Wielgolaski, 2003). Thus, the development of many species in alpine or Arctic regions is highly dependent on the timing of snowmelt (Inouye *et al.*, 2002; Stinson, 2004; Inouye, 2008). A prolongation in snow cover duration often delays plant phenology (Weaver and Collins, 1977; Inouye, 2008; Torp *et al.*, 2010; Cooper *et al.*, 2011), whereas a shortening of snow cover duration mostly advances the timing of plant development (e.g. Price and Waser, 1998; Dunne *et al.*, 2003; Inouye *et al.*, 2003; Wipf *et al.*, 2009; Lambert *et al.*, 2010; Wipf, 2010; Chen *et al.*, 2011). However, phenological responses are highly species specific and differ among functional groups (Wipf and Rixen, 2010). An advanced snowmelt could potentially increase plant fitness by prolonging the growth period and hence resource allocation (Galen and Stanton, 1993; Stinson, 2004). However, an earlier start of flowering also increases the risk of late frost damage in spring. Thus, an earlier snowmelt may not necessarily lead to advanced flowering (Inouye, 2008). In the Australian Alps, for example, the timing of snowmelt only slightly affected the timing of flowering for the tested species (Venn and Morgan, 2007).

As with other plants, the responses of alpine plants to drought include wilting and reduced plant growth (Sangtarash *et al.*, 2009) and seed set, or even extinction (Galen, 2000). Phenological responses to drought, however, are not consistent for alpine and other plants. Jentsch *et al.* (2009) reported an advance of the mid-flowering date by 4 d after a drought event, whereas Bloor *et al.* (2010) did not detect a significant effect of drought on grasses. In contrast, a delay in flowering phenology under dry conditions was reported for Mediterranean plants (Penuelas *et al.*, 2004; Llorens and Penuelas, 2005; Prieto *et al.*, 2008; Miranda *et al.*, 2009).

In general, there have been several studies dealing with the impacts of a changing abiotic environment (shifts in the date of snowmelt or the occurrence of drought) on plant phenology. However, as far as we know, there have been only a few studies combining manipulative experiments with an altitudinal gradient (but see Dunne *et al.*, 2003; Stinson, 2004) to assess whether impacts due to climate change differ between lower and higher altitudes. Altitudinal gradients naturally provide different temperature scenarios, because air temperature decreases by 0.54–0.58 °C per 100 m increase in altitude (Rolland, 2003). Thus, the current study focused not only on treatment effects but also on combined temperature changes, which are derived indirectly from altitudinal change. Consequently, the aims of this study were to test whether shifts in the date of snowmelt and drought events affected (i) the timing and (ii) the length of flowering phenology of different grassland species, and whether those impacts changed with (iii) elevation and (iv) season.

Materials and methods

Study site and experimental design

The study area was located in the northern part of the Berchtesgaden National Park, which is the only German national park in the Alps and is characterized by a large altitudinal range within a small area (StMUG, 2001).

Eleven observational sites were located along two valleys in the national park and ranged from ~800 m to ~2000 m above sea level (a.s.l.). To ensure a larger altitudinal gradient, three sites below 800 m beyond the borders of the park were added, starting at ~600 m. One other site outside the two valleys was also included to ensure a site at approximately every 250 m altitude difference. Thus, observations were conducted at a total of 15 different sites. The aspects of the sites were different: eight faced north, three faced west, three faced south, and one was on level ground.

The annual mean temperature in the park ranges between –2 and 7 °C and annual mean precipitation is 1500–2600 mm depending on altitude (StMUG, 2001). For sites below 1000 m a.s.l., maximum snow cover is reached in February at a mean depth of about 50 cm. Sites over 1000 m have their maximum snow cover in March, ranging between 3 and 5 m at the highest altitudes (StMUG, 2001).

The lapse rate of air temperature (decrease in temperature with elevation) was about 0.45 °C per 100 m elevation (mean from March to August; Konnert, 2004). Growing season lengths (derived from days above a 10 °C threshold) varied from 5 months at 600 m to ~1 month at 2000 m (Konnert, 2004).

Experimental plots were established at each of the 15 study sites along the entire altitudinal gradient, consisting of three different treatments and a control, each plot sized 4 × 4 m. Plots were contained within a 10 × 10 m square, arranged in a 2 × 2 array. Treatments were the simulation of advanced and delayed snowmelt, as well as a drought event.

Advanced and delayed snowmelt

Advanced and delayed snowmelt was simulated by shovelling snow from advanced snowmelt plots onto delayed snowmelt plots until only a thin snow layer was left on the former; thus, the vegetation on the advanced snowmelt plots was not disturbed. Shovelling took place

between the end of February and the beginning of April in 2010, depending on altitude. Snow depth along the gradient varied from 15 to 214 cm on advanced snowmelt plots before shovelling. After shovelling, snow depth on delayed snowmelt plots ranged from 16 to 304 cm depending on altitude. Snow melting date was defined as the day when near-surface air temperatures reached more than +5 °C on at least three consecutive days (for description of temperature measurements, see Environmental data, below).

Drought event

The drought event was simulated by rain-out shelters, which were installed, on average, 4 weeks after snowmelt in control plots depending on altitude (installed end of April to end of June; removed beginning of June to beginning of August). The drought period lasted 43 ± 1 d, which is regarded as a 1000-year extreme event in this region (Jentsch and Beierkuhnlein, 2008). To allow air exchange, rain-out shelters were open at the front and rear. Rain-out shelters were 125 cm high and constructed with aluminium tubes and cast-iron key clamps (B-One key clamps, Montfoort, The Netherlands). Shelter poles were covered with a transparent plastic sheet (0.2 mm polyethylene; SPR 5, Hermann Meyer KG, Germany), which transfers nearly 90% of photosynthetically active radiation. The drought period ended when the shelters were removed. Over the altitudinal gradient, no significant difference in average or maximum near-surface air temperature (for description of temperature measurements, see Environmental data, below) between drought and control plots was detected with a paired t-test ($P=0.6$ and $P=0.9$, respectively) in the drought period. Minimum temperature, however, was significantly different between drought and control plots for the same period (paired t-test, $P=0.012$).

Species and phenological observations

Phenological observations of ten different species (eight herbs and two grasses) were conducted once a week from April to September 2010 on each plot following the Biologische Bundesanstalt, Bundessortenamt and Chemical Industry (BBCH) code. The BBCH code is a detailed growth stage key that includes intermediate stages as well as stages marking the end of phenophases. It allows the observation of the entire development cycle of all mono- and dicotyledonous plants using a decimal coding system (Meier, 2001). Using a detailed observation key like this, it is not necessary to be present at the exact start of the phenological stage, as the key allows recording of the frequency distribution of phenophases of a certain number of individual plants on each sampling date. Classical onset dates, as used in climate research studies, could be interpolated from these data using the ordinal logistic regression (OLR) method described by Cornelius *et al.* (2011). The OLR method provides information about the progression of stages (including the beginning, speed of passage, and end of secondary growth stages) and allows stages to be of unequal length (ordinal-scale approach). Furthermore, OLR is based on the frequency distribution over time, which includes the entire progression of plants in the model and not only the progression of a single stage.

In this study, the focus was on flower phenology, especially the beginning of flowering (forbs: first flowers open; grasses: first anthers visible), full flowering (forbs: 50% of flowers open; grasses: 50% of anthers mature), and end of flowering (forbs: petals dehydrated or fallen; grasses: all spikelets/panicles have completed flowering but some dehydrated anthers may remain). *Campanula scheuchzeri* Vill and *Ranunculus montanus* Willd. develop only one flower per individual, and thus definitions needed to be adjusted for the beginning of flowering (flower slightly open) and full flowering (flower expanded to full size). In each plot, 20 individuals per species were observed where possible. This number of individuals was considered large enough for further statistical analysis and small enough to make all observations achievable within a week. As plants of each species were not individually marked, partly different groups of individual plants were probably observed on consecutive sampling dates.

The average altitudinal range of species in this study was about 705 m but varied between 127 m for full flowering of *Ranunculus acris* L. and

1343 m for end of flowering of *Ranunculus montanus* (Table 1). All observed dates were converted to day of year (1 January=1, etc.; DOY).

Environmental data

Temperature data was derived from iButton data loggers (Thermochron iButtons DS1921G#F5; Maxim Integrated Products, Sunnyvale, CA, USA), which were located in the middle of each treatment plot, recording the temperature at 2 h intervals. For snowmelt treatments, iButton loggers were used to determine snow melting dates from subnivean temperatures, which were measured near the soil surface. Due to technical faults of the iButton data loggers, there was no information about snow melting dates for the sites at 817 and 1920 m. The amount of rain excluded from drought plots through rain-out shelters was estimated with the help of rain collectors next to the site. Averaged over all sites, mean precipitation was 379 ± 71 l m^{-2} during the drought period. Linear regression analysis revealed no significant relationship between the amount of precipitation among sites along the altitudinal gradient ($P=0.3$). Soil moisture content was measured with a portable soil moisture meter (Delta-T Devices type HH2 + ThetaProbe ML2x sensors, Cambridge, UK) on average four times per plot during the drought period.

Statistical analyses

Linear regression models with data from control plots over the entire altitudinal gradient were conducted to test the effect of altitude on the timing of phenophases (beginning of flowering, full flowering, and end of flowering) for each species. To test whether the response to altitude changed with the timing of mean onset dates, weighted linear regression of significant altitudinal regression coefficients on mean dates was carried out. We weighted the dependent variable in dependence on its residuals. A mixed-effect analysis of covariance (ANCOVA) with Type I sums of squares was used for each species and phenophase (beginning of flowering, full flowering, and end of flowering) separately to test whether there were differences in phenology due to experimental treatments. In this model, site nested within altitude was considered as a random factor and treatment as a fixed factor. Altitude was included as a covariate to remove the effect of altitude from the treatment comparison. Tukey's HSD for multiple comparisons was used when the model was significant. Mean onset dates were derived from the adjusted means from the mixed-effect model. ANCOVA was conducted separately for lower (600–1300 m) and higher (1300–2000 m) sites to detect changes in the response to experimental treatments over the altitudinal gradient.

Paired t-tests were used to test whether soil moisture content differed between control and treated plots during the drought period. Further t-tests were conducted to see whether there were differences in treatment effects between lower and higher sites.

All statistical analyses were performed with SPSS 19.0 (SPSS, Chicago, IL, USA).

Results

Abiotic treatment effects

Averaged over the lower gradient from 600 to 1300 m, snow melted ~18 d earlier on advanced snowmelt plots than on control plots [between 20 February (DOY 51) and 23 March (DOY 82)] (Figs 1 and 2). At higher altitudes (1300–2000 m), the snow melting date on advanced snowmelt plots was between 23 March (DOY 82) and 8 April (DOY 98), which was about 40 d earlier in comparison with control plots (Figs 1 and 2). A t-test showed a significant difference in the advance of snow melting dates in comparison with control plots at lower and higher sites on advanced snowmelt plots ($P=0.014$). On delayed snowmelt plots, the mean snow melting date was about 2 d later at lower

Table 1. Results of linear regression analysis of study site mean dates of three phenophases on altitude Numbers in bold are significant ($P < 0.05$). Altitudinal ranges show the maximum difference in elevation and the elevation of the lowest and highest site for each species and phenophase. BF, beginning of flowering; FF, full flowering; EF, end of flowering; #, no variation recorded in this variable for this event.

		N	R^2	*P*	Regression coefficients (±SE) (days/100 m)	Altitudinal ranges (low–high) (m)
Alchemilla vulgaris L. (Rosaceae)	BF	4	0.119	0.655	0.8 (±1.6)	534 (1045–1579)
	FF	7	0.827	**0.005**	4.8 (±1.0)	865 (714–1579)
	EF	7	0.550	**0.050**	2.4 (±1.0)	619 (960–1579)
Briza media L. (Poaceae)	BF	7	0.844	**0.003**	3.4 (±0.7)	689 (641–1330)
	FF	7	0.731	**0.014**	2.4 (±0.7)	689 (641–*1330*)
	EF	7	0.853	**0.003**	3.2 (±0.6)	689 (641–1330)
Campanula scheuchzeri Vill. (Campanulaceae)	BF	3	0.776	0.314	5.2 (±2.8)	273 (1552–1825)
	FF	5	0.535	0.160	1.4 (±0.8)	865 (960–1825)
	EF	8	0.642	**0.017**	1.9 (±0.6)	865 (960–1825)
Dactylis glomerata L. (Poaceae)	BF	5	0.713	0.072	3.9 (±1.4)	464 (641–1105)
	FF	5	0.526	0.166	2.5 (±1.4)	464 (641–1105)
	EF	5	0.331	0.311	1.3 (±1.1)	464 (641–1105)
Lotus corniculatus L. (Fabaceae)	BF	6	0.794	**0.017**	3.6 (±0.8)	1111 (714–1825)
	FF	6	0.878	**0.006**	3.1 (±0.6)	1111 (714–1825)
	EF	11	0.683	**0.002**	1.7 (±0.4)	1270 (714–1984)
Potentilla erecta (L.) Raeusch (Rosaceae)	BF	4	0.917	**0.043**	3.6 (±0.8)	762 (817–1579)
	FF	5	0.916	**0.011**	3.1 (±0.5)	762 (817–1579)
	EF	9	0.074	0.479	0.8 (±1.0)	1167 (641–1808)
Prunella vulgaris L. (Lamiaceae)	BF	3	0.900	0.205	7.0 (±2.3)	288 (817–1105)
	FF	5	0.816	**0.036**	2.7 (±0.7)	865 (714–1579)
	EF	8	0.769	**0.004**	2.5 (±0.6)	938 (641–1579)
Ranunculus acris L. (Ranunculaceae)	BF	#	#	#	#	#
	FF	3	0.894	0.211	7.9 (±2.7)	127 (714–841)
	EF	3	0.999	**0.019**	5.7 (±0.2)	246 (714–960)
Ranunculus montanus Willd (Ranunculaceae)	BF	#	#	#	#	#
	FF	3	0.953	0.139	5.1 (±1.1)	780 (1045–1825)
	EF	8	0.954	**<0.001**	4.9 (±0.4)	1343 (641–1984)
Trifolium pratense L. (Fabaceae)	BF	5	0.648	0.100	3.4 (±1.4)	984 (841 –1825)
	FF	7	0.647	**0.029**	4.1 (±1.3)	1111 (714–1825)
	EF	10	0.684	**0.003**	4.1 (±1.0)	1111 (714–1825)

and about 5 d later at higher sites than on control plots (Fig. 2). The date of snowmelt on delayed plots was between 22 February (DOY 53) and 16 April (DOY 106) at lower sites and between 23 April (DOY 113) and 5 June (DOY 156) at higher sites (Fig. 1). A *t*-test showed no significant differences in the delay of snowmelt in comparison with controls between the lower and higher sites on delayed snowmelt plots (P=0.157, Fig. 2). During the drought period, soil moisture content was, averaged over all sites, significantly different between control and drought plots (paired *t*-test, $P < 0.001$); however, the difference did not change with altitude, as a *t*-test was not significant different between the lower and higher sites (P=0.301, Fig. 3). No significant difference in soil moisture content was found between controls and either advanced or delayed snowmelt plots (paired *t*-test, P=0.786 or P=0.932, respectively).

Phenological shifts due to altitude

Linear regression models mostly showed significant responses of flowering phenology to altitude (Table 1). Averaged over all phenophases and species, there was a delay in onset dates of 3.4 d per 100 m increase in elevation. However, the altitudinal response differed strongly among species, being greatest for the end of flowering of *R. acris* (5.7 d per 100 m) and smallest for the end of flowering of *Lotus corniculatus* L. (1.7 d per 100 m).

Weighted linear regression analysis showed that phenophases occurring later in the year were significantly less responsive to altitudinal change than phenophases early in the year (P=0.043, R^2=0.593).

Phenological differences due to treatments

ANCOVA showed few significant differences in the timing of phenophases between treatments with differences found mainly at higher sites, except for *Prunella vulgaris* L., which showed a significant shift at the lower gradient (Tables 2 and 3).

Tukey's HSD post-hoc tests showed a significant advance of 6–12 d for the beginning of flowering and full flowering of *Alchemilla vulgaris* L. on advanced snowmelt plots in comparison with control and other treatment plots (Table 3). Full flowering and end of flowering of *R. montanus* were also 8–18 d earlier on advanced snowmelt plots in comparison with the
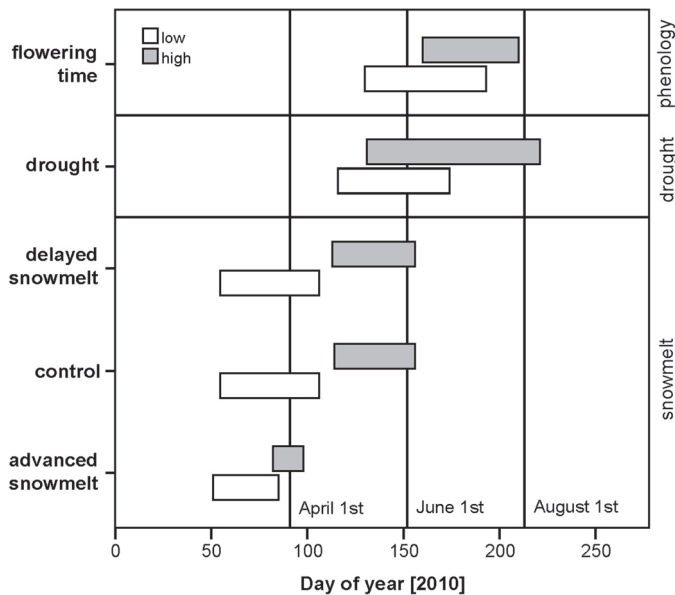
Fig. 1. Range in the date of snowmelt (advanced snowmelt, control, delayed snowmelt), duration of drought treatment, and flowering time of all species over the lower (600–1300 m) and the higher (1300–2000 m) altitudinal gradient in 2010.

Fig. 3. Deviations of soil moisture content on drought plots from controls, derived from each altitudinal site singly and then separated by low (600–1300 m) and high (1300–2000 m) sites.

other treatments (Table 3). A significant delay of 5–9 d in the end of flowering of *C. scheuchzeri* and *P. vulgaris* was recorded on
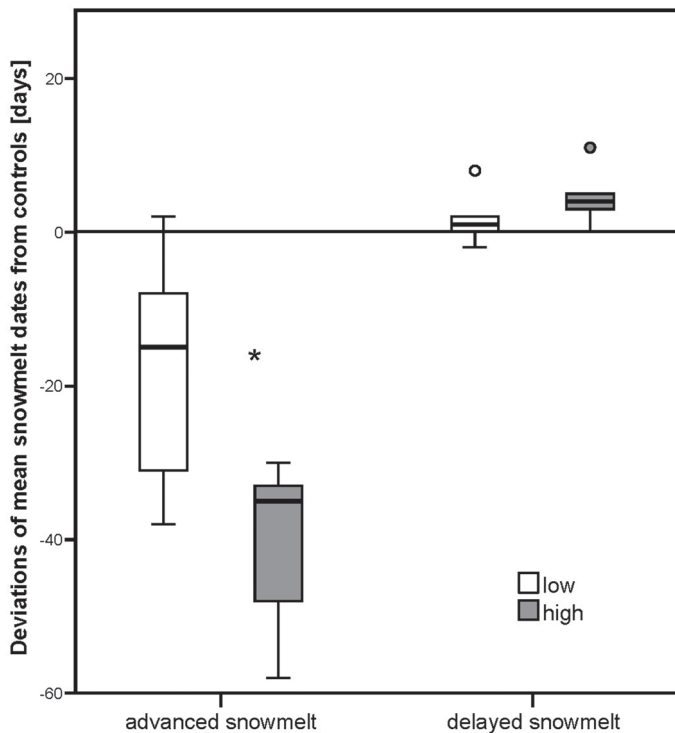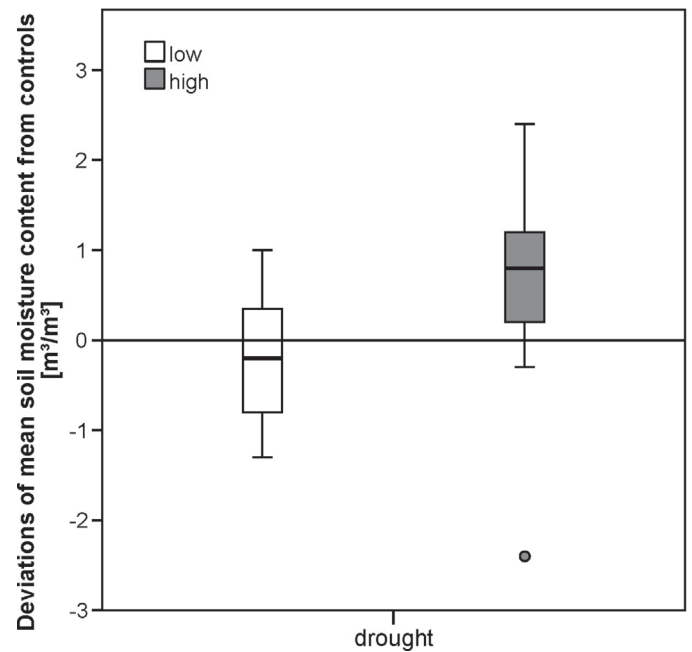

Fig. 2. Deviations from controls of mean snowmelt dates on advanced and delayed snowmelt plots, derived from each altitudinal site singly and then separated by low (600–1300 m) and high (1300–2000 m) altitudes. The asterisk indicates significant differences in snow melting date between lower and higher sites (*P* <0.05).

delayed snowmelt plots (Tables 2 and 3). For *Potentilla erecta* (L.) Raeusch, the end of flowering was significantly advanced on drought plots (by 3–8 d) in comparison with advanced and delayed snowmelt plots (no data available for control plots, Table 3).

The timing of phenophases, averaged over all species, was about 1–7 d earlier on advanced snowmelts plots in comparison with control plots (including non-significant results). The timing was 2–3 d later or about the same (0 to –2 d) on delayed snowmelt and drought plots, respectively.

On advanced snowmelt plots, effects were much greater at higher than at lower sites (mean response of –1 day on lower and –5 d on higher sites). On delayed snowmelt plots, the response was the same for lower and higher sites (mean delay of 3 d). The mean response to drought was –2 d for lower sites, but no significant difference in phenology was found at higher sites.

The effect of an advanced snowmelt appeared to be more pronounced earlier in the year, showing a response of –7 d on higher sites for the beginning of flowering and only –1 day for the end of flowering. The effect of delayed snowmelt and drought appeared to be consistent throughout the year.

Changes in duration of flower phenology

ANCOVA showed that, for all species, manipulative treatments had no significant effect on the duration of flower phenology except for *A. vulgaris* showing a prolongation of 7 d on advanced snowmelt plots in comparison with the control plots (Table 4). For *P. erecta*, flower duration was much longer at lower altitudes (33 d) than at higher altitudes (18 d) averaged over all treatments (Table 4).

Table 2. Mixed-effect ANCOVA showing differences in phenological onset dates (beginning of flowering, full flowering, and end of flowering) between treatments [control (co), advanced snowmelt (ad), delayed snowmelt (de), and drought (dr)] for the lower part (600–1300 m) of the altitudinal gradient. Numbers in bold are significant (P <0.05). NA, data not available. Mean onset dates are derived as adjusted means from the model. Tukey's HSD was conducted for multiple comparisons if the model was significant; letters indicate a significant difference between respective treatments.

	Beginning of flowering					Full flowering					End of flowering				
	P	co	ad	de	dr	P	co	ad	de	dr	P	co	ad	de	dr
Alchemilla vulgaris L.	0.622	140	137	NA	139	0.153	140	137	139	139	0.369	174	177	NA	177
Briza media L.	0.485	173	172	174	172	0.236	175	177	179	173	0.103	181	181	182	180
Campanula scheuchzeri Vill.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Dactylis glomerata L.	0.106	170	168	170	167	0.354	172	170	173	170	0.265	177	175	178	175
Lotus corniculatus L.	0.253	166	156	170	NA	0.223	170	162	178	NA	0.160	189	188	200	198
Potentilla erecta (L.) Raeusch	0.218	149	153	153	152	0.744	156	158	158	158	0.714	189	189	192	187
Prunella vulgaris L.	0.800	183	183	181	185	0.290	185	183	187	185	**0.047**	193	191	196	191
													a	a, b	b
Ranunculus acris L.	0.695	143	140	144	141	0.402	144	143	144	142	0.763	159	157	158	158
Ranunculus montanus Willd.	NA	NA	NA	NA	NA	0.590	130	128	130	130	0.801	136	133	137	136
Trifolium pratense L.	0.391	167	167	162	169	0.147	173	172	170	171	0.634	184	181	181	181

Discussion

The present study showed strong responses of the flower phenology of different grassland species to altitude. Furthermore, we demonstrated that advanced snowmelt had a greater influence on flower phenology at higher than at lower sites due to a stronger treatment effect at higher altitudes. However, altitude had no significant effect on responses to delayed snowmelt or drought,

Table 3. Mixed-effect ANCOVA showing differences in phenological onset dates (beginning of flowering, full flowering, and end of flowering) between treatments [control (co), advanced snowmelt (ad), delayed snowmelt (de), and drought (dr)] for the higher part (1300–2000 m) of the altitudinal gradient. Numbers in bold are significant (P <0.05). NA data not available. Mean onset dates are derived as adjusted means from the model. Tukey's HSD was conducted for multiple comparisons if the model was significant; letters indicate a significant difference between respective treatments.

	Beginning of flowering					Full flowering					End of flowering				
	P	co	ad	de	dr	*P*	co	ad	de	dr	*P*	co	ad	de	dr
Alchemilla vulgaris L.	**0.005**	160	154	166	161	**0.028**	170	161	172	169	0.255	187	187	189	185
		a	a b c	b	c		a	a b c	b	c					
Briza media L.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Campanula scheuchzeri Vill.	0.122	209	211	213	207	0.123	210	211	214	207	**<0.001**	216	219	225	217
												a	b	a b c	c
Dactylis glomerata L.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lotus corniculatus L.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.242	202	200	200	202
Potentilla erecta (L.) Raeusch	0.318	179	173	183	178	0.192	180	175	184	181	**0.036**	NA	195	200	192
													a	b	a b
Prunella vulgaris L.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Ranunculus acris L.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Ranunculus montanus Willd.	0.092	169	153	168	171	**0.005**	170	158	171	176	**0.006**	178	170	181	179
							a	a b c	b	c		a	a b c	b	c
Trifolium pratense L.	NA	NA	NA	NA	NA	0.610	199	196	201	198	0.410	210	207	211	210

Table 4. Mixed-effect ANCOVA showing differences in the length of flowering period (days from beginning of flowering to end of flowering) between treatments [control (co), advanced snowmelt (ad), delayed snowmelt (de), and drought (dr)] over a lower (l) (600–1300 m) and a higher (h) (1300–2000 m) altitudinal gradient. Numbers in bold are significant (P <0.05). Tukey's HSD was conducted for multiple comparisons if the model was significant; letters indicate a significant difference between respective treatments. NA, data not available.

		Duration (days)				
		P	co	ad	de	dr
Alchemilla vulgaris L.	Mean (l)	NA	NA	NA	NA	NA
	Treatment (l)					
	Mean (h)	**0.010**	30	37	25	27
	Treatment (h)		a	a b c	b	c
Briza media L.	Mean (l)		9	9	8	7
	Treatment (l)	0.552				
	Mean (h)	NA	NA	NA	NA	NA
	Treatment (h)					
Campanula scheuchzeri Vill.	Mean (l)	NA	NA	NA	NA	NA
	Treatment (l)					
	Mean (h)		11	11	12	14
	Treatment (h)	0.253				
Dactylis glomerata L.	Mean (l)		11	9	11	11
	Treatment (l)	0.396				
	Mean (h)	NA	NA	NA	NA	NA
	Treatment (h)					
Lotus corniculatus L.	Mean (l)		22	30	31	
	Treatment (l)	0.696				
	Mean (h)	NA	NA	NA	NA	NA
	Treatment (h)					
Potentilla erecta (L.) Raeusch	Mean (l)		33	31	35	31
	Treatment (l)	0.591				
	Mean (h)		18	22	17	15
	Treatment (h)	0.082				
Prunella vulgaris L.	Mean (l)		12	10	15	9
	Treatment (l)	0.935				
	Mean (h)	NA	NA	NA	NA	NA
	Treatment (h)					
Ranunculus acris L.	Mean (l)	NA	NA	NA	NA	NA
	Treatment (l)					
	Mean (h)	NA	NA	NA	NA	NA
	Treatment (h)					
Ranunculus montanus Willd.	Mean (l)	NA	NA	NA	NA	NA
	Treatment (l)					
	Mean (h)		10	20	16	9
	Treatment (h)	0.241				
Trifolium pratense L.	Mean (l)		12	12	15	10
	Treatment (l)	0.283				
	Mean (h)	NA	NA	NA	NA	NA
	Treatment (h)					

whereas treatment effects were rather small over the entire gradient. Flowering duration was mostly not influenced by manipulative treatments at both higher and lower sites.

Phenological response to altitudinal change

Averaged over all species and phenophases, there was a delay in flower phenology of 3.4 d per 100 m increase. This is in accordance with the results of Cornelius *et al.* (2012) who showed a delay in flower and leaf phenology of 3.8 d per 100 m increase for tree and herbaceous species in the same region. However, the response to altitude change is species specific, ranging between 1.7 and 5.7 d per 100 m, which is similar to the 1.7–6.9 d per 100 m shown by Cornelius *et al.* (2012). Most altitudinal studies refer to tree species (e.g. Roetzer and Chmielewski, 2001; Dittmar and Elling, 2006; Migliavacca *et al.*, 2008; Vitasse *et al.*, 2009; Moser *et al.*, 2010); however, Ziello *et al.* (2009) showed, based on COST725 data for the Alpine region, a delay in the beginning of flowering of *Dactylis glomerata* L. of 2.8 d per 100 m. This is slightly less sensitive to altitude than the

non-significant response of *D. glomerata* in our study (3.9 d per 100 m). We assume that if we had had a greater number of observations in the present study these values would have been more similar.

Phenophases later in the year were significantly less sensitive to altitude than phenophases early in the year, which was also confirmed by Cornelius *et al.* (2012). A weaker response to temperature of species flowering in May and June in comparison with earlier spring flowering species was also shown by Fitter and Fitter (2002) and Menzel *et al.* (2006), who found that, because of high temperature variability in spring, the earlier the species, the stronger the sensitivity to temperature. However, in the present study as well as that of Cornelius *et al.* (2012), early (March to May) and late (September to October) species and phases are missing. Thus, it appears that response to temperature is declining not only in spring but consistently throughout the year.

Phenological response to treatments

The experiment showed only a few significant differences in the timing of flowering due to the manipulative treatments. Earlier snowmelt advanced flower phenology in most cases, although the effect was only significant for four species and phenophases. An earlier snowmelt is in accordance with the results of other studies (Price and Waser, 1998; Dunne *et al.*, 2003; Lambert *et al.*, 2010; Wipf, 2010). For example, Wipf *et al.* (2009) showed an advance of flower phenology of up to 10 d (present study 1–7 d). The response of species to later snowmelt was rather small; only the end of flowering phenophase was sometimes significantly delayed. Delayed timing due to later snowmelt was also shown in other studies (Weaver and Collins, 1977; Torp *et al.*, 2010; Chen *et al.*, 2011; Cooper *et al.*, 2011) that demonstrated a delay in the beginning of flowering and peak flowering of about 6–8 d for alpine species. In our study, the response was smaller with a non-significant delay of 2–3 d between delayed snowmelt and control plots. Hoye *et al.* (2007), however, showed that the result of delayed snowmelt was not necessarily later flowering but could also be unchanged. Thus, the response to delayed snowmelt also appears to be species specific. Wipf and Rixen (2010) suggested that, in general, the least responsive and least consistent responses to shifts in the date of snowmelt were in the grasses, whilst forbs were a little more responsive. Furthermore, the advanced snowmelt treatment was very early in the year, thus early flowering species such as *A. vulgaris* or *R. montanus* were affected, whereas an effect on late flowering species such as *C. scheuchzeri* or *P. vulgaris* was rather unlikely. Late-flowering species as well as phenophases later in the season were less responsive to snowmelt than early-flowering species or phenophases early in the season because these are controlled by temperature (Price and Waser, 1998; Dunne *et al.*, 2003; Wipf, 2010).

Across species and phenophases, drought treatment did not influence flowering significantly except for *P. vulgaris*. No effect of drought on plant phenology was also found for different grass species in an alpine meadow in France (Bloor *et al.*, 2010) and for the onset of growth of *Globularia alypum* L. in a Mediterranean shrubland (Bernal *et al.*, 2011). However, flowering of *G. alypum* was delayed by drought (Prieto *et al.*, 2008). A delay in flowering time after a drought period was also demonstrated for other Mediterranean plants (Llorens and Penuelas, 2005). In contrast, Jentsch *et al.* (2009) showed an advance of the mid-flowering date by 4 d after a drought period of 32 d. Thus, plant response to drought appears to be highly species specific (Bernal *et al.*, 2011) and ecosystem dependent. In the present study, soil moisture content on drought plots was 42% on average, which was probably not low enough to simulate a drought event that affects plant phenology (Fig. 3).

The flowering durations of species were mostly not significantly affected by the manipulative treatments. As far as we know, studies dealing with the impacts of snowmelt date on flower duration are rare and contradictory. Price and Waser (1998) showed that early snowmelt was associated with a longer flowering duration, which agrees with our prolongation of the flowering duration of *A. vulgaris* on advanced snowmelt plots. However, Wipf (2010) demonstrated that flowering duration was not affected by snowmelt timing, which agrees with the results of all other species in our study. Studies dealing with the impacts of drought on flowering duration are also rare and contradictory. Jentsch *et al.* (2009) reported a lengthening of the flowering period after a drought event, whereas Llorens and Penuelas (2005) reported both a shortening and a lengthening of the flowering duration of two different Mediterranean dwarf shrubs. In our study, the intensity of drought was probably not sufficient to cause shifts in flowering duration. However, general conclusions from ambiguous results as shown in these studies should be drawn with care due to slight differences in flowering duration definitions among studies.

Shifts in the phenological response due to changes in altitude

We had data for both the lower and the higher altitudes for only a few species. Ideally, species would have been distributed over the entire altitudinal gradient and also located in each treatment plot. However, due to restrictions in their natural distribution, species are often not spread over the entire gradient. Thus, only four species were monitored on both lower and higher sites. For these species, the impacts of treatments on flower phenology are additionally illustrated in Fig. 4. For advanced snowmelt plots, treatment effects were more pronounced at higher sites; however, other treatments showed no significant difference between altitude bands. Thus, on advanced snowmelt plots, the phenological response was most likely stronger at higher altitudes due to a larger treatment effect and not because species reacted more sensitively at higher than at lower altitudes. For delayed snowmelt and drought plots, no significant differences in treatment effects between lower and higher altitudes were detected. Thus, phenological differences were not significant, which indicates that species responded similarly at different altitudes. Defila and Clot (2005) showed from a 50-year time series in Switzerland that the total proportion of significant trends was higher in alpine regions (higher than 1000 m a.s.l.; 42%) and lower in lowland regions (lower than 600 m a.s.l.; 33%). However, considering the intensity of trends, the results showed an advance of full flowering of 32 d in the lowland and 20 d in the alpine region.
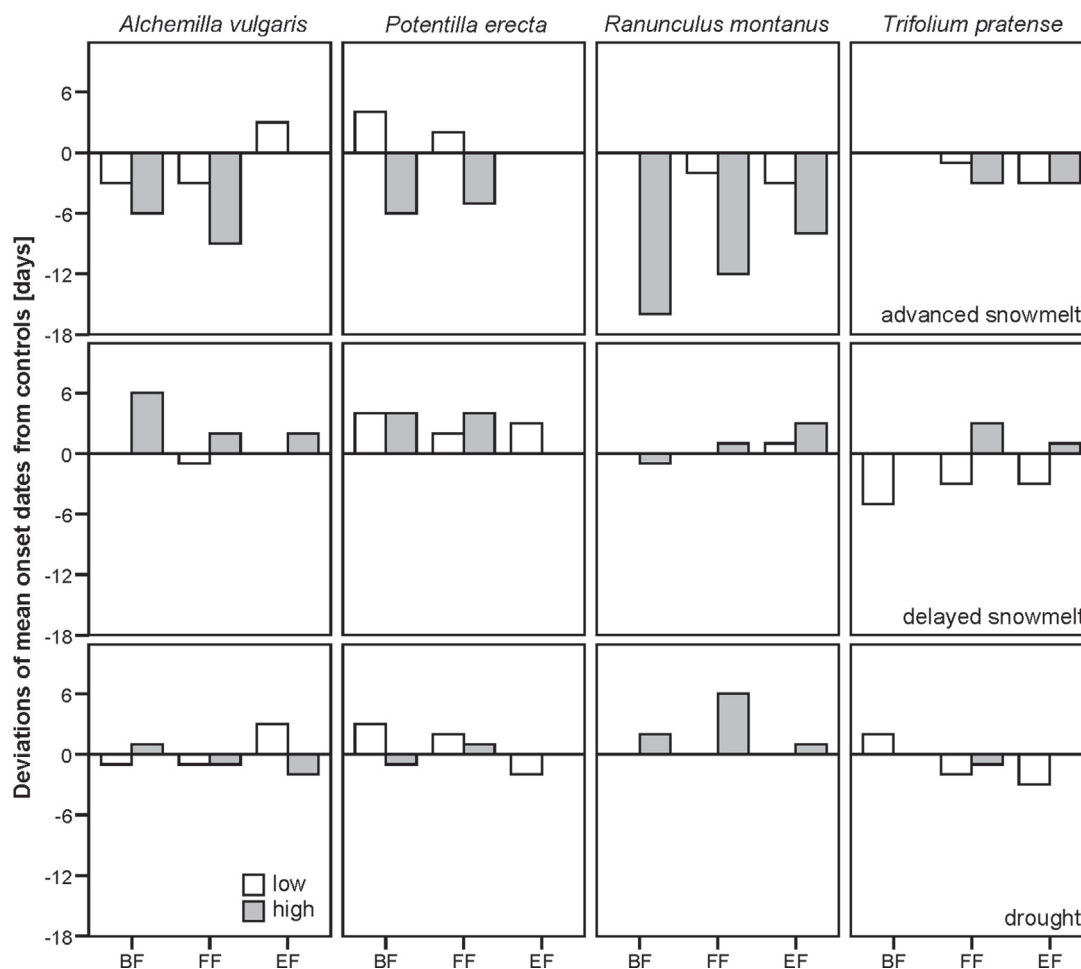
Fig. 4. Deviations from controls of mean onset dates from the ANCOVA model for each studied phenophase (BF, beginning of flowering; FF, full flowering; EF, end of flowering) separately by low (600–1300 m) and high (1300–2000 m) sites for the species *Alchemilla vulgaris* L., *Potentilla erecta* (L.) Raeusch, *Ranunculus montanus* Willd, and *Trifolium pratense* L., observed at low and high altitudes.

The length of flowering of *P. erecta* was greater at lower altitudes for all treatments, which led to the conclusion that duration was probably influenced by higher temperatures at lower sites. Tyler (2001) showed that the length of the flowering period was only slightly influenced by temperature because the timing of the onset of both start and end of phenophases advances in response to temperature increase; thus, the total length is not affected. However, Cornelius *et al.* (2012) showed that, although for most species flowering duration was not influenced by temperature, some species prolonged their flowering duration mainly due to a weaker response of end of flowering, which is related to the declining sensitivity to temperature change over the season, as also shown in the present study.

Conclusion

Our results suggest that changes in the abiotic environment such as shifts in the date of snowmelt only influence the timing of flowering if the effect is rather distinctive. As this will probably be the case at higher altitudes, species there may be more affected by global climate change. Furthermore, this study showed that a

1000-year extreme drought event in the Bavarian Alps did not substantially influence the phenology of grassland species. Thus, the risk of severe impacts of droughts on flowering phenology will be rather low here. Consequently, shifts in temperature and in the date of snowmelt will constitute the main factors that alter plant phenology under future climate change; however, the magnitude of change will depend strongly on the species.

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